

## First Record of the Pathogenic Protist *Labyrinthula* sp. Infecting the Seagrass *Enhalus acoroides* (L.f.) Royle

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### ABSTRACT

*Labyrinthula* is a globally distributed pathogen known to cause wasting disease and large-scale die-offs in various seagrass species. However, infection in *Enhalus acoroides* has not been previously documented. In this study, the marine slime mold *Labyrinthula* sp., was isolated from a lesion leaf of *Enhalus acoroides* collected at Pa Khlok Beach, Phuket, Thailand in February 2024. Leaf sections with lesions or suspected affected areas were cut and placed on serum seawater agar for cultivation and examination. The isolate was subsequently inoculated onto axenic *E. acoroides* plantlets to assess pathogenicity. Within 24–48 h of incubation, spindle-shaped cells of *Labyrinthula* sp. formed dense colonies embedded in ectoplasmic networks emerging from leaf edges. By the third week, brown lesions appeared on inoculated plantlets, expanding into band-like patterns by the fourth week. These symptoms confirm the ability of the isolated *Labyrinthula* sp. to induce lesions and contribute to wasting disease in *E. acoroides*. However, despite its pathogenic potential, there is not yet conclusive evidence linking this organism to the broader seagrass die-off observed in this region. This study presents the first report of *Labyrinthula* sp. infecting the seagrass, *E. acoroides*, and the first documented case of seagrass infection by *Labyrinthula* in Southeast Asia.

**Keywords:** Marine pathogen, Seagrass diseases, Thailand, Tropical seagrass, Wasting disease

### INTRODUCTION

The marine slime mold *Labyrinthula*, a unicellular saprophytic or parasitic protist in the phylum Labyrinthulomycota, is widely distributed in coastal areas worldwide. It thrives in various marine habitats, including organic detritus, diatoms, macroalgae, and marine vascular plants such as seagrasses (Vergeer and den Hartog, 1994; Raghukumar, 2002; Bergmann *et al.*, 2011). As an opportunistic pathogen, *Labyrinthula* affects not

only seagrasses but also marine algae and certain invertebrates (Wang *et al.*, 2024).

In the early 1930s, *Labyrinthula* caused the infamous "wasting disease," which led to the die-off of up to 90% of *Zostera marina* populations along the Atlantic coasts of Europe and North America (Renn, 1936; Short *et al.*, 1987; Muehlstein, 1989). Since then, the disease has continued to spread along coastlines, causing significant damage to seagrass populations in the northern hemisphere.

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The first report of pathogenic *Labyrinthula* in the western Pacific came from the southern coast of Japan, although no widespread die-offs were observed (Short *et al.*, 1993). Subsequently, *Labyrinthula* was found in the southern hemisphere of the western Pacific region in New Zealand and Australia (Armiger, 1964; Vergeer and den Hartog, 1994).

*Labyrinthula* does not exclusively infect only *Zostera* spp.; it has also been found in various other seagrass species, including *Heterozostera tasmanica*, *Posidonia oceanica*, *Cymodocea nodosa*, and tropical seagrasses such as *Halodule uninervis*, *Halophila ovalis*, and *Syringodium isoetifolium* (Vergeer and den Hartog, 1994). This broad host range suggests that any seagrass species, in any location, could be at risk of infection.

Since late 2024, Thailand's Department of Marine and Coastal Resources (DMCR) has reported a decline and widespread die-off of seagrass beds in the Andaman Sea, affecting approximately 106.5 km<sup>2</sup> across the provinces of Trang, Phang Nga, Phuket, and Krabi (Department of Marine and Coastal Resources, 2025). This loss has significant ecological and socio-economic consequences, disrupting marine animal habitats, fisheries, and coastal livelihoods. One suspected cause of this decline is wasting disease associated with *Labyrinthula* spp. We hypothesized that *Labyrinthula* would be present in natural symptomatic

seagrass plants. This study aimed to investigate the presence of *Labyrinthula* in *Enhalus acoroides* leaves and to determine its potential to cause wasting disease. It represents a novel contribution by providing the first recorded evidence of *Labyrinthula* infecting *E. acoroides*, offering valuable insights for future disease surveillance and monitoring efforts.

## MATERIALS AND METHODS

### Isolation and cultivation

*E. acoroides* leaves with lesions were collected from Pa Khlok Beach, Phuket, Thailand (8.033572N, 98.417935E) in February 2024. *Labyrinthula* sp. was isolated by cutting 10 mm × 10 mm sections from areas with lesions or suspected affection (Figure 1). These leaf pieces were placed on serum seawater agar, modified from Muehlstein and Porter (1991), containing 1% horse serum, 1.2% agar in 28 psu (practical salinity unit) seawater, 0.25 g·L<sup>-1</sup> amoxicillin trihydrate, and 0.25 g·L<sup>-1</sup> oxolinic acid. The culture plates were sealed with Parafilm and incubated at room temperature for three days. The plates were then examined, and *Labyrinthula* sp. was successfully isolated and transferred to a pure culture plate. On cultured agar, *Labyrinthula* cells form colonies surrounded by an ectoplasmic net (Moss, 1985; Wang *et al.*, 2024), which is visible to the naked eye. For morphological observation, the wet-mount preparation technique



Figure 1. *Enhalus acoroides* leaves with lesions or suspected leaf area (arrow). Scale bars represent 2 cm.

was used: a small piece of agar containing the ectoplasmic net colony was placed in a drop of water, covers with a coverslip, and observed under a light microscope. If the cells are *Labyrinthula*, their characteristic fusiform shape can be readily identified, as described by Sullivan *et al.* (2023).

#### *Axenic Enhalus acoroides* plantlet preparation

The *E. acoroides* plantlet culture technique was conducted using the method described by Tongkok *et al.* (2018). Mature fruits of *E. acoroides* were cleaned using a surface sterilization procedure with 70% ethanol (v/v) and 1.5% sodium hypochlorite (NaOCl). The seeds were then cultured on solid MS medium (Murashige and Skoog, 1962), with the pH adjusted to 6.5 and salinity to 28 psu. Plantlets were incubated under a 16-hour photoperiod with a light intensity of 70–100  $\mu\text{mol m}^{-2}\text{s}^{-1}$  at  $25\pm 2^\circ\text{C}$ . After 64 days of incubation, three plantlets were used for pathogenicity testing, while another three plantlets without inoculation of the pathogen were served as the control group.

#### *Inoculation of the pathogen*

Small agar pieces (10 mm  $\times$  20 mm) containing *Labyrinthula* sp., were cut and inoculated onto axenic plantlets by placing them near the plantlet shoots. Both inoculated and control plantlets were incubated under a 16-h photoperiod with a light intensity of 70  $\mu\text{mol m}^{-2}\text{s}^{-1}$  at room temperature for three weeks to observe pathogen transmission.

## RESULTS AND DISCUSSION

When a piece of *E. acoroides* leaf with lesions was transferred onto serum seawater agar, a mucus-like substance exuded from the leaf edge within 24–48 h (Figure 2a). Fusiform or spindle-shaped cells of *Labyrinthula* sp. subsequently formed dense colonies within ectoplasmic networks. These individual cells are colorless, measuring 20–30  $\mu\text{m}$  in length and 3–8  $\mu\text{m}$  in width (Figure 2b–2d). The ectoplasmic network is also referred to as “slimeways”, which facilitate gliding motility, as described by Porter (1969).

*Labyrinthula* has been identified in various marine environments, including sediments, detritus, macroalgae, mangrove leaves, and even plastic waste (Vergeer and den Hartog, 1994; Wahid *et al.*, 2007; Martin *et al.*, 2016; Wang *et al.*, 2019; 2024). Pathogenic species of *Labyrinthula* isolated from seagrass are known to cause leaf lesions in both host-specific and non-specific seagrass species (Vergeer and den Hartog, 1994; Garcias-Bonet and Sherman, 2011). However, under normal conditions, *Labyrinthula* does not harm healthy seagrasses (Vergeer and den Hartog, 1994). Sullivan *et al.* (2013) explained this phenomenon using Robinson (1976) plant pathosystem concept, suggesting that the occurrence of wasting disease depends on the interaction among the seagrass defense mechanisms, environmental conditions, and the pathogenicity of the *Labyrinthula* strain.

To evaluate whether the isolated *Labyrinthula* could induce brown lesions and cause wasting disease in seagrass, agar containing *Labyrinthula* was inoculated onto an axenic *E. acoroides* plantlet. By week 3, a brown lesion appeared on the leaf, approximately 3–4 cm above the site of the inoculated *Labyrinthula* agar. By week 4, the brown lesions had expanded into larger band-like lesions on the attached leaves (Figure 3), ultimately leading to the death of the infected plantlet within eight weeks. These symptoms confirm that the isolated *Labyrinthula* can induce lesions and contribute to wasting disease in *E. acoroides*. Based on this observation, *Labyrinthula* required approximately three weeks to grow from the inoculated agar at the base of plantlet to the leaf tissue where lesions became visible.

The time from inoculation to lesion appearance in this study was longer than that reported in previous studies, where symptoms typically developed within 2 to 16 days, depending on the *Labyrinthula* species, seagrass host, and inoculation methods, primarily surface-to-surface or waterborne transmission. (Muehlstein *et al.*, 1989; Garcias-Bonet and Sherman, 2011; Trevathan *et al.*, 2011; Brakel *et al.*, 2014; Venkataraman *et al.*, 2023; Eisenlord *et al.*, 2024). This extended duration may be attributed to the time required for



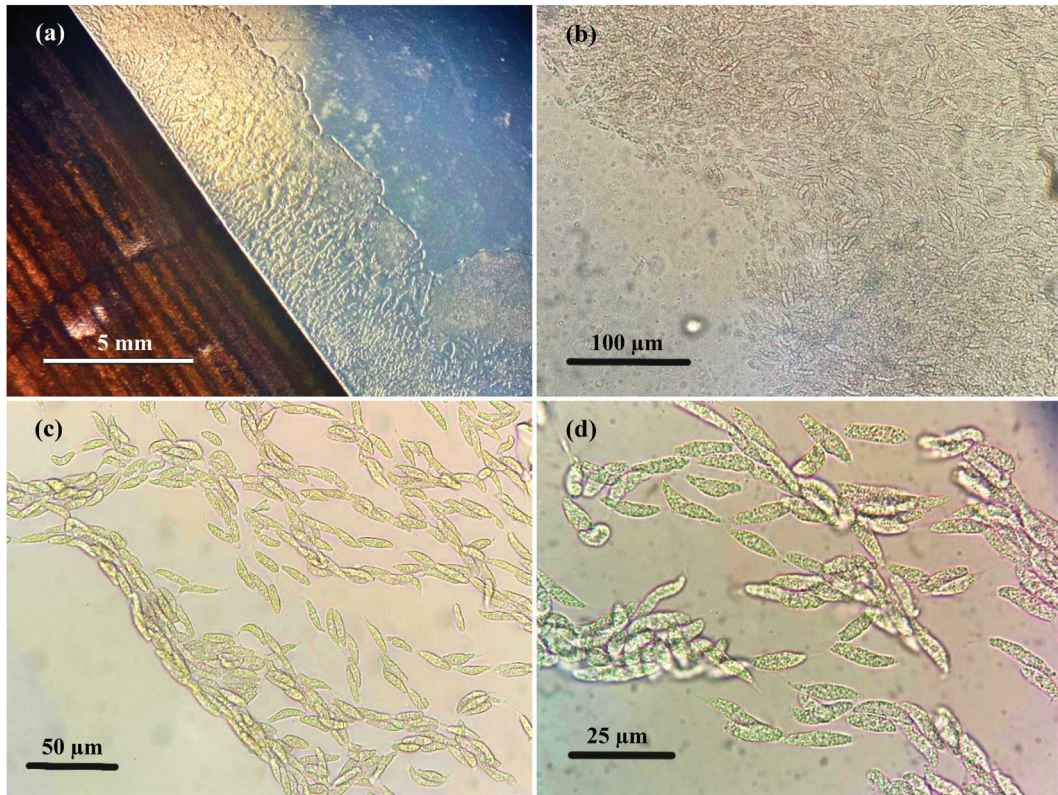


Figure 2. *Labyrinthuhula* sp. colony with surrounded ectoplasmic membrane (a, b) exuding from *Enhalus acoroides* leaf margin. Spindle-shaped cells of isolated *Labyrinthuhula* sp. (c, d). Scale bars represent 5 mm (a), 100 μm (b), 50 μm (c) and 25 μm (d).

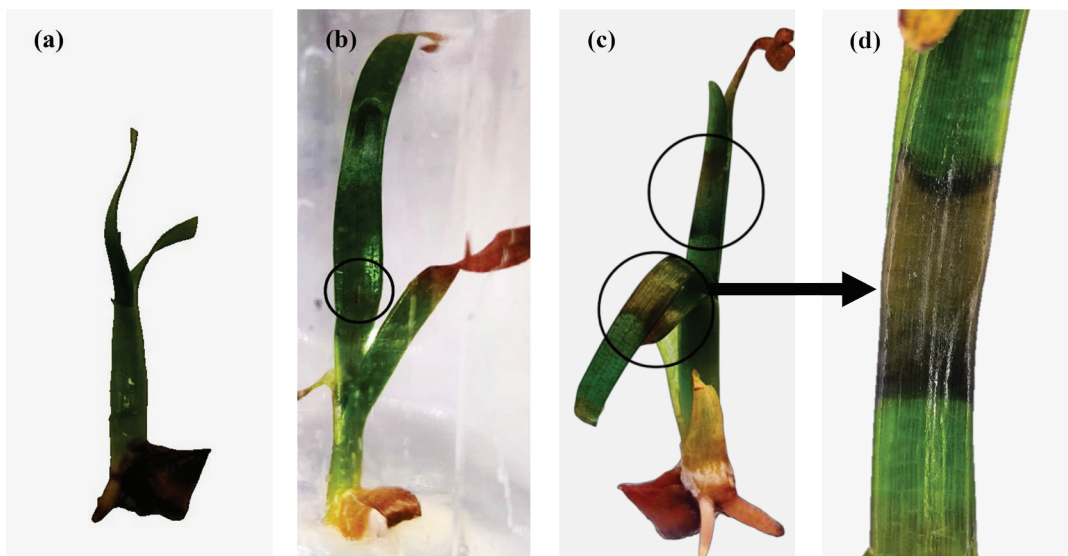


Figure 3. Axenic *Enhalus acoroides* plantlet before inoculation (a). Leaf lesions occurred after inoculation in week 3 (lesions size 3×4 mm) (b) and week 4 (lesions size 13–18×8 mm) (c, d).

*Labyrinthula* to migrate from the inoculated agar near the plantlet shoots, along the leaf sheath, to the target leaf tissue. In *E. acoroides*, the leaf sheath, composed of fibrous remnants of older leaves, encloses the leaf base, providing structural support and protecting developing leaves, which may hinder pathogen progression.

This study represents the first report of *Labyrinthula* sp. infecting the seagrass *E. acoroides*, and the first documented case of seagrass infection

by *Labyrinthula* in Southeast Asia. Previous records from the region identified *Labyrinthula* sp. in *Rhizophora* mangroves in the Philippines and from an unspecified source in Vietnam, as reported by Trevathan-Tackett *et al.* (2018) and Wahid *et al.* (2007). However, no prior evidence has confirmed its presence in seagrasses within this area. In contrast, *Labyrinthula* infections have been widely documented in Western Pacific coastal regions, particularly in Japan and Australia (Table 1). The organism has been found in diverse marine habitats,

Table 1. Summarized *Labyrinthula* spp. reported in Western Pacific Ocean, Asia and Australia.

Species	Samples / host	Location	Seagrass disease symptom	References
<i>Labyrinthula</i>	<i>Amphibolis antarctica</i>	The coast of	Black leaf lesions occur after 12 h to 3 days of infection.	Trevathan-Tackett <i>et al.</i> (2018)
	<i>Halophila australis</i>	Victoria, Australia		
	<i>Halohila ovalis</i>			
	<i>Heterozostera nigricaulis</i> ,			
	<i>Posidonia australis</i>			
	<i>Zostera muelleri</i>			
	Mangrove <i>Rhizophora</i> sp.	Philippines, Japan	-	
	Macroalgae	Japan	-	
	Not mention	Viet Nam	-	
<i>Labyrinthula</i> sp.	<i>Zostera muelleri</i> ,	Victoria and	-	Sullivan <i>et al.</i> (2017)
	<i>Halophila ovalis</i> ,	New South Wales,		
	<i>Heterozostera nigricaulis</i> ,	Southern Australia		
	<i>Posidonia australis</i>			
<i>Labyrinthula</i> sp.	Mangrove leaves	Panay Island, Philippines	-	Wahid <i>et al.</i> (2007)
<i>Labyrinthula zosterae</i>	<i>Zostera marina</i>	Gyeongnam Province, Korea	Black leaf lesions	Lee <i>et al.</i> (2021)
<i>Labyrinthula</i> sp.	Plastic bottle waste	Wuyuan Bay, Xiamen, China	-	Zhang <i>et al.</i> (2023)
<i>Labyrinthula</i> sp.	Mangrove leaves	Hainan, Guangxi, China	-	Wang <i>et al.</i> (2019; 2024)
<i>Labyrinthula zosterae</i>	<i>Zostera marina</i> ,	South coast of Japan	Black spot leaf	Short <i>et al.</i> (1993)
	<i>Zostera caulescens</i> ,			
	<i>Zostera japonica</i>			
<i>Labyrinthula</i> spp.	<i>Zostera mucronata</i>	Western Australia	Leaf lesions	Vergeer and de Hartog (1994)
	<i>Heterozostera tasmanica</i>	Western Australia	Leaf lesions	
	<i>Halophila ovalis</i>	Western Australia	No lesions with green healthy tissue	

including sediments, detritus, and macroalgae, with its morphology varying depending on species, geographic location, and host seagrass (Vergeer and den Hartog, 1994). These findings suggest that although *Labyrinthula* is distributed across the Western Pacific, no evidence of its infection in Southeast Asian seagrasses has been documented until now. Despite its ability to produce leaf lesions, evidence directly linking *Labyrinthula* to large-scale seagrass die-off, known as "wasting disease," remains inconclusive.

Symptoms of *Labyrinthula* infection typically begin as small brown lesions that gradually expand across one or more leaves. This infection disrupts photosynthesis and damages the air lacunar system, impairing both vascular and air transport functions (Sullivan *et al.*, 2013). Recurrent infections can cause necrosis of the rhizome, eventually leading to plant death. In meadows where few reproductive plants remain, natural recovery becomes limited, increasing the risk of acute disease outbreaks (Short *et al.*, 1986; 1988).

If wasting disease affects *E. acoroides*, it could pose significant serious ecological threats to coastal ecosystems in Southeast Asia, as this species is the largest and most widespread seagrass in the region (Bujang and Zakaria, 2003; Green and Short, 2003; Kuriandewa *et al.*, 2003; Supanwanid and Lewmanomont, 2003). Its leaves and detritus serve as important food sources and provide habitat for a variety of marine organisms, particularly dugongs (Hines *et al.*, 2005). In Thailand, *E. acoroides* has been identified in the stomach contents of dugongs (Adulyanukosol *et al.*, 2001). Notably, *E. acoroides* exhibits a very slow shoot multiplication rate, ranging from 7 months to 11 years (Rollón, 1998; Tongkok *et al.*, 2022). Tongkok *et al.* (2022) further estimated that four *E. acoroides* plants patch was at least three years old. Furthermore, surviving plants may not fully recover or become vigorous enough to produce male and female flowers limiting reproductive potential and long-term meadow resilience.

The spread of *Labyrinthula* could result in significant die-offs of *E. acoroides* in natural habitats, posing a serious threat to tropical seagrass ecosystems in Southeast Asia, including the

Philippines, Indonesia, Vietnam, and Malaysia. However, there is currently no evidence of *Labyrinthula* causing epidemic seagrass die-offs in Thailand. Environmental factors such as elevated water temperatures due to global warming, hypersalinity, oxygen depletion, and sulfide toxicity, are known to weaken seagrass health and promote the onset of wasting disease epidemics (Robblee *et al.*, 1991; Short and Neckles, 1999; Pedersen *et al.*, 2004; Frederiksen *et al.*, 2006; Ehlers *et al.*, 2008; Trevathan *et al.*, 2011; Sullivan *et al.*, 2013).

Regular monitoring of seagrass meadows and the development of effective restoration techniques are essential for mitigating potential wasting disease outbreaks in Southeast Asian countries.

## CONCLUSIONS

This study provides the first evidence of *Labyrinthula* sp. infecting *E. acoroides*, representing a significant finding for Southeast Asia. The infection initiates as small brown lesions, which gradually expand and disrupt photosynthesis and vascular function, potentially leading to plant death. The slow recovery and low reproductive rate of *E. acoroides* amplify the ecological risk, particularly in regions such as the Philippines, Indonesia, Vietnam, and Malaysia. Although, no epidemic-scale die-offs have been observed in Thailand to date, proactive monitoring and disease surveillance, along with improved restoration techniques, are critical for safeguarding the resilience of these vital seagrass ecosystems.

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## LITERATURE CITED

- Adulyanukosol, K., S. Poovachiranon and P. Natakuthug. 2001. Analysis of stomach contents of dugongs (*Dugong dugon*) from Trang Province. **Thai Fishery Gazette** 54: 129–137.
- Armiger, L.C. 1964. An occurrence of *Labyrinthula* in New Zealand *Zostera*. **New Zealand Journal of Botany** 2(1): 3–9. DOI: 10.1080/0028825X.1964.10428713.
- Bergmann, N., B. Fricke, M.C. Schmidt, V. Tames, K. Beining and H. Schwitte. 2011. A quantitative real-time polymerase chain reaction assay for the seagrass pathogen *Labyrinthula zosterae*. **Molecular Ecology Resources** 11: 1076–1081. DOI: 10.1111/j.1755-0998.2011.03051.x.
- Brakel, J., F.J. Werner, V. Tams, T.B.H. Reusch and A.C. Bockelman. 2014. Current European *Labyrinthula zosterae* are not virulent and modulate seagrass (*Zostera marina*) defense gene expression. **PLOS One** 9(4): e92448. DOI: 10.1371/journal.pone.0092448.
- Bujang, J.S. and M.H. Zakaria. 2003. **The seagrasses of Malaysia**. In: World Atlas of Seagrasses (eds. E. Green and F.T. Short), pp. 152–160. University of California Press, Berkeley, California, USA.
- Department of Marine and Coastal Resources. 2025. **Current status and counter measures seagrass die-off and dugong crisis in the lower Andaman Sea**. In: The First Asian Regional Dialogue on Seagrass and Dugong Conservation: From Gaps to Impactful Action, 20-21 February 2025, Bangkok Thailand. <https://www.dugongseagrass.org/media/2025/02/Thailand.pdf>. Cited 19 June 2025.
- Ehlers, A., B. Worm and T.B.H. Reusch. 2008. Importance of genetic diversity in eelgrass *Zostera marina* for its resilience to global warming. **Marine Ecology Progress Series** 355: 1–7. DOI: 10.3354/meps07369.
- Eisenlord, M.E., M.V. Agnew, M. Winningham, O.J. Lobo, A.D. Vompe, B. Wippel, C.S. Friedman, C.D. Harvell and C.A. Burge. 2024. High infectivity and waterborne transmission of seagrass wasting disease. **Royal Society Open Science** 11: 240663. DOI: [epdf/10.1098/rsos.240663](https://doi.org/10.1098/rsos.240663).
- Frederiksen, M.S. and R.N. Glud. 2006. Oxygen dynamics in the rhizosphere of *Zostera marina*: a two-dimensional planer optode study. **Limnology Oceanography** 51(2): 1072–1083. DOI: 10.4319/lo.2006.51.2.1072.
- Garcias-Bonet, N. and T.D. Sherman. 2011. Distribution and pathogenicity of the protist *Labyrinthula* sp. in western Mediterranean seagrass meadows. **Estuaries and Coasts** 34: 1161–1168. DOI: 10.1007/s12237-011-9416-4.
- Green, E. and F.T. Short. 2003. **The seagrasses of the Philippines and Vietnam**. In: World Atlas of Seagrasses (eds. E. Green and F.T. Short), pp. 183–184. University of California Press, Berkeley, California, USA.
- Hines, E.M., K. Adulyanukosol and E.A. Duffus. 2005. Dugong (*Dugong dugon*) abundance along the Andaman coast of Thailand. **Marine Mammal Science** 21: 536–549. DOI: 10.1111/j.1748-7692.2005.tb01247.x.
- Kuriandewa, T.E., W. Kiswara, M. Hotomo and S. Saemodihard. 2003. **The seagrasses of Indonesia**. In: World Atlas of Seagrasses (eds. E. Green and F.T. Short), pp. 171–178. University of California Press, Berkeley, California, USA.
- Lee, S.J., J.B. Shim and S. Lee. 2021. First report of *Labyrinthula zosterae* (Labyrinthulomycetes) as the causal pathogen of wasting disease in the seagrass *Zostera marina* in Korea. **Plant Disease** 105: 2251. DOI: 10.1094/PDIS-12-20-2751-PDN.



- Martin, D.L., Y. Chiaril, E. Boone, T.D. Sherman, C. Ross, S. Wyllie-Echeverria, J.K. Gaydos and A.A. Boettcher. 2016. Functional, phylogenetic and host-geographic signatures of *Labyrinthula* spp. provide for putative species delimitation and a global-scale view of seagrass wasting disease. **Estuaries and Coasts** 39: 1403–1421. DOI: 10.1007/s12237-016-0087-z.
- Moss, S.T. 1985. An ultrastructural study of taxonomically significant characters of the Thraustochytriales and the Labyrinthulales. **Botanical Journal of the Linnean Society** 91: 329–357. DOI: 10.1111/j.1095-8339.1985.tb01154.x.
- Muehlstein, L.K. 1989. Perspectives on the wasting disease of eelgrass *Zostera marina*. **Diseases of Aquatic Organisms** 7: 211–221. DOI: 10.3354/dao007211.
- Muehlstein, L.K. and D. Porter. 1991. *Labyrinthula zosterae* sp. nov., the causative agent of wasting disease of eelgrass, *Zostera marina*. **Mycologia** 82(2): 180–191. DOI: 10.2307/3759933.
- Murashige, T. and F. Skoog. 1962. A revised medium for rapid growth bioassays with tobacco tissue cultures. **Physiologia Plantarum** 15: 473–497. DOI: 10.1111/j.1399-3054.1962.tb08052.x.
- Pedersen, O., T. Binzer and J. Borum. 2004. Sulfide intrusion in eelgrass. **Plant, Cell and Environment** 27: 595–602. DOI: 10.1111/j.1365-3040.2004.01173.x
- Porter, D. 1969. Ultrastructure of *Labyrinthula*. **Protoplasma** 67: 1–19. DOI: 10.1007/BF01256763.
- Raghukumar, S. 2002. Ecology of the marine protists, the Labyrinthulomycetes (thraustochytrids and labyrinthulids). **European Journal of Protistology** 38: 127–145. DOI: 10.1078/0932-4739-00832.
- Renn, C.E. 1936. The wasting disease of *Zostera marina*: a phytological investigation of the disease plant. **Biology Bulletin** 70: 148–158. DOI: 10.2307/1537320.
- Robblee, M.B., T.R. Barber, P.R. Carlson Jr., M.J. Durako, J.W. Fourqurean, L.K. Muehlstein and J.C. Zieman. 1991. Mass mortality of the tropical seagrass *Thalassia testudinum* in Florida Bay (USA). **Marine Ecology Progress Series** 71(3): 297–299. DOI: 10.3354/meps071297.
- Robinson, R.A. 1976. **Plant Pathosystems**. Springer-Verlag, Berlin. 186 pp. DOI: 10.1007/978-3-642-66359-8.
- Rollón, R.N. 1998. **Spatial variation and seasonality in growth and reproduction of *Enhalus acoroides* (L.f.) Royle populations in the coastal waters off Cape Bolinao, NW Philippines**. PhD Thesis, Wageningen Agricultural University, Wageningen, the Netherlands. 135 pp.
- Short, F.T., A.C. Mathieson and J.I. Nelson. 1986. Recurrence of the eelgrass wasting disease at the border of New Hampshire and Maine, USA. **Marine Ecological Progress Series** 29: 89–92. DOI: 10.3354/meps029089.
- Short, F.T., L.K. Muehlstein and D. Porter. 1987. Eelgrass wasting disease: Cause and recurrence of a marine epidemic. **Biology Bulletin** 173: 557–562. DOI: 10.2307/1541701.
- Short, F.T., B.W. Ibelings, C. Den Hartog. 1988. Comparison of a current eelgrass disease to the wasting disease in the 1930s. **Aquatic Botany** 30(4): 295–304. DOI: 10.1016/0304-3770(88)90062-9.
- Short, F.T., D. Porter, H. Iizumi and K. Aioi. 1993. Occurrence of the eelgrass pathogen *Labyrinthula zosterae* in Japan. **Disease of Aquatic Organisms** 16: 73–77. DOI: 10.3354/dao016073.
- Short, F.T. and H.A. Neckles. 1999. The effects of global climate change on seagrasses. **Aquatic Botany** 63: 169–196. DOI: 10.1016/S0304-3770(98)00117-X.
- Sullivan, B.K., T.D. Sherman, V.S. Damare, O. Lilje and F.H. Gleason. 2013. Potential roles of *Labyrinthula* spp. in global seagrass population declines. **Fungal Ecology** 6(5): 328–338. DOI: 10.1016/j.funeco.2013.06.004.



- Sullivan, B.K., L. Robinson, S.M. Trevathan-Tackett, E.S. Lilje, F.H. Gleason and O. Lilje. 2017. The first isolation and characterization of the protist *Labyrinthula* sp. In Southeastern Australia. **Journal of Eukaryotic Microbiology** 64: 504–513. DOI: 10.1111/jeu.12387.
- Sullivan, B.K., D.L. Martin, R.M. Yoshioka, J. Brakel, S. Jakobsson-Thor, M. Eisenlord and S.M. Trevathan-Tackett. 2023. Standard ecological and molecular research methods and techniques for *Labyrinthula* spp. **Frontiers in Marine Science** 10:1092587. DOI: 10.3389/fmars.2023.1092587.
- Supanwanid, C. and K. Lewmanomont. 2003. **The seagrasses of Thailand**. In: World Atlas of Seagrasses (eds. E. Green and F.T. Short), pp. 144–151. University of California Press, Berkeley, California, USA.
- Trevathan, S.M., A. Kahn and C. Ross. 2011. Effects of short-term hypersalinity exposure on the susceptibility to wasting disease in the subtropical seagrass *Thalassia testudinum*. **Plant Physiology and Biochemistry** 49(9): 1051–1058. DOI: 10.1016/j.plaphy.2011.06.006.
- Trevathan-Tackett, S.M., B.K. Sullivan, K. Robinson, Osu Lilje, P.I. Macreadie and F.H. Gleason. 2018. Pathogenic *Labyrinthula* associated with Australian seagrasses: Considerations for seagrass wasting disease in the southern hemisphere. **Microbiology Research** 206: 74–81. DOI: 10.1016/j.micres.2017.10.003.
- Tongkok, P., P. Kermanee and C. Kaewsuralikhit. 2018. Effects of N6-(2-Isopentenyl) Adenine (2iP) on the growth of tropical seagrass *Enhalus acoroides* after germination. **Journal of Fisheries and Environment** 42(1): 14–23.
- Tongkok, P., J. Chusrisoml, Y. Munthum, C. Roengthong, A. Khantavong and C. Kaewsuralikhit. 2022. **Enhalus acoroides shoot multiplication in seagrass beds: the truth for seagrass transplantation and restoration**. The Proceedings of the 7<sup>th</sup> Marine Science Conference: Science, Technology and Innovation for Sustainable Seas 2022: 165–172. (in Thai)
- Venkataraman, Y.R., A. Shore, S. Dayal, *et al.* 2023. Characterizing host-pathogen interactions between *Zostera marina* and *Labyrinthula zosterae*. **Frontiers in Marine Science** 10: 1152647. DOI: 10.3389/fmars.2023.1152647.
- Vergeer, L.H.T. and C. de Hartog. 1994. Omnipresence of Labyrinthulaceae in seagrasses. **Aquatic Botany** 48: 1–20. DOI: 10.1016/0304-3770(94)90070-1.
- Wahid, M., T. Yoshikawa and T. Sakata. 2007. Bacteriolytic activity and growth of marine isolates of labyrinthulids on dead bacterial cells. **Fisheries Science** 73: 1286–1294. DOI: 10.1111/j.1444-2906.2007.01467.x.
- Wang, Q., Y. Huike, X. Yunxuan, H. Yaodong, S. Biswarup and Guangyi Wang. 2019. Culturable diversity and lipid production profile of Labyrinthulomycete protists isolated from coastal mangrove habitats of China. **Marine Drugs** 17: 268. DOI: 10.3390/md17050268.
- Wang, Q., X. Yu, Y. He, Y. Zhang, R. Hui, C. Wang and M. Bai. 2024. Review of the protist *Labyrinthula* spp. and its relationship to seagrass disease under the influence of anthropogenic activities. **Frontiers in Microbiology** 15: 1410195. DOI: 10.3389/fmicb.2024.1410195.
- Zhang, X., P. Zhang, Z. Deng, R. Huang, D. Zhang and Y. Tian. 2023. Ocean acidification has a strong effect on communities living on plastic in mesocosms. **Limnology and Oceanography Letters** 8: 675–684. DOI: 10.1002/lol2.10329.