doi: https://doi.org/10.15407/microbiolj82.05.065

HALOTOLERANT YEASTS: BIODIVERSITY AND POTENTIAL APPLICATION

O.D. Ianieva

Zabolotny Institute of Microbiology and Virology, NAS of Ukraine,
154 Acad. Zabolotny Str., Kyiv, 03143, Ukraine
Ianieva@nas.gov.ua

Halotolerant yeasts represent a heterogeneous group of unicellular fungi able to survive and thrive under hypersaline conditions. This review examines the biodiversity of halotolerant yeasts in various habitats with high salt content and the potential practical applications of this group of microorganisms in industry and agriculture. Halotolerant yeasts are found in various habitats with elevated salt content, including seawater, hypersaline ponds and salterns, saline soils and wastewaters, salt-containing foods. Habitats with moderate salinity, e.g. seawater, food products, olive fermentation wastewaters can boast a comparatively large biodiversity of yeasts both ascomycetes and basidiomycetes. Hypersaline niches are mostly inhabited by pigmented and melanized yeasts and yeast-like fungi. The adaptability and robustness of halotolerant yeasts could be exploited in several biotechnological fields, mainly the food industry and bioremediation. Yeasts isolated from food products with elevated salt content are studied as potential starter cultures in the corresponding fermenting products due to their enzymatic and antimicrobial activity and probiotic characteristics. Marine yeasts are of an increasing interest due to their production of various hydrolytic enzymes, biofuel production using seawater, bioremediation of saline wastewaters and the probiotic potential in aquaculture. Halotolerant yeasts found in various saline wastewaters could be used in bioremediation of wastewaters with high salinity containing various organic pollutants. However more research is required to achieve practical utilization of this group of microorganisms.

Keywords: halotolerant yeasts, hypersaline habitats, potential applications, bioremediation, enzymes, food industry.

Yeasts are a non-taxonomical group of unicellular fungi able to reproduce asexually either by budding or fission and inhabit various ecological niches. They are usually found in high numbers in habitats with high nutrient content e.g. plants and their roots, flowers, fruits, insect guts, various food products. However, in smaller numbers yeasts are also ubiquitous in soil, air, water and living organisms [1]. Extremotolerant and extremophilic yeasts constitute a large part of known yeasts, e.g. they often possess tolerance to low pH (acidophiles/acid-tolerant) and high sugar concentrations (osmophiles/osmotolerant) [2]. However tolerance to several other stress factors is less frequently observed, for example tolerance to the elevated temperature or alkaline conditions in yeasts is detected to much lesser degree.

Many types of yeast possess osmotolerance, e.g. the ability to grow at high osmotic pressure usually caused by high levels of sugar and salt [1]. Halotolerance, e.g. the ability to tolerate high salt content is less wide-spread among yeasts though a high proportion of known species can grow at 10 % NaCl [1]. Extremely halotolerant yeasts, those able to tolerate sodium chloride at concentrations higher than 15 % are much rarer [3].

Halotolerant yeasts are a widely heterogeneous group that includes representatives from both main taxonomic groups – Ascomycota and Basidiomycota [4]. This group of microorganisms possesses robustness and ability to thrive under harsh conditions and is characterized by different mechanisms and ways to cope with osmotic stress and sodium toxicity that is often accompanied by low pH. They are often characterized by unique biochemical processes and adaptation techniques that allow them to survive under extreme conditions. Such characteristics could be exploited in several biotechnological fields [5].

Environments with elevated salt content include a wide range of habitats such as food products and beverages, fermented or salt-cured, seawater and its plants and fauna, hypersaline water reservoirs and soils and man-made hypersaline sources such as salt-containing wastewaters [6]. The specific extreme environments could establish conditions unique for a certain group of microorganisms that could determine the physiological characteristics of yeasts and in prospect their biotechnological potential.

This review explores the biodiversity of yeasts in various saline and hypersaline environments with the focus on halotolerant yeasts and their potential practical applications related to their habitat.

1. Foods with high salt content as a reservoir of biotechnologically important yeasts. Historically humans prolonged the storage and microbiological safety of various food products by decreasing water activity in the corresponding foods, e.g. by addition of salt and/or sugar or by dehydration thus increasing osmotic pressure in the preserved foods and inhibiting the growth of undesirable microorganisms. Another way of increasing the shelf-life of foods is the fermentation process that results in low pH of the final product thus ensuring the microbiological safety of the foods [7]. The conditions specific for certain food products, e.g. low pH, the presence of certain chemical compounds, low water activity due to high sugar or salt concentration would be selective for the survival and proliferation of yeasts with unique characteristics suitable for their biotechnological application.

It should be noted that there are several sources of microorganisms that participate in the fermentation or maturation of salt-containing products. The main sources of yeasts in various food products are natural yeast populations in the initial substrates and environmental contamination of the processing facilities [8]. Some yeasts that thrive under saline conditions during the production of various food products and participate in various biochemical processes during the production could be the part of autochthonous mycobiota of the corresponding initial food substrate – olives, vegetables, fruits, milk, etc. [9–12]. The spontaneous fermentation of these substrates results in the creation of the specific conditions (low pH, high salinity, high osmotic pressure, the presence of various chemical compounds) unfavourable for the survival of the majority of the autochthonous microbiota and the selection of few groups of microorganisms that could thrive under such pressure, e.g. extremotolerant yeasts, lactic acid bacteria and other gram-negative bacteria [13]. However microorganisms that are dominant on the surface of the corresponding vegetable or fruit are not necessarily the same that would be the main players in the process of the spontaneous fermentation [9]. Although fermentation processes could employ the specifically selected cultures of microorganisms that does not preclude the participation of other fungi and bacteria initially present in the food substrate and even successfully overpowering the starter cultures [14]. For example a large study of the surface microbiota of smear-ripened cheeses resulted in the detection of 55 bacterial and 30 yeast species with only few of those being deliberately inoculated as starter cultures [15]. Another important source of various yeasts in food products would be the surrounding areas in the sites of production (air, surfaces, equipment, brines, etc.) where stable associations of microorganisms have evolved over many years [14, 16].

However every food product is characterized by the specific physicochemical parameters during production that would determine the diversity and biotechnological traits of the corresponding yeast microbiota. Yeasts that inhabit salt-containing products and their potential use in biotechnology will be discussed.

1.1. *Biodiversity and the biotechnological potential of yeasts from fermented olives.* Olive fermentation is a complex biochemical process of transformation of table olives with the bitter taste and high oil content into the final product suitable for human consumption. Yeasts play a dual role during olive fermentation – as participants in the fermentation process due to their fermenting, hydrolytic activities and production of various aromatic substances, vitamins and other compounds and as potential spoilage microorganisms [9].

Olive fermentation brines contain up to 10 % NaCl that inhibits the growth of various undesirable microorganisms and allows reproduction and dominance of the starter culture microorganisms that among other valuable characteristics must possess halotolerance. Fermentation of olives is usually performed by the indigenous microbiota of olives which include lactic acid bacteria, yeasts, enterobacteria, and other bacteria [19]. Yeast biodiversity of fermented olives is of increasing interest due to their role in olive fermentation and potential valuable biotechnological traits. A great variety of various yeast species is detected during table olive fermentation depending on the region, type of olives, and stage of fermentation, most of them being ascomycetous yeasts and belonging to *Pichia, Candida* and *Saccharomyces genera* (Table 1).

Table 1

Biodiversity of yeasts isolated from fermented olives

Product origin	Dominant yeast species / genera																							Reference	
	Saccharomyces cerevisiae	*Zygosaccharomyces/ Zygotorulaspora mrakii*	*Pichia galeieformis/manshurica*	*Pichia membranifaciens*	*Pichia kurdriavzevii*	*Pichia fermentans*	*Pichia spp.*	*Pichia/Wickerhamomyces anomalus*	*Torulaspora delbrueckii*	*Debaryomyces etchelsii*	*Debaryomyces hansenii/ Candida famata*	*Kluyveromyces marxiamus*	*Kluyveromyces lactis*	*Metschnikowia pulcherrima*	*Zygoascus hellenicus/ Candida hellencia*	*Candida naeodendra*	*Candida apicola*	*Candida boidinii*	*Candida diddensiae*	*Candida oleophila*	*Candida tropicalis*	*Candida aaseri*	*Nakazawaea/Candida molendini-olei*	*Aureobasidium pullulans*	*Cryptococcus laurentii*	
Spain	■		■	■														■								[19]
	■		■	■				■		■			■						■		■					[20]
	■	■	■				■										■									[21]
Portugal						■		■																		[22]
	■							■				■				■									■	[12]
	■			■		■														■						[23]
Italy	■	■						■										■	■				■			[24]
	■		■					■										■								[25]
	■				■			■							■			■	■		■	■				[26]
Greece				■				■			■			■										■		[27]
	■		■	■												■		■					■	■		[28]
									■		■														■	[29]
Turkey	■							■										■								[30]
								■			■				■											[31]

The autochthonous microbiota of fermented olives would be well-adapted to survive and thrive under the conditions of table olive fermentation – high salinity, phenolic content, low pH, low sugar content [32]. Yeasts isolated from different stages of olive fermentation are studied as potential candidates as starter co-cultures alongside lactic acid bacteria in olive fermentation due to their fermenting characteristics, production of aromatic and volatile compounds, the probiotic potential and killer activity and also as promising producers of hydrolytic enzymes. Several works highlighted the decrease in fermentation time and improvement in organoleptic characteristics of fermented olives as a result of the use of yeasts as starter co-cultures. Also a high proportion of strains with killer activity (antimicrobial activity against fungi) were detected by several authors in yeasts isolated from fermented olives (Table 2).

As it can be concluded from the presented data yeasts that are isolated from table olive processing and belong to the representatives of *P./W. anomalus, S. cerevisiae* and *C. boidinii* species are especially promising regarding their biotechnological potential.

1.2. *Yeasts from fermented vegetables and fruits.* A wide variety of yeasts are detected in various foods and beverages with the elevated salt content and it should be noted that the vast majority of those belong to ascomycetous yeasts. The most frequently detected yeasts in fermented vegetables and fruits belonged to *Pichia/Kodamea, Wickerhamomyces, Debaryomyces, Saccharomyces* and *Candida* genera, while basidiomycetous yeasts were detected infrequently and belonged to *Trichosporon* spp. and *Rhodotorula* spp. (Table 3).

Table 2

Biotechnological traits of yeasts in table olive processing

Biotechnological trait		Yeast species														Reference
		S. cerevisiae	*P./W. anomalus*	*D. hansenii*	*P. fermentans*	*P. galeieformis*	*P. guilliermondii*	*P.membranifaciens*	*K. lactis*	*K. marxianus*	*C.boidinii*	*C. diddensiae*	*Candida norvegica*	*C. oleophila*	*A. pullulans*	
Enzymatic activities	β-glucosidase		■			■										[25]
			■													[33]
			■									■				[34]
	lipase								■							[19]
					■											[35]
			■						■							[34]
											■					[36]
	esterase		■													[34]
Antibacterial activity					■			■						■		[23]
				■												[37]
Killer activity			■													[22]
		■	■	■			■			■						[38]
				■												[37]
			■	■				■								[38]
Probiotic potential		■									■				■	[24]
							■								■	[40]
		■						■						■		[23]
Potential starter co-cultures		■	■	■												[41]
			■													[42]
		■														[43]
		■		■												[44]
			■						■			■				[45]
				■												[46]

Table 3

Yeast biodiversity in fermented vegetables and fruits

Yeast genus	Yeast species	Source				Reference
		cucumber	cabbage	pepper	radish	
Debaryomyces	*D. hansenii*	■				[47,48]
	Debaryomyces spp.			■		[10]
					■	[49]
Pichia	*P.(Kodamea) ohmeri*	■				[47]
				■		[50]
	P. anomala / W. anomalus	■				[48]
				■		[51]
	P. kluyveri		■			[52]
	P. onychis		■			[53]
	P. kudriavzevii/ Isaatchenkia orientalis	■				[47]
				■		[51]
	Pichia spp.	■				[47,48]
				■		[10]
					■	[49]
Hanseniaspora	*H. opuntiae*			■		[51]
	H. pseudiguilliermondii			■		[50]
	Hanseniaspora spp.			■		[10]
Saccharomyces	*S. cerevisiae*	■				[54]
			■			[53]
	S. castellii		■			[52]
	S. unisporus		■			[52]
	Saccharomyces spp.		■			[55]
Zygosaccharomyces	*Z. rouxii*	■				[47]
	Zygosaccharomyces spp.	■				[47]
Kluyveromyces marxianus			■			[52]
Torulaspora spp.		■				[47]
Kazachstania spp.					■	[49]
Millerozyma spp.					■	[49]
Candida	*C. albicans*		■			[53]
	C. sake		■			[52]
	Candida spp.	■				[47]
			■			[55]
					■	[49]
Lodderomyces elongisporus			■			[52]
Trichosporon spp.			■			[52]
				■		[10]
Rhodotorula spp.				■		[10]

Fermented vegetables and fruits are considered probiotic foods [56]. Halotolerant yeasts are known to play a role in the production of several traditional fermented vegetable and fruit products and are studied as potential probiotic microorganisms. Several yeast strains have been investigated as co-starter cultures alongside lactic acid bacteria for the production of a traditional Korean dish kimchi that contains salted and fermented vegetables, usually cabbage and radish [57]: *Galactomyces geotrichum* and *P. anomala* [58], *S. cerevisiae* [59]. It is assumed that yeasts could improve the quality of the products due to their enzymatic activities, prolong its shelf-life and microbiological safety. The probiotic potential of several yeast strains isolated from various foods with the elevated salt content has been demonstrated: *S. cerevisiae* isolated from traditional Korean fermented cucumbers [54], *P. kudriavzevii, H. opuntiae, W. anomalus* isolated from fermented pepper [51].

However works focusing on the biotechnological potential of yeasts from various fermented fruits and vegetables are comparatively scarce presumably due to an enormous amount and diversity of such traditional food products in different parts of the world that are customarily obtained by spontaneous fermentation [7].

1.3. *Yeasts in salt-cured meat and fish products.* The production of various fermented and preserved meat and fish products often requires the addition of salt that improves the taste and microbiological safety of the product [60]. Although the main groups of microorganisms responsible for the maturation process of fermented meat and fish products are lactic acid bacteria and staphylococci, high numbers of yeasts are found during the production of these foods that could reflect some role of yeasts in flavor and aroma formation [7]. Several yeast species, mainly belonging to ascomycetes have been reported in various salt-cured and preserved fish and meat products (Table 4). The most frequently detected yeasts in foods of fish origin are *Pichia* spp., *Candida* spp., *D. hansenii, Y. lipolytica* while a variety of ascomycetous and basidiomycetous yeasts are usually isolated from sausages.

Microbiota of salt-supplemented meat products has been studied for various potential applications, especially in the food industry as starter cultures for sausages maturation and to inhibit the development of undesirable microorganisms, mainly molds. Halotolerant yeasts *D. hansenii* are known to play an important role in the maturation of fermented meat products probably due to their lipolytic and proteolytic activities [69, 71]. Several studies demonstrated the biotechnological potential of these yeasts for aroma improvement and anti-mold effect [68, 72, 73]. The potential of yeasts to combat spoilage microorganisms in cured meat products, especially toxigenic *Penicillum* molds is researched, the promising results are shown by halotolerant yeast *D. hansenii* against toxigenic mold *Penicillum verrucosum* in dry-fermented sausages [74] and *Penicillum nordicum* in ham [75], although it is not clear whether the inhibitory effect was based on killer protein production or other mechanisms. Yeast strains isolated from dry-cured ham exhibited antagonistic activity against mold *P. nordicum* which was enhanced by addition of sodium chloride [76]. The ubiquitous yeast *Y. lipolytica* has been evaluated for potential use in sausage production due to its well-known high lipolytic activity and high incidence in meat products, however contradictory reports show the positive effect of inoculation [77] and no effect at all [78].

1.4. Halotolerant yeasts as spoilage microorganisms in the food industry. Halotolerant yeasts were first isolated from various food products as spoilage microorganisms [47] and for a long time it has been considered as an established fact that hypersaline environments apart from food do not contain yeasts or fungi [79]. Halotolerant yeasts can be responsible for spoilage of some salt-containing foods including salad dressings, mayonnaise, fermented fruits and vegetables, salt-cured meat and cheese. Food spoilage by yeasts mostly occurs due to the appearance of undesirable odour and taste, the softening of the product texture, the expansion of the packaging due to gas formation, or the appearance of yeast film on the surface of the product [47]. The most frequently isolated yeasts that lead to spoilage of salt-containing foods belong to ascomycetous yeast of *Saccharomyces, Debaryomyces, Pichia, Candida, Yarrowia* genera and some others (Table 5). Interestingly, very rarely basidiomycetous yeasts are held responsible for spoilage of foods in general and salt-containing foods in particular; usually representatives of *Geotrichum candidum, Rhodotorula* spp. and *Cryptococcus* spp. are detected in such foods undergoing spoilage [47]. Such a phenomenon could be partially explained by the observation that basidiomycetous yeasts are more sensitive to osmotic stress that is one of the common stress factors encountered by microorganisms in food when compared to ascomycetes [80]. That would also explain a much higher frequency and biodiversity of ascomycetous yeasts in most food products.

It should be emphasized that some yeasts species can play a dual role in the food industry: to be responsible for the product spoilage and at the same time be also proposed as potential starter cultures or could possess valuable biotechnological traits (Table 6). Especially such phenomenon is reported for yeasts commonly found in fermented olives. The same traits that could be beneficial for the fermentation or maturation process during production (hydrolytic and fermenting activities, production of aromatic and volatile compounds) could also lead to the appearance of undesirable characteristics, e.g. gas formation, change in texture or unpleasant odour or taste, especially if they continue long after the completion of the fermentation process [99].

Table 4

Biodiversity of yeasts in meat and fish salt-containing food products

Yeast genus	**Yeast species**	**Salted fish**			**Traditional fish and seafood fermented foods**			**Sausages**			
Saccharomyces	*S. cerevisiae*	■									
	Saccharomyces spp.		■								
Zygosaccharomyces	*Zygosaccharomyces spp.*		■								
	Z. rouxii						■	■	■		■
Debaryomyces	*D. hansenii*	■		■						■	
	Debaryomyces spp.										
Pichia	*P. membranifaciens*	■									
	P. fabianii					■					
Yarrowia	*Y. lipolytica*	■		■					■	■	
	Yarrowia spp.							■			
Saccharomycopsis	*Saccharomycopsis spp.*				■						
Metschnikowia	*Metschnikowia spp*							■			
Candida	*C. glabrata*	■									
	C. zeylanoides		■	■					■		
	C. sake			■					■		
	C. tropicalis					■					
	C. papapsilosis								■	■	
	Candida spp.		■		■			■			
Cryptococcus	*Cryptococcus spp.*							■			
Rhodotorula	*R.mucilaginosa*								■	■	
	Rhodotorula spp							■			
Rhodosporidium	*Rhodosporidium spp*							■			
Trichosporon	*T. cutaneum*								■		
	Trichosporon spp							■			

Table 5

Spoilage yeasts in food products with elevated salt content

Food	Yeast species	Reference
Fermented olives	*S. cerevisiae, P. manshurica, C. boidinii*	[81]
	S. cerevisiae, P. membranifaciens	[82]
	P. membranifaciens, Candida etchellsii, Candida pararugosa	[83]
Fermented fruits and vegetables	*Saccharomyces bayanus, S. unisporus, Hansenula anomala, Debaryomyces sp.*	[84]
	P. manshurica, Issatchenkia occidentalis	[85]
	P. kudriavzevii	[86]
	Kazachstania exigua, Kazachstania pseudohumilis	[87]
	P. membranifaciens, D. hansenii	[88]
	K. ohmeri, G. candidum, Candida spp.	[89]
	Hanseniaspora uvarum, Pichia kluyveri, Y. lipolytica, Kazachstania servazzi, C. sake	[90]
Processed meat products	*C. sake*	[91]
Soy sauces, mayonnaise and salad dressings	*P. membranifaciens, Saccharomyces exiguus*	[92]
	Zygosacharomyces bailii, Zygosacharomyces bisporus	[93]
	T. delbrueckii	[94]
Cheese	*T. delbrueckii, C. parapsilosis, P. fermentans, D. hansenii, P. membranifaciens, Pichia norvegensis, P. guilliermondii, Pichia jadinii, Rhodotorula glutinis, P. anomala, Saccharomyces dairensis, Rhodotorula minuta, S. unisporus, Y. lipolytica, Cryptococcus sp.*	[95]
	D. hansenii, K. marxianus, Y. lipolytica, T. delbrueckii, P. anamola, P.guilliermondii, G. geotrichum, Williopsis californica, C. sake, Candida versatilis, C. diddensiae, C. zeylanoides	[96]
	D. hansenii, C. parapsilosis, K. marxianus, P. fermentans, R. mucilaginosa, Trichosporon asahii, Sporodiobolus salmonicolor, Y. lipolytica	[97]
	Y. lipolytica	[98]

Table 6

Yeast species as spoilage yeasts and potential biotechnological cultures in food industry

Yeast species	Olive fermentation		Fermented vegetables		Meat products	
	potential use	spoilage	potential use	spoilage	potential use	spoilage
D. hansenii	■			■	■	
S. cerevisiae	■	■				
W/P. anomalus	■			■		
P. membranifaciens	■	■		■		
P. kudriavzevii			■	■		
C. boidinii	■	■				
Y. lipolytica				■	■	

2. Marine yeasts: biodiversity and future perspective. Seawater represents a huge reservoir of various ascomycetous and basidiomycetous yeasts; altogether more than 200 yeast species have been reported to be found in marine environments [100]. 220 yeast species belonging to 74 genera in 9 classes are currently described as marine yeasts [101].

Low yeast numbers (below 10–100 cells/l) are usually found in oceans and seas water although higher yeast cell concentrations are often associated with seaweeds and various marine animals [102]. Frequently novel yeast species are discovered in marine environments. New basidiomycetous yeast species *Naganishia qatarensis* and *Kondoa qatarensis* were isolated from seawater in Qatar [103, 104], *Rhodotorula pacifica* – from sediments in the North-West Pacific Ocean [105]. New ascomycetous species *Candida oceani* was isolated from a deep-sea hydrothermal vent in the Atlantic Ocean [76].

Most studies performed on the biodiversity of marine yeasts are done using genetic approaches as isolation and cultivation of fungi from seawater is often difficult and time-consuming. It has been shown than yeast forms dominate fungal diversity in deep-sea water and sediments around the world [106]. Yeast distribution and biodiversity in seas and oceans are greatly dependent on the isolation source (sea, sediments, algae, invertebrates, fish, and mammals), geographical location, nutrient availability and many other factors [107]. A large study of microbial biodiversity in European coastal sea waters resulted in the detection of yeasts belonging to basidiomycetous genera *Rhodotorula, Rhodosporidium, Sporobolomyces, Kondoa,* and *Cryptococcus* and ascomycetous genera *Geotrichum, Debaryomyces, Saccharomyces, Candida* and *Pichia* [109].

Several reviews indicate that the most frequently detected marine yeasts are represented by ascomycetous genera *Debaryomyces, Candida (Torulopsis), Pichia, Kluveromyces, Metschnikowia,* and basidiomycetous genera *Cryptococcus, Rhodotorula, Leucosporidium, Rhodosporidium, Sporobolomyces, Trichosporon* [100, 108, 110]. Most such yeasts especially *Candida, Pichia,* and *Debaryomyces* and pigmented basidiomycetes are not exclusively confined to marine environments and are common in most terrestrial habitats [100]. It should be emphasized that marine yeasts were the subject of several comprehensive and extensive reviews that cover various topics on their isolation, ecology, metabolic traits, and biotechnological potential [100, 108, 110, 111] and this work does not aim to review all the available information on biodiversity of yeasts in the marine environment instead focusing on some biotechnological traits of marine yeasts.

Seas and oceans provide a unique reservoir of microorganisms, sometimes previously unknown and adapted to ever-changing surrounding conditions, e.g. temperature, osmolarity, nutrient availability, pressure, and salinity [100]. As marine yeasts are poorly studied compared to their terrestrial relatives their biotechnological relevance became a subject of increasing scientific inte-rest.

Marine yeasts are extensively studied as producers of extracellular hydrolytic enzymes as enzymes synthesized by them are expected to retain activity under varying temperature, pressure and salinity [111]. Large screening studies are performed on marine yeasts in search for novel promising enzymes. More than 300 marine yeast strains were screened for inulinase production and yeast strain *C. aureus* was found to produce the highest quantities of extracellular inulinase [112]. Among 427 yeast strains isolated from seawater, sea sediments, fish, and algae four strains secreted extracellular inulinase in the seawater-based medium and were identified as *Cryptococcus aureus, D. hansenii, Y. lipolytica,* and *P. guilliermondii* [113]. The screening for proteolytic enzymes among these yeasts revealed four yeasts strains *C. aureus, A. pullulans, Y. lipolytica* and *I. orientalis* which produced extracellular alkaline proteases [114]. Extracellular hydrolytic enzymes produced by marine-derived yeasts include inulinase, protease, lipase, pullulanase, amylase, and several others (Table 7).

As production of biofuels requires large quantities of water the potential use of seawater as the basis for fermentation medium for biofuel production using halotolerant yeasts is researched [111]. Most industrially relevant *S. cerevisiae* strains lack tolerance to high salt content thus making the fermentation in seawater-based media inefficient. Marine yeasts with high fermentative capacity could be employed for biofuel production using seawater [111]. A marine strain *S. cerevisiae* AZ 65 was an efficient producer of ethanol in seawater based medium converting sugars to ethanol with 83.3 % theoretical yield [122]. Also high ethanol yields were obtained by this yeast strain using sugarcane molasses in seawater.

Marine-derived yeast strains *Candida* sp. have been shown to efficiently ferment various sugars and seaweed hydrolysate to ethanol in the presence of up to 11% NaCl [123]. Non-diluted seaweed hydrolysate containing 11.25% salt and 5.5% reducing sugars was fermented by the isolated yeast with 50% conversion efficiency while thrice diluted hydrolysate was fermented with 100% conversion efficiency in 2 days. Several ethanol-producing yeasts strains were isolated from marine sediments in India, and the most efficient producer was *Pichia salicaria* strain [124]. A marine yeast *M. guilliermondii* was studied for ethanol production from spent seaweed hydrolysate in combination with the marine bacterial consortium [125].

Marine yeasts have recently become the subject of research as possible candidates for biodiesel production. Oleaginous yeasts including *Rhodotorula, Cryptococcus,* and *Rhodosporidium* are among the most frequently found yeast species in seawater and sediments [102]. Several oleaginous yeasts belonging to *Rhodosporidium* and *Cryptococcus* sp. were isolated from seawater in Northern China; the highest lipid accumulation was observed in *Rhodosporidium* strain up to 44% of dry cell weight and the cultivation in medium with salinity similar to seawater did not affect biomass yield or lipid accumulation [126]. The use of seawater as the medium for lipid production was studied for wild-type and genetically engineered strains of *Y. lipolytica* [127] and *R. mucilaginosa* [128].

Table 7

Hydrolytic enzymes produced by marine yeasts

Enzyme	Yeast producer	Source of isolation	Reported activity	Reference
Inulinase	*C. aureus*	Sea sediment, China	85.0 U/ml	[112]
	C. aureus, D. hansenii, Y. lipolytica, P. guilliermondii	Algae, sea sediment, China	39.56-62.85 U/ml	[113]
	P. guilliermondii	Marine alga, China	60 U/ml	[115]
Protease	*Metschnikowia reukaufii*	Sea sediment, China	72.5 U/ml	[116]
	R. mucilaginosa	Sea invertebrates, Antarctica	11.12 U/ml	[117]
	R. mucilaginosa	Marine alga, Antarctica	up to 48.55 U/ml	[118]
	C. aureus, A. pullulans, Y. lipolytica, I. orientalis	Seawater and sea sediments, China	26.7-127 U/mg protein	[114]
Lipase	*Cryptococcus laurentii, Leucosporidium scottii*	Sea invertebrates, Antarctica	0.143-0.23 U/ml	[117]
Endoxylanase	*Cryptococcus adeliensis*	Sea invertebrates, Antarctica	0.43 U/ml	[117]
β-xylosidase	*C. laurentii*	Sea invertebrates, Antarctica	1.09 U/ml	[117]
Glucoamylase	*A. pullulans*	Sea water, Pacific Ocean	10 U/ml	[119]
Phytase	*K. ohmeri*	Marine fish	0.557 U/ml	[120]
Pullulanase	*A. pullulans*	Sea mud	-	[121]

Marine yeasts would be well-adapted to the conditions of the open sea and, as such, are studied as producers of antifungal substances – killer proteins for aquaculture. Yeasts can be pathogenic for marine invertebrates thus causing economic losses in aquaculture, for example *M. bicuspidate* causes so-called emulsification disease in crab *Portunus trituberculatus* [110]. Several marine yeast strains with killer activity against this pathogen have been isolated and described including *P. anomala* strain isolated from sea [129], psychrotolerant Antarctic yeast strain *Mrakia frigid* with killer activity against *M. bicuspidate*, *C. albicans,* and *C. tropicalis* [130], marine-derived *Williopsis saturnus* strain with a broad spectrum of killer activity besides *M. bicuspidate* against *C. aureus, L. elongisporus, C. albicans, C. tropicalis,* and *R. mucilaginosa* [131]. For most described strains the optimal conditions for killer protein production included the supplementation of the medium with sodium chloride at 2–8 % concentrations. The use of these compounds against pathogenic yeasts could provide a safe and effective strategy of biocontrol in aquaculture [110].

Marine environments could be heavily polluted by various contaminants including hydrocarbons, heavy metals, and various other organic substances. Marine yeasts can possess the ability to degrade organic pollutants or remove heavy metal ions from the environment [110]. Bioremediation of oil spills in seawater requires microorganisms that would successfully remove hydrocarbons in the presence of salt. Halotolerant yeast strain *Lipomyces tetrasporus* isolated from the Red Sea could degrade crude oil more efficiently in the presence of 25 and 45 g/l NaCl than in the salt-free medium [132]. *C. tropicalis* strain isolated from motor oil-polluted area in the Mediterranean Sea demonstrated a high hydrocarbon-degrading activity in the seawater-based medium [133].

Textile wastewaters are characterized not only by various dye content but also by high salinity [134] so yeasts with the bioremedial potential should also possess halotolerance to be efficient under such conditions. The potential to degrade various textile dyes was studied in several marine-derived yeast strains. Salt-tolerant yeast *Scheffersomyces spartinae* isolated from sea mud successfully degraded more than 90% of aze dye

Acid Scarlet 3R under optimal conditions [135]. Another halotolerant strain *C. tropicalis* SYF-1 isolated from sea mud could decolorize six different azo dyes thereby reducing the toxicity of the dye-containing solutions [136]. Halotolerant strain *P. occidentalis* G-1 isolated from sea mud effectively degraded more than 98% of azo dye Acid Red B in the presence of 3% NaCl due to its high ligninase activity [137]. Other examples of halotolerant yeasts efficiently degrading different azo dyes under high salinity conditions include *Cyberlindnera samutprakarnensis* [138], *G. geotrichum* [139].

As several marine yeasts including *Rhodotorula* spp., *Candida* spp., *Saccharomyces* spp, *Debaryomyces* spp. are known to colonize the gut of marine animals and to produce extracellular proteases, siderophores and killer proteins thus inhibiting pathogenic microbiota [110] their probiotic potential is researched. *D. hansenii* is one of the most frequently isolated yeast species in seawater and also in the fish gut [140] and was shown to exert a beneficial effect on fish *S. aurata* [141], and also in newborn goats [142]. Other examples of marine yeasts with the immunomodulating effect on aquaculture include *C. sake* [143], *Rhodosporidium paludigenum* [144], *Candida aquaetextoris* [145].

So it could be concluded that marine yeasts represent a heterogeneous group of ascomycetes and basidiomycetes that are still poorly researched and could be promising sources of novel enzymes, probiotics, and bioremedial agents.

3. Yeasts in hypersaline habitats: salterns, hypersaline ponds and halophytes

Seawater usually has salinity on the average 3.5 % of salts, mainly NaCl, per liter. There are several natural environments on the Earth that are characterized by even higher salinity that include salterns and saltern ponds, hypersaline lakes, and surrounding soils and halophitic plants [6]. Only recently the presence of fungi and, yeasts in particular, in hypersaline environments apart from food products has been detected. Ascomycetous yeasts in hypersaline habitats are usually represented by pigmented yeasts of *Rhodotorula, Rhodosporidium, Aureobasidium,* and *Naganishia/ Cryptococcus* genera while ascomycetes include representatives of *Candida, Pichia/Meyerozyma,* and *Debaryomyces* (Table 8).

Gunde-Cimerman et al. described fungal biodiversity in hypersaline waters of saltern ponds with the salinity of 3–35 % NaCl which included melanized yeastlike fungi *Hortaea werneckii, Phaeotheca triangularis, Trimmatostroma salinum* and *A. pullulans* [79]. Strains of black yeast *H. werneckii* were dominant in the salterns throughout the year. Halophilic dimorphic fungus *H. werneckii* is one of the most halotolerant eukaryotic microorganisms isolated from very diverse environments – from hypersaline water in salterns, seawater and human skin where it can cause superficial infection tinea nigra [154].

159 fungal strains were isolated from hypersaline Inland Sea in Qatar characterized by high salinity up to saturation, red-pigmented yeasts *R. mucilaginosa* and *Symmetrospora marina* being the most frequently isolated strains [150]. Ascomycetous and basidiomycetous yeasts were isolated with similar frequency.

Yeast biodiversity was studied in hypersaline soils surrounding salt lake Urmia Lake in Iran, where salinity is recorded in the range 12–30 %, the basidiomycetous yeasts represented the majority of isolates (92.4 %) [151, 152]. 43 strains of halophilic and halotolerant fungi have been isolated from soil in a man-made saltern in Thailand where salinity reached 13.11 %, most belonging to filamentous fungi of *Aspergillus* genus [155]. The only isolated yeast belonged to *S. halophilus* and was the most frequent halophilic fungus in soil samples. In the soils in the Dead Sea region, Israel with various salinity levels only one yeast strain *Rhodotorula* sp. among 329 fungal isolates has been identified [156]. Several non-identified yeast isolates were isolated alongside microscopic fungi belonging to 23 different species from hypersaline soil and water of the Mono Lake area, USA [157].

Halophytic plants are adapted to saline soils by excreting excess salt or by accumulating salt in their tissues or organs. Fungal biodiversity of halophytes has been described in several studies however most studies are focused on mycelial mycobiota [6]. Among various fungal species of salt-excreting desert tree of *Tamarix* genus traces of *Saccharomyctotina* and representatives of *Bensingtonia* and *Sporobolomyces* have been detected [158]. *Sporobolomyces* yeasts have also been found on leaves of *Phragmites australis* in brackish marshes [159]. Among 320 fungal strains from halophyte *Salicornia europaea* 6 strains of yeastlike black fungus *Aureobasidium* have been isolated [160].

Very few studies are focused on the biotechnological potential of yeasts isolated from various hypersaline habitats. As these habitats

Table 8

Yeast biodiversity in hypersaline water and soils

Source	Sampling sites	Yeast species	Reference
Salterns and associated habitats	Salterns in Slovenia, Spain, Israel, France, Namibia, Portugal The Dead Sea, the Great Salt Lake (USA), Enriquillo Lake (Dominican Republic)	*P. guilliermondii, D. hansenii, Y. lipolytica, M. bicuspidata, C. parapsilosis, Rhodosporidium sphaerocarpum, Rhodosporidium babjevae, Rhodotorula laryngis, Trichosporon mucoides*	[146]
	Hyper saline ponds in Marakkanam and Tuticorin saltpans, India	*Cryptococcus neoformans, R. sphaerocarpum, D. hansenii, S. cerevisiae, Y. lipolytica, H. werneckii, C. albicans, Candida sp.*, *Aureobasidium* sp.	[147]
Hypersaline waters	Antarctic brines from Tarn Flat (Northern Victoria Land)	*Candida* sp., *Leucosporidium* sp., *Naganishia* sp., *Sporobolomyces* sp., *Malassezia* sp.	[148]
	Wadi ElNatrun, Egypt	*C. tropicalis, Meyerozyma caribbica, M. guilliermondii, R. mucilaginosa*	[149]
	The Inland Sea, Qatar	*Aureobasidium iranianum, Aureobasidium melanogenum, A. pullulans, Candida metapsilosis, Candida orthopsilosis, C. parapsilosis, D. hansenii, Debaryomyces nepalensis, H.werneckii, Kondoa spp., Naganishia (Cryptococcus) albida, Naganishia albidosimilis, N. qatarensis, Papilliotrema (Cryptococcus) laurentii, Rhodotorula diobovata, R. mucilaginosa*	[150]
Hypersaline soils	Urmia Lake, Iran	*Candida baotianensis, T. delbrueckii, M. guilliermondii, Metschnikowia sinensis, D. hansenii, Naganishia (Cryptococcus)* spp., *Cystobasidium* spp., *Rhodotorula* spp., *Holtermanniella* spp., *Naganishia* spp., *Saitozyma* spp., *Tausonia* spp., *Vanrija* spp., *Vishniacozyma* spp.	[151, 152]
	The Great Salt Plains of Oklahoma, USA	*Debaryomyces* spp.	[153]

are characterized by extremely high salinity the possibility of using such microorganisms as producers of industrially relevant enzymes active at high salt concentrations has been raised. Halotolerant strain *Usilago cynodontis* isolated from soil of salt lake in Algeria exhibited high cellulose, lipase, and protease activity [161]. Six strains of halophilic fungi isolated from the man-made saltern in Thailand were screened for the production of enzymes, antioxidants and antimicrobial agents, the only yeast strain belonging to *S. halophilus* [155]. This yeast demonstrated low to moderate antimicrobial activity and weak lipolytic activity.

Yeast strain *Sterigmatomyces halophilus* isolated from saltern sediments in Mexico was evaluated for its probiotic potential in aquaculture and has been shown to boost immunity in fish *Sparus aurata* as a dietary supplement [162].

4. Wastewaters as a source of yeasts with the bioremedial potential

Several industries generate vast amounts of wastewaters with high salt content either due to the specific use of salt in the production process or by using seawater to substitute drinking water. The main examples of such industries are table olive fermentation, oil refinery, chemical, and dyeing industries [134].

Large quantities of saline wastewaters are generated by table olive fermentation and thriving yeast communities are found there. 23 fungal strains were isolated from olive brine wastewaters with 4.7 % salinity including *C. boidinii, C. diddensiae, Candida bombi* and *Citeromyces matritensis* [163]. Up to 5 lg CFU/ml of fungi were found in table olive wastewaters and *Pichia* spp. were dominant fungal isolates [164].Wastewaters generated by olive fermentation are characterized by high salt and phenol content, high chemical oxygen demand (COD), and biological oxygen demand (BOD), often highly acidic. There is no generally accepted strategy for treating these wastewaters; usually they are stored in the evaporation ponds during warmer periods of the year [165]. The extreme conditions in these wastewaters facilitate the survival of extremophilic or extremotolerant microorganisms that could be of use in bioremediation [166]. Red-pigmented yeast *R. mucilaginosa* isolated from olive wastewater stored in the evaporation pond completely degraded following phenolic compounds: f-protocatechuic, vanillic, and p-coumaric acids and reduced COD up to 50 % in olive mill wastewater [167]. Other examples of halotolerant yeasts isolated from wastewaters and able to reduce COD, dye content, and concentration of phenolic compounds include fungi *Candida rugosa, Candida cylindracea,* and *Y. lipolytica* [168]. *G. candidum* [169].*C. matritensis* and *Aspergillus fumigatus*[163].

Yeast biodiversity in saline wastewaters generated by other industries is usually very scarce due to harsh conditions and low carbon content and mostly represented by extremotolerant yeast strains. Fungal load in alkaline wastewaters with high salt and ammonium content was very low and represented mostly by filamentous fungi although one ascomycetous yeast *C. parapsilosis* and two basidiomycetes *G. geotrichum* and *R. minuta* were isolated [170]. Two halo- and osmotolerant yeast strains *P. guilliermondii* and *R. mucilaginosa* isolated from chemical wastewater evaporation ponds exhibited extremely high salt tolerance up to 3.5 M NaCl [171]. Halotolerant *Debaryomyces* sp. strain isolated from phenolic sludge with high salinity was also highly tolerant to heavy metals and phenolic compounds [172]. In oil refinery wastewater in Brazil a low fungal diversity was observed and three phenol-degrading yeast strains tentatively identified as *P. membranifaciens, C. rugosa* and *C. tropicalis* were isolated [173].

Such autochthonous for wastewaters extremotolerant strains could possess tolerance to several stress factors and the ability to degrade various toxic organic compounds that are present in industrial wastewaters. *Pichia* and *Rhodotorula* yeasts isolated from chemical evaporation ponds were capable of degrading a number of polycyclic aromatic hydrocarbons including anthracene and phenanthrene [171]. Halotolerant *Debaryomyces* sp. strain isolated from phenolic sludge with high salinity completely degraded 500 mg/l of phenol in the presence of 1% sodium chloride, the presence of Mn (II) and Zn (II) ions did not noticeably affect the efficiency of phenol degradation [172], phenol degradation was considerably increased by yeast cells immobilization in Ca-alginate [174]. Phenol-degrading yeast strain *C. tropicalis* was considered for the remediation of phenol-containing wastewaters due to its efficient phenol removal and biosurfactant production [173].

Conclusions. Halotolerant yeasts represent a heterogeneous group of yeasts and yeastlike fungi belonging to ascomycetes and basidiomycetes. They are found in many saline and hypersaline habitats including various food products, hypersaline ponds and salterns, saline soils and wastewaters, the surface of halophytic plants, and some others. A high diversity of yeasts is observed in habitats with moderate salinity, e.g. seas and oceans, various food products. Interestingly the majority of yeasts detected in foods with high salt content belong to ascomycetous species while marine environments and the associated animals and plants are populated by both ascomycetes and basidiomycetes. Several halotolerant yeast genera, mostly *Candida, Pichia,* and *Debaryomyces* could be considered real cosmopolites as they inhabit very different and often inhospitable for most yeasts habitats. Very low yeast loads are detected in hypersaline niches where salinity exceeds that of seawater. Saline wastewaters are characterized not only by high salinity but also often by the presence of other contaminants like phenolic compounds and heavy metal salts thus creating very harsh conditions for the survival of microorganisms. Yeasts present in salterns are mainly represented by pigmented yeasts and melanized yeast-like fungi [175] that could be explained by the role of pigment formation under conditions of high salinity [176].

The extreme conditions created in the specific saline environments result in the survival and selection of highly tolerant and adapted to such conditions microbiota that could be of use in the corresponding fields. As an example halotolerant yeasts isolated from olive processing wastewaters are proposed as bioremedial agents to decrease COD, dye, and phenolic content in such wastewaters. Yeast strains found in large quantities in various food products are considered as potential starter cultures in the corresponding fermentation and preservation processes due to their possession of the necessary characteristics, e.g. enzymatic and fermenting activities, probiotic qualities

and antimicrobial activity against undesirable microorganisms. Marine yeasts are proposed as a novel source of biofuel production using seawater due to their adaptation to the conditions, as producers of novel hydrolytic enzymes active at high salinity and pressure and also as probiotics in aquaculture. Yeasts isolated from habitats with extremely high salinity higher than 10% are very few and only a handful of works deal with their biotechnological potential usually concerning their enzymatic activities.

ГАЛОТОЛЕРАНТНІ ДРІЖДЖІ: БІОРІЗНОМАНІТТЯ ТА ПЕРСПЕКТИВИ ЗАСТОСУВАННЯ

О.Д. Янєва

Інститут мікробіології і вірусології
ім. Д.К. Заболотного НАН України,
вул. Академіка Заболотного, 154,
Київ, 03143, Україна

Резюме

Галотолерантні дріжджі представляють гетерогенну группу одноклітинних грибів, здатних виживати та розмножуватися за умов високої солоності. У цьому огляді розглядається біорізноманіття галотолерантних дріжджів у різних джерелах з високим вмістом солі та потенційне практичне застосування цієї групи мікроорганізмів у промисловості та сільському господарстві. Галотолерантні дріжджі виділяють з різних джерел з підвищеним вмістом солі, включаючи морську воду, гіперсалінові водойми та соляники, солоні грунти та стічні води, харчові продукти з високим вмістом солі. Джерела з помірною солоністю, такі як морська вода, харчові продукти, стічні води ферментації оливок характеризуються доволі значним біорізноманіттям дріжджів як аскоміцетів, так і базідіоміцетів. Гіперсалінові джерела переважно містять пігментовані та меланизовані дріжджі та дріжджоподібні гриби. Здатність до адаптації та стійкість галотолернатних дріжджів до стресу може бути застосована в різних біотехнологічних галузях, зокрема в харчовій та біоремедіаційній промисловості. Дріжджі, ізольовані з харчових продуктів з підвищеним вмістом солі, розглядають як потенційні стартові культури для ферментації відповідних продуктів через їх ферментативну та антимікробну активність та пробіотичні властивості. Морські дріжджі викликають інтерес завдяки продукуванню різноманітних гідролітичних ферментів, отриманню біопалив з використанням морської води, біоремедіації солоних стічних вод та пробіотичному потенціалу в аквакультурі. Галотолеранті дріжджі зі стічних вод з підвищеною солоністю можуть бути застосовані для очистки солоних стічних вод, що містять органічні сполуки. Однак подальші дослідження потрібні для дослідження можливості практичного застосування цієї групи мікроорганізмів.

Ключові слова: галотолерантні дріжджі, гіперсалінові джерела, перспективи застосування, біоремедіація, ферменти, харчова промисловість.

1. The Yeasts A Taxonomic Study. Fifth edition. In: C.P. Kurtzman, J.W. Fell, T. Boekhout, Editors. Amsterdam: Elsevier, 2011. 2354 p.
2. Peter G, Takashima M, Cadez N. Yeast habitats: different but global. In: Yeasts in Natural Ecosystems: Ecology. 2017. p. 39–71
3. Kurtzman CP, Mateo RQ, Kolecka A, Theelen B, Robert V, Boekhout T. Advances in yeast systematics and phylogeny and their use as predictors of biotechnologically important metabolic pathways. FEMS Yeast Res; 15(6).
4. Buzzini P, Turchetti B, Yurkov A. Extremophilic yeasts: the toughest yeasts around? Yeast. 2018; 35(8):487–97.
5. Vashishtha A, Meghwanshi GK. Fungi Inhabiting in Hypersaline Conditions: An Insight. In: Gehlot P, Singh J, editors. Fungi and their role in sustainable sevelopment: surrent perspectives. Singapore: Springer; 2018. p. 449–65.
6. Zajc J, Zalar P, Gunde-Cimerman N. Yeasts in hypersaline habitats. In: Buzzini P, Lachance M-A, Yurkov A, editors. Yeasts in natural ecosystems: diversity. Cham: Springer International Publishing; 2017. p. 293–329.
7. Tamang JP, Watanabe K, Holzapfel WH. Review: Diversity of microorganisms in global fermented foods and beverages. Front Microbiol. 2016; 7:377.

8. Hernández A, Pérez-Nevado F, Ruiz-Moyano S, Serradilla MJ, Villalobos MC, Martín A, et al. Spoilage yeasts: What are the sources of contamination of foods and beverages? Int J Food Microbiol. 2018; 286:98–110.
9. Botta C, Cocolin L. Microbial dynamics and biodiversity in table olive fermentation: culture-dependent and -independent approaches. Front Microbiol. 2012; 3:245.
10. Zhao L, Li Y, Jiang L, Deng F. Determination of fungal community diversity in fresh and traditional Chinese fermented pepper by pyrosequencing. FEMS Microbiol Lett. 2016; 363.
11. Lavoie K, Touchette M, St-Gelais D, Labrie S. Characterization of the fungal microflora in raw milk and specialty cheeses of the province of Quebec. Dairy Sci Technol. 2012; 92(5):455–68.
12. Hernández A, Martín A, Aranda E, Pérez-Nevado F, Córdoba MG. Identification and characterization of yeast isolated from the elaboration of seasoned green table olives. Food Microbiol. 2007; 24(4):346–51.
13. Tofalo R, Fusco V, Böhnlein C, Kabisch J, Logrieco AF, Habermann D, et al. The life and times of yeasts in traditional food fermentations. Crit Rev Food Sci Nutr. 2019 Oct 26;1–30.
14. Goerges S, Mounier J, Rea MC, Gelsomino R, Heise V, Beduhn R, et al. Commercial ripening starter microorganisms inoculated into cheese milk do not successfully establish themselves in the resident microbial ripening consortia of a south german red smear cheese. Appl Environ Microbiol. 2008; 74(7):2210–7.
15. Cogan TM, Goerges S, Gelsomino R, Larpin S, Hohenegger M, Bora N, et al. Biodiversity of the Surface Microbial Consortia from Limburger, Reblochon, Livarot, Tilsit, and Gubbeen Cheeses. Microbiol Spectr. 2014; 2(1):CM-0010–2012.
16. Mounier J, Goerges S, Gelsomino R, Vancanneyt M, Vandemeulebroecke K, Hoste B, et al. Sources of the adventitious microflora of a smear-ripened cheese. J Appl Microbiol. 2006; 101 (3):668–81.
17. Arroyo-López FN, Querol A, Bautista-Gallego J, Garrido-Fernández A. Role of yeasts in table olive production. Int J Food Microbiol. 2008; 128(2):189–96.
18. Bonatsou S, Tassou C, Panagou E, Nychas G-J. Table olive fermentation using starter cultures with multifunctional potential. Microorganisms. 2017; 5:30.
19. Rodriguez-Gómez F, Arroyo-López F, López-López A, Bautista-Gallego J, Garrido Fernández A. Lipolytic activity of the yeast species associated with the fermentation/storage phase of ripe olive processing. Food Microbiol. 2010; 27:604–12.
20. Bautista-Gallego J, Rodriguez-Gómez F, Barrio E, Querol A, Garrido Fernández A, Arroyo-López F. Exploring the yeast biodiversity of green table olive industrial fermentations for technological applications. Int J Food Microbiol. 2011; 147:89–96.
21. Abriouel H, El Bakali N, Lucas R, Gálvez A. Culture-independent study of the diversity of microbial populations in brines during fermentation of naturally-fermented Aloreña green table olives. Int J Food Microbiol. 2011; 144:487–96.
22. Marquina D, Peres C, Caldas FV, Marques JF, Peinado JM, Spencer-Martins I. Characterization of the yeast population in olive brines. Lett Appl Microbiol. 1992; 14(6):279–83.
23. Silva T, Reto M, Sol M, Peito A, Peres C, Malcata F. Characterization of yeasts from Portuguese brined olives, with a focus on their potentially probiotic behavior. LWT - Food Sci Technol. 2011; 44:1349–54.
24. Porru C, Rodríguez-Gómez F, Benítez-Cabello A, Jiménez-Díaz R, Zara G, Budroni M, et al. Genotyping, identification and multifunctional features of yeasts associated to Bosana naturally black table olive fermentations. Food Microbiol. 2018; 69:33–42.
25. Tofalo R, Perpetuini G, Schirone M, Suzzi G, Corsetti A. Yeast biota associated to naturally fermented table olives from different Italian cultivars. Int J Food Microbiol. 2012; 161:203–8.
26. Sidari R, Martorana A, De Bruno A. Effect of brine composition on yeast biota associated with naturally fermented Nocellara messinese table olives. LWT. 2019; 109:163–70.
27. Nisiotou AA, Chorianopoulos N, Nychas G-JE, Panagou EZ. Yeast heterogeneity during spontaneous fermentation of black Conservolea olives

in different brine solutions. J Appl Microbiol. 2010; 108(2):396–405.

28. Bonatsou S, Paramithiotis S, Panagou EZ. Evolution of yeast consortia during the fermentation of Kalamata natural black olives upon two initial acidification treatments. Front Microbiol. 2018; 8:2673.
29. Kotzekidou P. Identification of yeasts from black olives in rapid system microtitre plates. Food Microbiol. 1997; 14(6):609–16.
30. Leventdurur S, Sert-Aydın S, Boyaci-Gunduz CP, Agirman B, Ben Ghorbal A, Francesca N, et al. Yeast biota of naturally fermented black olives in different brines made from cv. Gemlik grown in various districts of the Cukurova region of Turkey. Yeast. 2016; 33(7):289–301.
31. Mujdeci G, Arévalo-Villena M, Ozbas ZY, Briones Pérez A. Yeast Identification During Fermentation of Turkish Gemlik Olives. J Food Sci. 2018; 83(5):1321–5.
32. Bonatsou S, Tassou CC, Panagou EZ, Nychas G-JE. Table olive fermentation using starter cultures with multifunctional potential. Microorganisms. 2017; 5(2):30.
33. Restuccia C, Muccilli S, Palmeri R, Randazzo CL, Caggia C, Spagna G. An alkaline β-glucosidase isolated from an olive brine strain of Wickerhamomyces anomalus. FEMS Yeast Res. 2011;11(6):487–93.
34. Rodríguez-Gómez F, Romero-Gil V, Bautista-Gallego J, Garrido-Fernández A, Arroyo-López FN. Multivariate analysis to discriminate yeast strains with technological applications in table olive processing. World J Microbiol Biotechnol. 2012; 28(4):1761–70.
35. Papagora C, Roukas T, Kotzekidou P. Optimization of extracellular lipase production by Debaryomyces hansenii isolates from dry-salted olives using response surface methodology. Food Bioprod Process. 2013; 91:413–420.
36. Bataiche I, Kacem-chaouche N, Destain J, Lejeune A, Thonart P. Screening of Candida boidinii from Chemlal spent olive characterized by higher alkaline-cold adapted lipase production. Afr J Biotechnol. 2014; 13(11):1287–1294.
37. Psani M, Kotzekidou P. Technological characteristics of yeast strains and their potential as starter adjuncts in Greek-style black olive fermentation. World J Microbiol Biotechnol. 2006; 22(12):1329–36.
38. Hernández A, Martín A, Córdoba MG, Benito MJ, Aranda E, Pérez-Nevado F. Determination of killer activity in yeasts isolated from the elaboration of seasoned green table olives. Int J Food Microbiol. 2008; 121(2):178–88.
39. Llorente P, Marquina D, Santos A, Peinado JM, Spencer-Martins I. Effect of salt on the killer phenotype of yeasts from olive brines. Appl Environ Microbiol. 1997; 63(3):1165–7.
40. Bonatsou S, Karamouza M, Zoumpopoulou G, Mavrogonatou E, Kletsas D, Papadimitriou K, et al. Evaluating the probiotic potential and technological characteristics of yeasts implicated in cv. Kalamata natural black olive fermentation. Int J Food Microbiol. 2018; 271:48–59.
41. Tufariello M, Durante M, Ramires F, Grieco F, Tommasi L, Perbellini E, et al. New process for production of fermented black table olives using selected autochthonous microbial resources. Front Microbiol. 2015; 6:1007.
42. De Angelis M, Campanella D, Cosmai L, Summo C, Rizzello CG, Caponio F. Microbiota and metabolome of un-started and started Greek-type fermentation of Bella di Cerignola table olives. Food Microbiol. 2015; 52:18–30.
43. Tufariello M, Anglana C, Crupi P, Virtuosi I, Fiume P, Di Terlizzi B, et al. Efficacy of yeast starters to drive and improve Picual, Manzanilla and Kalamàta table olive fermentation. J Sci Food Agric. 2019; 99(5):2504–12.
44. Chytiri A, Tasioula-Margari M, Bleve G, Kontogianni VG, Kallimanis A, Kontominas MG. Effect of different inoculation strategies of selected yeast and LAB cultures on Conservolea and Kalamàta table olives considering phenol content, texture, and sensory attributes. J Sci Food Agr. 2020; 100(3):926–35.
45. Bevilacqua A, Beneduce L, Sinigaglia M, Corbo MR. Selection of yeasts as starter cultures for table olives. J Food Sci. 2013; 78(5):742–751.
46. Tsapatsaris S, Kotzekidou P. Application of central composite design and response surface methodology to the fermentation of olive juice by *Lactobacillus plantarum* and *Debaryomyces han-*

senii. Int J Food Microbiol. 2004; 95(2):157–68.

47. Deak T. Handbook of food spoilage yeasts. Boca Raton, USA: CRC Press, 2007. 352 p.
48. Ianieva O. Tolerance of yeasts isolated from pickled cucumbers to stress factors. Mikrobiol Z. 2017; 79:34–45.
49. Tang Y, Zhou X, Huang S, Li Y, Long M, Zhao X, et al. Microbial community analysis of different qualities of pickled radishes by Illumina MiSeq sequencing. J Food Saf. 2019; 39(2):e12596.
50. González-Quijano GK, Dorantes-Alvarez L, Hernández-Sánchez H, Jaramillo-Flores ME, de Jesús Perea-Flores M, Vera-Ponce de León A, et al. Halotolerance and survival kinetics of lactic acid bacteria isolated from jalapeño pepper (*Capsicum annuum* L.) fermentation. J Food Sci. 2014; 79(8):1545–1553.
51. Lara-Hidalgo CE, Dorantes-Álvarez L, Hernández-Sánchez H, Santoyo-Tepole F, Martínez-Torres A, Villa-Tanaca L, et al. Isolation of yeasts from guajillo pepper (*Capsicum annuum* l.) fermentation and study of some probiotic characteristics. Probiotics Antimicro Prot. 2019; 11(3):748–64
52. Chang H-W, Kim K-H, Nam Y-D, Roh SW, Kim M-S, Jeon C, et al. Analysis of yeast and archaeal population dynamics in Kimchi using denaturing gradient gel electrophoresis. Int J Food Microbiol. 2008; 126:159–66.
53. Lee KW, Shim JM, Kim DW, Yao Z, Kim JA, Kim H-J, et al. Effects of different types of salts on the growth of lactic acid bacteria and yeasts during kimchi fermentation. Food Sci Biotechnol. 2018; 27(2):489–98.
54. Lee N-K, Hong J-Y, Yi S-H, Hong S-P, Lee J-E, Paik H-D. Bioactive compounds of probiotic *Saccharomyces cerevisiae* strains isolated from cucumber jangajji. J Functional Foods. 2019; 58:324–9.
55. Jeong S, Lee SH, Jin HM, Jeon C. Microbial succession and metabolite changes during fermentation of dongchimi, traditional Korean watery kimchi. Int J Food Microbiol. 2013; 164:46–53.
56. Panghal A, Janghu S, Virkar K, Gat Y, Kumar V, Chhikara N. Potential non-dairy probiotic products – A healthy approach. Food Biosci. 2018; 21:80–9.
57. Lee M-E, Jang J-Y, Lee J-H, Park H-W, Choi H-J, Kim T-W. Starter cultures for kimchi fermentation. J Microbiol Biotechnol. 2015; 25(5):559–68.
58. Mo E-K, Ly S-Y, JeGal S-A, Sung C-K. Effects of addition of *Pichia anomala* SKM-T and *Galactomyces geotrichum* SJM-59 on baechu kimchi fermentation. Korean J Food Preserv. 2007; 14(1):94-9.
59. Kim Y-C, Jung E-Y, Kim H-J, Jung D-H, Hong S-G, Kwon T-J, et al. Improvement of kimchi fermentation by using acid-tolerant mutant of *Leuconostoc mesenteroides* and aromatic yeast *Saccharomyces fermentati* as starters. J Microbiol Biotechnol. 1999; 9:22–31.
60. Tamang J. Diversity of Fermented Foods. In: Fermented foods and beverages of the world. CRC Press; 2010. p. 41–84.
61. Paškevičius A, Varnaite R. Yeast occurrence in herring products and processing environment and their biochemical peculiarities. Pol J Food Nutr Sci. 2010; 60:369–73.
62. Dąbrowski W., Różycka-Kasztelan K., Czeszejko K., Mędrala D. Microflora of lawsalt herring. The influence of sodium benzoate on microflora of low-salt herring. Electr J Po Agric Univ. 2002; 5(2):14.
63. Ianieva O, Ogirchuk KS. Yeasts associated with salted herring and brine, Ukraine. Mikrobiol Z. 2018; 80(2): 40–51.
64. Thapa N, Pal J, Tamang JP. Microbial diversity in ngari, hentak and tungtap, fermented fish products of north-east India. World J Microbiol Biotechnol. 2004; 20(6): 599.
65. Roh SW, Kim K-H, Nam Y-D, Chang H-W, Park E-J, Bae J-W. Investigation of archaeal and bacterial diversity in fermented seafood using barcoded pyrosequencing. The ISME Journal. 2010; 4(1):1–16.
66. Paludan-Müller C, Madsen M, Sophanodora P, Gram L, Møller PL. Fermentation and microflora of plaa-som, a Thai fermented fish product prepared with different salt concentrations. Int J Food Microbiol. 2002; 73(1):61–70.
67. Mendoza LM, Padilla B, Belloch C, Vignolo G. Diversity and enzymatic profile of yeasts isolated from traditional llama meat sausages from

north-western Andean region of Argentina. Food Res Int. 2014; 62:572–9.

68. Murgia MA, Marongiu A, Aponte M, Blaiotta G, Deiana P, Mangia NP. Impact of a selected Debaryomyces hansenii strain's inoculation on the quality of Sardinian fermented sausages. Food Res Int. 2019; 121:144–50.
69. Mendonça RCS, Gouvêa DM, Hungaro HM, Sodré A de F, Querol-Simon A. Dynamics of the yeast flora in artisanal country style and industrial dry cured sausage (yeast in fermented sausage). Food Control. 2013; 29(1):143–8.
70. Baruzzi F, Matarante A, Caputo L, Morea M. Molecular and physiological characterization of natural microbial communities isolated from a traditional Southern Italian processed sausage. Meat Sci. 2006; 72(2):261–9.
71. Flores M, Corral S, Cano-García L, Salvador A, Belloch C. Yeast strains as potential aroma enhancers in dry fermented sausages. Int J Food Microbiol. 2015; 212:16–24.
72. Corral S, Belloch C, López-Díez JJ, Salvador A, Flores M. Yeast inoculation as a strategy to improve the physico-chemical and sensory properties of reduced salt fermented sausages produced with entire male fat. Meat Sci. 2017; 123:1–7.
73. Andrade M, Córdoba J, Casado E, Córdoba M, Rodríguez M. Effect of selected strains of *Debaryomyces hansenii* on the volatile compound production of dry fermented sausage "salchichón". Meat Sci. 2010; 85:256–64.
74. Núñez F, Lara MS, Peromingo B, Delgado J, Sánchez-Montero L, Andrade MJ. Selection and evaluation of *Debaryomyces hansenii* isolates as potential bioprotective agents against toxigenic penicillia in dry-fermented sausages. Food Microbiol. 2015; 46:114–20.
75. Andrade MJ, Thorsen L, Rodríguez A, Córdoba JJ, Jespersen L. Inhibition of ochratoxigenic moulds by *Debaryomyces hansenii* strains for biopreservation of dry-cured meat products. Int J Food Microbiol. 2014; 170:70–7.
76. Virgili R, Simoncini N, Toscani T, Camardo Leggieri M, Formenti S, Battilani P. Biocontrol of *Penicillium nordicum* growth and ochratoxin A production by native yeasts of dry cured ham. Toxins. 2012; 4(2):68–82.
77. Iucci L, Patrignani F, Belletti N, Ndagijimana M, Elisabetta Guerzoni M, Gardini F, et al. Role of surface-inoculated *Debaryomyces hansenii* and *Yarrowia lipolytica* strains in dried fermented sausage manufacture. Part 2: Evaluation of their effects on sensory quality and biogenic amine content. Meat Science. 2007; 75(4):669–75.
78. Selgas MD, Ros J, García ML. Effect of selected yeast strains on the sensory properties of dry fermented sausages. Eur Food Res Technol. 2003; 217(6):475–80.
79. Gunde-Cimerman N, Zalar P, de Hoog S, Plemenitas A. Hypersaline waters in salterns - natural ecological niches for halophilic black yeasts. FEMS Microbiol Ecol. 2000; 32(3):235–40.
80. Tekolo OM, McKenzie J, Botha A, Prior BA. The osmotic stress tolerance of basidiomycetous yeasts. FEMS Yeast Res. 2010; 10(4):482–91.
81. Golomb BL, Morales V, Jung A, Yau B, Boundy-Mills KL, Marco ML. Effects of pectinolytic yeast on the microbial composition and spoilage of olive fermentations. Food Microbiol. 2013; 33(1):97–106.
82. Bautista-Gallego J, Arroyo-López FN, Romero-Gil V, Rodríguez-Gómez F, García-García P, Garrido-Fernández A. Microbial stability and quality of seasoned cracked green Aloreña table olives packed in diverse chloride salt mixtures. J Food Prot. 2013; 76(11):1923–32.
83. de Castro A, Sánchez AH, López-López A, Cortés-Delgado A, Medina E, Montaño A. Microbiota and Metabolite Profiling of Spoiled Spanish-Style Green Table Olives. Metabolites. 2018; 8(4).
84. Savard T, Beaulieu C, Gardner N, Champagne C. Characterization of spoilage yeasts isolated from fermented vegetables and Inhibition by lactic, acetic and propionic acids. Food Microbiol. 2002; 19:363–73.
85. Franco W, Pérez-Díaz IM, Johanningsmeier SD, McFeeters RF. Characteristics of spoilage-sssociated secondary cucumber fermentation. Appl Environ Microbiol. 2012; 78(4):1273–84.
86. Moon SH, Chang M, Kim HY, Chang HC. *Pichia kudriavzevii* is the major yeast involved in film-formation, off-odor production, and texture-softening in over-ripened Kimchi. Food Sci

Biotechnol. 2014; 23(2):489–97.

87. Suzuki A, Muraoka N, Nakamura M, Yanagisawa Y, Amachi S. Identification of undesirable white-colony-forming yeasts appeared on the surface of Japanese kimchi. Biosci Biotech Bioch. 2018; 82(2):334–42.
88. Zhang F, Tang Y, Ren Y, Yao K, He Q, Wan Y, et al. Microbial composition of spoiled industrial-scale Sichuan paocai and characteristics of the microorganisms responsible for paocai spoilage. Int J Food Microbiol. 2018; 275:32–8.
89. Ao X, Yan J, Chen C, Zhao J, Liu S, Zhao K, et al. Isolation and identification of the spoilage microorganisms in Sichuan homemade Paocai and their impact on quality and safety. Food Sci Nutr. 2019; 7(9):2939–47.
90. Kim JY, Kim J, Cha I-T, Jung MY, Song HS, Kim YB, et al. Community structures and genomic features of undesirable white colony-forming yeasts on fermented vegetables. J Microbiol. 2019; 57(1):30–7.
91. Nielsen DS, Jacobsen T, Jespersen L, Koch AG, Arneborg N. Occurrence and growth of yeasts in processed meat products – Implications for potential spoilage. Meat Sci. 2008; 80(3):919–26.
92. Brocklehurst TF, Lund BM. Microbiological changes in mayonnaise-based salads during storage. Food Microbiol. 1984; 1(1):5–12.
93. Baleiras Couto MM, Hartog BJ, Huis in't Veld JHJ, Hofstra H, van der Vossen JMBM. Identification of spoilage yeasts in a food-production chain by microsatellite polymerase chain reaction fingerprinting. Food Microbiol. 1996; 13(1):59–67.
94. Waite JG, Jones JM, Yousef AE. Isolation and identification of spoilage microorganisms using food-based media combined with rDNA sequencing: Ranch dressing as a model food. Food Microbiol. 2009; 26(3):235–9.
95. Westall S, Filtenborg O. Spoilage yeasts of decorated soft cheese packed in modified atmosphere. Food Microbiology. 1998 Apr 1; 15(2):243–9.
96. Yalcin HT, Ucar FB. Isolation and characterization of cheese spoiler yeast isolated from Turkish white cheeses. Ann Microbiol. 2009; 59(3):477–83.
97. Garnier L, Valence F, Pawtowski A, Auhustsinava-Galerne L, Frotté N, Baroncelli R, et al. Diversity of spoilage fungi associated with various French dairy products. Int J Food Microbiol. 2017; 241:191–7.
98. Ross H, Harden T, Nichol A, Deeth H. Isolation and investigation of micro-organisms causing brown defects in mould-ripened cheeses. Aust J Dairy Technol. 2000; 55:5–8.
99. Arroyo-López FN, Romero-Gil V, Bautista-Gallego J, Rodríguez-Gómez F, Jiménez-Díaz R, García-García P, et al. Yeasts in table olive processing: desirable or spoilage microorganisms? Int J Food Microbiol. 2012; 160(1):42–9.
100. Raghukumar S. Fungi in Coastal and Oceanic Marine Ecosystems: Marine Fungi. Springer, Cham, 2017. 343 p.
101. Jones EBG, Pang K-L, Abdel-Wahab MA, Scholz B, Hyde KD, Boekhout T, et al. An online resource for marine fungi. Fungal Divers. 2019; 96(1):347–433.
102. Nagahama T. Yeast Biodiversity in Freshwater, Marine and Deep-Sea Environments. In Biodiversity and Ecophysiology of Yeasts, The Yeast Handbook. Berlin Heidelberg : Springer, 2006. p. 241–62.
103. Fotedar R, Kolecka A, Boekhout T, Fell J, Anand A, Malaki A, et al. *Naganishia qatarensis* sp. nov., a novel basidiomycetous yeast species from a hypersaline marine environment in Qatar. Int J Syst Evol Microbiol. 2018; 68(9): 2924–9.
104. Fotedar R, Kolecka A, Boekhout T, Fell JW, Zeyara A, Al Malki A, et al. *Kondoa qatarensis* f.a., sp. nov., a novel yeast species isolated from marine water in Qatar. Int J Syst Evol Microbiol. 2019; 69(2):486–92.
105. Nagahama T, Hamamoto M, Horikoshi K. *Rhodotorula pacifica* sp. nov., a novel yeast species from sediment collected on the deep-sea floor of the north-west Pacific Ocean. Int J Syst Evol Microbiol. 2006; 56(Pt 1):295–9.
106. Burgaud G, Arzur D, Sampaio J, Barbier G. *Candida oceani* sp. nov., a novel yeast isolated from a Mid-Atlantic Ridge hydrothermal vent (− 2300 meters). Antonie van Leeuwenhoek. 2011; 100:75–82.

107. Bass D, Howe A, Brown N, Barton H, Demidova M, Michelle H, et al. Yeast forms dominate fungal diversity in the deep oceans. Proc Biol Sci. 2007; 274(1629):3069–77.
108. Kutty SN, Philip R. Marine yeasts-a review. Yeast. 2008; 25(7):465–83.
109. Richards TA, Leonard G, Mahé F, del Campo J, Romac S, Jones MDM, et al. Molecular diversity and distribution of marine fungi across 130 European environmental samples. Proc Roy Soc B-Biol Sci. 2015; 282(1819):20152243.
110. Chi Z-M, Liu G, Zhao S, Li J, Peng Y. Marine yeasts as biocontrol agents and producers of bio-products. Appl Microbiol Biotechnol. 2010; 86(5):1227–41.
111. Zaky AS, Tucker GA, Daw ZY, Du C. Marine yeast isolation and industrial application. FEMS Yeast Res. 2014; 14(6):813–25.
112. Sheng J, Chi Z, Li J, Gao L, Gong F. Inulinase production by the marine yeast *Cryptococcus aureus* G7a and inulin hydrolysis by the crude inulinase. Process Biochem. 2007; 42:805–11.
113. Gao L, Chi Z, Sheng J, Wang L, Li J, Gong F. Inulinase-producing marine yeasts: evaluation of their diversity and inulin hydrolysis by their crude enzymes. Microb Ecol. 2007; 54:722–9.
114. Li J, Chi Z, Wang X, Peng Y, Chi Z. The selection of alkaline protease-producing yeasts from marine environments and evaluation of their bioactive peptide production. Chin J Oceanol Limn. 2009; 27:753–61.
115. Gong F, Sheng J, Chi Z, Li J. Inulinase production by a marine yeast *Pichia guilliermondii* and inulin hydrolysis by the crude inulinase. J Ind Microbiol Biotechnol. 2007; 34(3):179–85.
116. Li J, Peng Y, Wang X, Chi Z. Optimum production and characterization of an acid protease from marine yeast *Metschnikowia reukaufii* W6. J Ocean Univ China. 2010; 9:359–64.
117. Duarte AWF, Dayo-Owoyemi I, Nobre FS, Pagnocca FC, Chaud LCS, Pessoa A, et al. Taxonomic assessment and enzymes production by yeasts isolated from marine and terrestrial Antarctic samples. Extremophiles. 2013; 17(6):1023–35.
118. Chaud LCS, Lario LD, Bonugli-Santos RC, Sette LD, Pessoa Junior A, Felipe M das G de A. Improvement in extracellular protease production by the marine antarctic yeast *Rhodotorula mucilaginosa* L7. N Biotechnol. 2016; 33(6):807–14.
119. Li H, Chi Z, Duan X, Wang L, Sheng J, Wu LF. Glucoamylase production by the marine yeast *Aureobasidium pullulans* N13d and hydrolysis of potato starch granules by the enzyme. Process Biochem. 2007; 42:462–5.
120. Li X, Chi Z, Liu Z, Yan K, Li H. Phytase production by a marine yeast *Kodamea ohmeri* BG3. Appl Biochem Biotechnol. 2008; 149(2):183–93.
121. Wu S-J, Chen J. Preparation of maltotriose from fermentation broth by hydrolysis of pullulan using pullulanase. Carbohydr Polym. 2014; 107:94–97.
122. Zaky A, Greetham D, Tucker G, Du C. The establishment of a marine focused biorefinery for bioethanol production using seawater and a novel marine yeast strain. Sci Rep. 2018; 8:121–27.
123. Khambhaty Y, Upadhyay D, Kriplani Y, Joshi N, Mody K, Gandhi M. Bioethanol from macroalgal biomass: utilization of marine yeast for production of the same. Bioenerg Res. 2012; 6(1):188–95.
124. Kandasamy K, Saravanakumar K. Bio-ethanol production by marine yeasts isolated from coastal mangrove sediment. IRMJ-Biotechnology. 2011; 1:19–24.
125. Sudhakar MP, Jegatheesan A, Poonam C, Perumal K, Arunkumar, K. Biosaccharification and ethanol production from spent seaweed biomass using marine bacteria and yeast. Renew Energy. 2016; 105:133–39.
126. Wang Q, Cui Y, Sen B, Ma W, Zheng RL, Liu X, et al. Characterization and robust nature of newly isolated oleaginous marine yeast *Rhodosporidium* spp. from coastal water of Northern China. AMB Express. 2017; 7:30.
127. Dobrowolski A, Drzymała K, Rzechonek DA., Mituła P, Mirończuk AM. Lipid production from waste materials in seawater-based medium by the yeast *Yarrowia lipolytica*. Front Microbiol. 2019; 10:547.
128. Yen H-W, Liao Y-T, Liu YX. Cultivation of oleaginous *Rhodotorula mucilaginosa* in airlift bioreactor by using seawater. J Biosci Bioeng. 2016; 121(2):209–12.

129. Wang X, Chi Z, Yue L, Li J. Purification and characterization of killer toxin from a marine yeast *Pichia anomala* YF07b against the pathogenic yeast in crab. Curr Microbiol. 2007; 55(5):396–401.

130. Hua M-X, Chi Z, Liu G-L, Buzdar MA, Chi Z-M. Production of a novel and cold-active killer toxin by *Mrakia frigida* 2E00797 isolated from sea sediment in Antarctica. Extremophiles. 2010; 14(6):515–21.

131. Wang X-X, Chi Z, Peng Y, Wang X-H, Ru S-G, Chi Z-M. Purification, characterization and gene cloning of the killer toxin produced by the marine-derived yeast *Williopsis saturnus* WC91-2. Microbiol Res. 2012; 167(9):558–63.

132. Shetaia Y, Khalik W, Mohamed T, Farahat L, ElMekawy A. Potential biodegradation of crude petroleum oil by newly isolated halotolerant microbial strains from polluted Red Sea area. Mar Pollut Bull. 2016; 111(1–2):435–42.

133. Farag S, Soliman NA. Biodegradation of crude petroleum oil and environmental pollutants by *Candida tropicalis* strain. Braz Arch Biol Technol. 2011; 54:821–830.

134. Lefebvre O, Moletta R. Treatment of organic pollution in industrial saline wastewater: a literature review. Water Res. 2006; 40(20):3671–82.

135. Tan L, He M, Song L, Fu X, Shi S. Aerobic decolorization, degradation and detoxification of azo dyes by a newly isolated salt-tolerant yeast *Scheffersomyces spartinae* TLHS-SF1. Biores Technol. 2016; 203:287–94.

136. Tan L, Xu B, Hao J, Wang J, Shao Y, Mu G. Biodegradation and Detoxification of azo dyes by a newly isolated halotolerant yeast *Candida tropicalis* SYF-1. Envir Eng Sci. 2019; 36(9):999–1010.

137. Song L, Shao Y, Ning S, Tan L. Performance of a newly isolated salt-tolerant yeast strain *Pichia occidentalis* G1 for degrading and detoxifying azo dyes. Biores Technol. 2017; 233:21–9.

138. Song Z, Song L, Shao Y, Liang T. Degradation and detoxification of azo dyes by a salt-tolerant yeast *Cyberlindnera samutprakarnensis* S4 under high-salt conditions. World J Microb Biot. 2018; 34(9):131.

139. Guo G, Tian F, Zhao Y, Tang M, Liu W, Liu C, et al. Aerobic decolorization and detoxification of Acid Scarlet GR by a newly isolated salt-tolerant yeast strain *Galactomyces geotrichum* GG. Int Biodeter Biodegr. 2019; 145:104818.

140. Navarrete, P, Tovar-Ramírez D. Use of yeasts as probiotics in fish aquaculture. In: Sustainable Aquaculture Techniques, 2014. p. 135–172.

141. Tapia Paniagua ST, Reyes-Becerril M, Ascencio F, Esteban M, Clavijo E, Balebona M. Modulation of the intestinal microbiota and immune system of farmed Sparus aurata by the administration of the yeast *Debaryomyces hansenii* L2 in conjunction with inulin. J Aquac Res Development. 2011; S1:012.

142. Angulo M, Reyes-Becerril M, Cepeda-Palacios R, Tovar-Ramírez D, Esteban MÁ, Angulo C. Probiotic effects of marine *Debaryomyces hansenii* CBS 8339 on innate immune and antioxidant parameters in newborn goats. Appl Microbiol Biotechnol. 2019; 103(5):2339–52.

143. Sajeevan TP, Philip R, Singh ISB. Immunostimulatory effect of a marine yeast *Candida sake* S165 in Fenneropenaeus indicus. Aquaculture. 2006; 257(1):150–5.

144. Yang S-P, Wu Z-H, Jian J-C, Zhang X-Z. Effect of marine red yeast *Rhodosporidium paludigenum* on growth and antioxidant competence of *Litopenaeus vannamei*. Aquaculture (Amst). 2010; 309(1–4):62–5.

145. Babu DT, Antony SP, Joseph SP, Bright AR, Philip R. Marine yeast *Candida aquaetextoris* S527 as a potential immunostimulant in black tiger shrimp Penaeus monodon. J Invertebr Pathol. 2013; 112(3):243–52.

146. Butinar L, Santos S, Spencer-Martins I, Oren A, Gunde-Cimerman N. Yeast diversity in hypersaline habitats. FEMS Microbiol Lett. 2005; 244(2):229–34.

147. Rani MHS, Kalaiselvam M. Diversity of halophilic mycoflora habitat in saltpans of Tuticorin and Marakkanam along southeast coast of India. Int J Micro Myco. 2018; 7(1):1–17.

148. Borruso L, Sannino C, Selbmann L, Battistel D, Zucconi L, AZZARO di Rosamarina M, et al. A thin ice layer segregates two distinct fungal

communities in Antarctic brines from Tarn Flat (Northern Victoria Land). Sci Rep. 2018; 8:6582.

149. Moubasher A-AH, Abdel-Sater MA, Soliman ZSM. Diversity of yeasts and filamentous fungi in mud from hypersaline and freshwater bodies in Egypt. Czech Mycol. 2018; 26:70:1–32.

150. Fotedar R, Kolecka A, Boekhout T, Fell JW, Al-Malki A, Zeyara A, Marri MA. Fungal diversity of the hypersaline Inland Sea in Qatar. Botanica Mar. 2018; 61 (6):595–609.

151. Mokhtarnejad L, Arzanlou M, Babai-Ahari A. Molecular and phenotypic characterization of ascomycetous yeasts in hypersaline soils of Urmia Lake basin (NW Iran). Rostaniha. 2015; 16:174–85.

152. Mokhtarnejad L, Arzanlou M, Babai-Ahari A, Di Mauro S, Onofri A, Buzzini P, et al. Characterization of basidiomycetous yeasts in hypersaline soils of the Urmia Lake National Park, Iran. Extremophiles. 2016; 20(6):915–28.

153. Evans S, Hansen RW, Schneegurt MA. Isolation and Characterization of Halotolerant Soil Fungi from the Great Salt Plains of Oklahoma. Cryptogamie Mycol. 2013; 34(4):329–41.

154. Marchetta A, Gerrits van den Ende B, Al-Hatmi AMS, Hagen F, Zalar P, Sudhadham M, et al. Global molecular diversity of the halotolerant fungus Hortaea werneckii. Life (Basel). 2018; 8(3).

155. Ali I, Kanhayuwa L, Rachdawong S, Rakshit S. Identification, phylogenetic analysis and characterization of obligate halophilic fungi isolated from a man-made solar saltern in Phetchaburi province, Thailand. Ann Microbiol. 2012; 63:887–95.

156. Steiman R, Guiraud P, Sage L, Seigle-Murandi F. Soil mycoflora from the Dead Sea Oases of Ein Gedi and Einot Zuqim (Israel). Antonie Van Leeuwenhoek. 1997; 72(3):261–70.

157. Steiman R, Ford L, Ducros V, Lafond J-L, Guiraud P. First survey of fungi in hypersaline soil and water of Mono Lake area (California). Antonie Van Leeuwenhoek. 2004; 85(1):69–83.

158. Finkel O, Burch A, Lindow S, Post A, Belkin S. Finkel OM, Burch AY, Lindow SE, Post AF, Belkin S. Geographical location determines the population structure in phyllosphere microbial communities of a salt-excreting desert tree. Appl Environ Microbiol. 2011; 77(21):7647–55.

159. Van Ryckegem G, Gessner MO, Verbeken A. Fungi on leaf blades of Phragmites australis in a brackish tidal marsh: diversity, succession, and leaf decomposition. Microb Ecol. 2007; 53(4):600–11.

160. Furtado B, Szymańska S, Hrynkiewicz K. A window into fungal endophytism in Salicornia europaea: deciphering fungal characteristics as plant growth promoting agents. Plant Soil. 2019; 445:577–94.

161. Chamekh R, Deniel F, Donot C, Jany J-L, Nodet P, Belabid L. Isolation, Identification and Enzymatic Activity of Halotolerant and Halophilic Fungi from the Great Sebkha of Oran in Northwestern of Algeria. Mycobiology. 2019; 47(2):230–41.

162. Reyes-Becerril M, Guluarte C, Ceballos-Francisco D, Angulo C, Esteban MÁ. Dietary yeast *Sterigmatomyces halophilus* enhances mucosal immunity of gilthead seabream (*Sparus aurata* L.). Fish Shellfish Immunol. 2017; 64:165–75.

163. Crognale S, Pesciaroli L, Petruccioli M, D’Annibale A. Phenoloxidase-producing halotolerant fungi from olive brine wastewater. Process biochem. 2012; 47:1433–7.

164. Papadelli M, Ntougias S. Microbial community structure and disposal issues of table olive wastewaters generated from the fermentation of the olive cultivar ‘Kalamon’. Ann Microbiol. 2014; 64:1483–92.

165. Rincón-Llorente B, De la Lama-Calvente D, Fernández-Rodríguez MJ, Borja-Padilla R. Table olive wastewater: problem, treatments and future strategy. A review. Front Microbiol. 2018; 9:1641.

166. Yang Q, Angly F, Wang Z, Zhang H. Wastewater treatment systems harbor specific and diverse yeast communities. Biochem Eng J. 2011; 58:168–76.

167. Jarboui R, Baati H, Fetoui F, Gharsallah N, Ammar E. Yeast performance in wastewater treatment: Case study of Rhodotorula mucilaginosa. Envir Technol. 2012; 33:951–60.

168. Gonçalves C, Lopes M, Ferreira J, Belo I. Biological treatment of olive mill wastewater by non-conventional yeasts. Biores Technol. 2009; 100:3759–63.

169. Ayed L, Asses N, Chammem N, Hamdi M. Improvement of green table olive processing wastewater decolorization by *Geotrichum candidum*. Desalin Water Treat. 2015; 57(37):17322-17332.

170. Tigini V, Prigione V, Varese GC. Mycological and ecotoxicological characterisation of landfill leachate before and after traditional treatments. Sci Total Environ. 2014; 487:335–41.

171. Lahav R, Fareleira P, Nejidat A, Abeliovich A. The identification and characterization of osmotolerant yeast isolates from chemical wastewater evaporation ponds. Microb Ecol. 2002; 43(3):388–96.

172. Jiang Y, Shang Y, Yang K, Wang H. Phenol degradation by halophilic fungal isolate JS4 and evaluation of its tolerance of heavy metals. Appl Microbiol Biotechnol. 2016; 100(4):1883–90.

173. Rocha LL, de Aguiar Cordeiro R, Cavalcante RM, do Nascimento RF, Martins SCS, Santaella ST, et al. Isolation and characterization of phenol-degrading yeasts from an oil refinery wastewater in Brazil. Mycopathologia. 2007;164(4):183–8.

174. Jiang Y, Deng T, Shang Y, Yang K, Wang H. Biodegradation of phenol by entrapped cell of Debaryomyces sp. with nano-Fe 3 O 4 under hypersaline conditions. Int Biodeter Biodegr. 2017; 123:37–45.

175. Zajc J, Zalar P, Plemenitaš A, Gunde-Cimerman N. The Mycobiota of the Salterns. In: Biology of Marine Fungi. Berlin, Heidelberg: Springer; 2012. p. 133–58.

176. Kejžar A, Gobec S, Plemenitaš A, Lenassi M. Melanin is crucial for growth of the black yeast Hortaea werneckii in its natural hypersaline environment. Fungal Biol. 2013; 117(5):368–79.

Received 20.01.2020