



Dictyotaceae (Dictyotales, Phaeophyceae) species from French Polynesia: current knowledge and future research

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Abstract

The coral reefs of French Polynesia (FP) have experienced repeated macroalgal blooms over the last decades. These events have prompted intense efforts in fundamental and applied research on macroalgae in this ecoregion, especially regarding species of the order Fucales (*Turbinaria ornata* and *Sargassum pacificum*). Recently, however, these proliferations have occurred with a higher frequency, and they now involve additional species. Specifically, over the past decade, the abundance of species belonging to the Dictyotaceae family (e.g., *Dictyota bartayresiana* and *Spatoglossum asperum*) has increased on coral reefs around Tahiti Island, the largest and most inhabited island in FP. On the course of evolution, these species have developed physical and chemical defenses to deter grazers, including the production of a wide array of specialized metabolites. These molecules are of particular interest for their promising biological activities as well as for the new Blue Economy opportunities they can offer to FP. We review the current state of knowledge on the diversity, ecology, and potential uses of Dictyotaceae species present in FP. The first section focuses on the diversity and distribution of the family Dictyotaceae in FP. The second part examines the ecological dynamics of Dictyotaceae species in the coral reef ecosystem and their response to various environmental factors. The third and final part reviews the metabolites known from Dictyotaceae species that are present in FP, their associated biological activities, and potential for the development of biotechnological applications in FP.

1. Introduction

French Polynesia (FP) is a vast territory (5.5 million km²) in the South Pacific Ocean (7°S–28°S; 134°W–155°W) consisting of 118 islands (34 high volcanic islands and 84 atolls) that belong to five archipelagos (Austral, Gambier, Marquesas, Society, and Tuamotu; [Andréfouët & Adjeroud, 2019, Fig. 1](#)). It harbors a wide variety of habitats and climates, ranging from high volcanic islands with fringing and barrier reefs in the Society Islands to low-lying coral atolls in the Tuamotus, and from equatorial conditions in the Marquesas to sub-tropical environments in the Austral Islands ([Andréfouët & Adjeroud, 2019](#)).

A remarkable floristic effort has been conducted to record the marine macroalgae in FP, and more than 40 relevant studies have been published since the 19th-century pioneering work made by [Bory De Saint-Vincent](#)

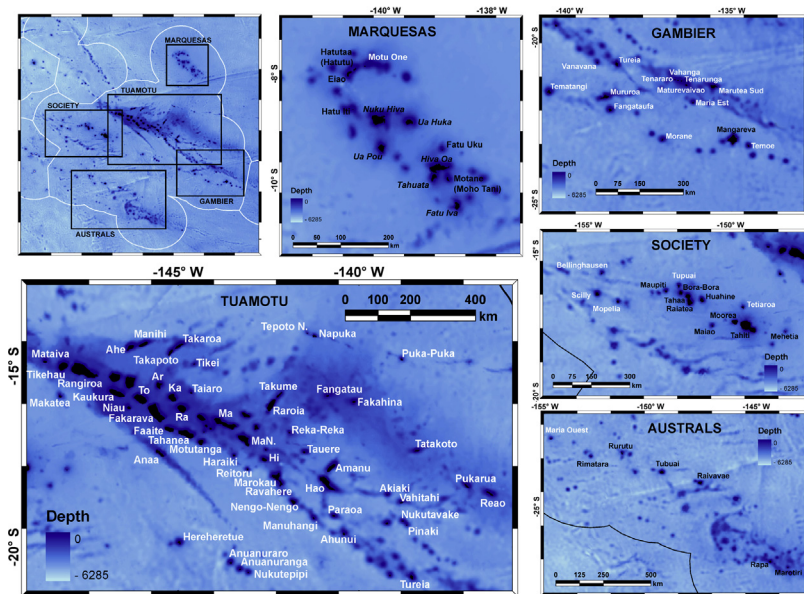


Fig. 1 Map showing the five archipelagos of French Polynesia.

(1828) (Table S1). The most comprehensive contributions were by Setchell (1926), Payri (1982), Payri and Meinesz (1985), Payri and Denizot (1993), Payri and N'Yeurt (1997), and N'Yeurt and Payri (2006; 2007; 2010). Based on previously published records, Payri and N'Yeurt (1997) provided a checklist of 425 taxa including 42 Phaeophyceae, 96 Chlorophyceae, 170 Rhodophyceae, and 117 Cyanophyceae. Using more in-depth analyses and extensive new field collections, N'Yeurt and Payri (2006; 2007; 2009; 2010) then revised the total number of marine macroalgal species known from FP to 312, including 32 Phaeophyceae, 82 Chlorophyceae, and 198 Rhodophyceae (Table S1).

The largest macroalgal diversity is recorded for the Society and the Austral Archipelagos, with the latter harboring 20% of endemic species (N'Yeurt & Payri, 2006). The remoteness of these islands is likely to explain this high level of endemism (Gillespie, Foody, Rocchini, Giorgi, & Saatchi, 2008; Kier et al., 2009). In their study, N'Yeurt and Payri (2006) also stressed the role of water temperature and the availability of specific habitats in shaping species distribution across the French Polynesian archipelago. For instance, in the Marquesas Islands, the absence of barrier reefs and lagoons, and the exposure to oceanic swell have been put forward to explain the dominance of crustose coralline algae and the low Phaeophyceae specific richness (Payri, N'Yeurt, Fiat, & Andréfouët, 2016). Because the Society, Austral, and Gambier archipelagos harbor more substantial habitat diversity

(e.g., lagoons, fringing, and barrier reefs) compared to the Tuamotus, only consisting of atolls, it is expected that they harbor higher biodiversity (Sanciango, Carpenter, Etnoyer, & Moretzsohn, 2013). They also happen to have received most of the sampling effort (Table S1). Since 2003, a series of scientific expeditions and research programs using both morphological and molecular approaches (the *Biocode* project in Moorea, the *Pakaihi i te Moana* expedition in the Marquesas, the *Global Reef Expedition of the Khaled bin Sultan Living Ocean Foundation* in the Gambier Islands, and the *AlgalReef* project in the Tuamotus) have been carried out to increase sampling efforts and better understand the distribution of macroalgal diversity in FP. The first published studies to use a molecular-based approach for the taxonomic revision of FP macroalgae focused on the Sargassaceae family (Fucales, Phaeophyceae; Rohfritsch, Payri, Stiger, & Bonhomme, 2007, 2010; Mattio, Payri, & Stiger-Pouvreau, 2008). Other molecular investigations of FP species appeared sporadically as a component of regional or global studies, for example for the red encrusting algal Order Corallinales (Rhodophyceae; Bittner et al., 2010; Caragnano et al. 2018), the red algal genus *Asparagopsis* (Bonnemaisoniales, Rhodophyceae; Dijoux, Viard, & Payri, 2014), the green algal genus *Halimeda* (Verbruggen, De Clerck, N'Yeurt, Spalding, et al., 2006) or the brown algal genera *Dictyota* (Dictyotales, Phaeophyceae; De Clerk et al., 2006) and *Lobophora* (Dictyotales, Phaeophyceae; Vieira, Camacho et al., 2016).

In general, Phaeophyceae is the group that has received the most attention in FP. Indeed, despite being the least diverse lineage compared to Chlorophyceae and Rhodophyceae, Phaeophyceae species often represent the most abundant biomass, are particularly significant ecologically (e.g., *Sargassum* beds provide food, habitat and nursery grounds for a wide array of marine organisms; Chaves, Pereira, & Feitosa, 2013), and have also been put forward for their economic potential (Zubia, Payri, Deslandes, & Guezennec, 2003; Zubia, Payri, & Deslandes, 2008; Zubia, Andréfouët, & Payri, 2014). Currently, taking into account the latest molecular work on *Lobophora* (Vieira, Camacho et al., 2016; 2017), the diversity of Phaeophyceae in FP accounts for 44 species (26 Dictyotales, 8 Ectocarpales, 4 Fucales, 1 Ralpsiales, 1 Scytothamiales, 2 Sphacelariales, 2 Tilopteridales) (Table 1). The highest Phaeophyceae diversity is reported for the Society Archipelago with 22 species. *Turbinaria ornata* and *Sargassum pacificum* (Fucales) are the most prevalent species, particularly in the case of abnormal proliferation, during which they represent the main species involved (Stiger & Payri, 1999a, 1999b; Payri & Stiger, 2001). Their molecular diversity was assessed in detail (Mattio et al., 2008; Rohfritsch et al., 2007, 2010). In contrast, the more species-rich order Dictyotales has received little or no attention

Table 1 Phaeophyceae species of French Polynesia and their distribution across the five archipelagos (Mattio et al., 2008; N'Yeurt & Payri, 2006; 2010; Vieira, Camacho et al., 2016; 2017).

	Austral	Gambier	Marquesas	Society	Tuamotu
Dictyotales Bory					
<i>Dictyopteris repens</i> (Okamura) Børgesen				+	
<i>Dictyota acutiloba</i> * J.Agardh	+				
<i>Dictyota bartayresiana</i> J.V. Lamouroux	+			+	
<i>Dictyota ceylanica</i> Kützting		+		+	
<i>Dictyota friabilis</i> Setchell		+		+	+
<i>Dictyota hamifera</i> Setchell			+	+	
<i>Lobophora obscura</i> (Dickie) C.W.Vieira, De Clerck & Payri				+	
<i>Lobophora pacifica</i> (Setch.) C.W.Vieira, De Clerck & Payri				+	
<i>Lobophora</i> sp.6		+			
<i>Lobophora</i> sp.11	+	+			
<i>Lobophora</i> sp.13		+			
<i>Lobophora</i> sp.17					+
<i>Lobophora</i> sp.19		+		+	
<i>Lobophora</i> sp.31			+		
<i>Lobophora</i> sp.32			+		
<i>Lobophora</i> sp. 57			+		
<i>Lobophora</i> sp.70			+		
<i>Lobophora</i> sp.73			+		
<i>Lobophora</i> sp.74			+		
<i>Lobophora variegata</i> (J.V.Lamouroux) Womersley ex E.C.Oliveira	+	+		+	+
<i>Padina boryana</i> Thivy		+		+	
<i>Padina melemele</i> * I.A.Abbott & Magruder	+				
<i>Padina pavonica</i> (Linnaeus) Thivy				+	
<i>Padina stipitata</i> Tanaka & Nozawa	+				

(Continued)

Table 1 Phaeophyceae species of French Polynesia and their distribution across the five archipelagos (Mattio et al., 2008; N'Yeurt & Payri, 2006; 2010; Vieira, Camacho et al., 2016; 2017).—cont'd

	Austral	Gambier	Marquesas	Society	Tuamotu
<i>Spatoglossum asperum</i> J.Agardh		+		+	
<i>Styopodium</i> <i>australasicum</i> * (Zanardini) Allender & Kraft	+				
<i>Ectocarpales</i> Bessey					
<i>Chnoospora implexa</i> J.Agardh	+	+		+	
<i>Chnoospora minima</i> (Hering) Papenfuss	+		+	+	
<i>Cladosiphon novae-caledoniae</i> * Kylin	+				
<i>Colpomenia sinuosa</i> (Mertens ex Roth) Derbès & Solier	+	+		+	+
<i>Hincksia mitchelliae</i> (Harvey) P.C.Silva	+				+
<i>Hydroclathrus clathratus</i> (C.Agardh) M.Howe	+	+		+	
<i>Hydroclathrus tumulis</i> * Kraft & Abbott	+				
<i>Rosenvingea intricata</i> (J.Agardh) Børgesen	+			+	+
<i>Fucales</i> Bory					
<i>Sargassum echinocarpum</i> J.Agardh	+	+			
<i>Sargassum obtusifolium</i> J.Agardh	+				
<i>Sargassum pacificum</i> Bory		+		+	
<i>Turbinaria ornata</i> (Turner) J.Agardh	+			+	
<i>Ralfsiales</i> Nakamura ex P.-E.Lim & H.Kawai					
<i>Ralfsia expansa</i> (J.Agardh) J.Agardh				+	

Table 1 Phaeophyceae species of French Polynesia and their distribution across the five archipelagos (Mattio et al., 2008; N'Yeurt & Payri, 2006; 2010; Vieira, Camacho et al., 2016; 2017).—cont'd

	Austral	Gambier	Marquesas	Society	Tuamotu
Scytothamnales A.F.Peters & M.N.Clayton					
<i>Asteronema breviarticulatum</i> (J.Agardh) Ouriques & Bouzon		+		+	
Sphacelariales Migula					
<i>Sphacelaria rigidula</i> Kützing	+			+	
<i>Sphacelaria tribuloides</i> Meneghini				+	
Tilopteridales Bessey					
<i>Cutleria irregularis</i> I.A.Abbott & Huisman	+				
<i>Cutleria mollis</i> * Allender & Kraft		+			
Number of species per archipelago	21	15	8	22	6

(*) record is for Rapa Island only.

although a significant increase in their abundance has been observed on the reefs surrounding the island of Tahiti over the past decade (Zubia, pers. obs.). The present study reports the first detailed assessment of the family Dictyotaceae in FP and, as a background, provides a review of the current state of knowledge on the species diversity, ecology, and potential uses of Dictyotaceae species present in FP.



2. Diversity and distribution of the family Dictyotaceae in French Polynesia

The order Dictyotales is composed of only one family, the Dictyotaceae, which is subdivided into 19 genera (Bittner et al., 2008; Guiry & Guiry, 2019). Most Dictyotaceae belong to three genera, namely *Dictyota*, *Lobophora*, and *Padina*, mainly present in tropical regions (Silberfeld,

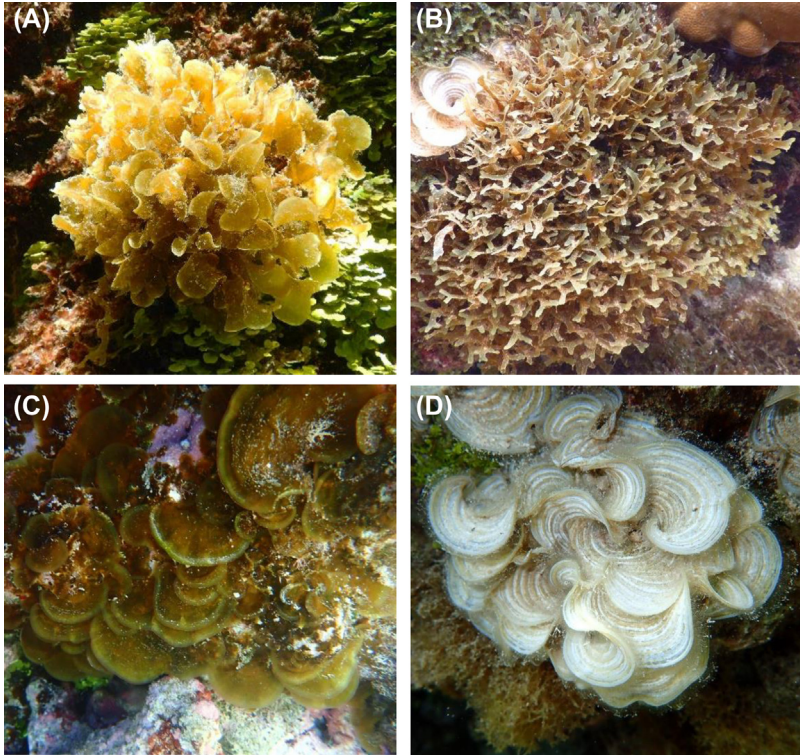


Fig. 2 Illustrations of the most abundant Dictyotaceae species in Tahiti Island: (A) *Spatoglossum asperum*; (B) *Dictyota bartayresiana*; (C) *Lobophora pacifica*; (D) *Padina borvana*. @: Zubia M., UPF.

Rousseau, & De Reviere, 2014; Vieira et al., 2017). Based on the available literature, we listed a total of 26 Dictyotaceae species recorded from FP that belong to six genera: *Dictyopteris* (1 species), *Dictyota* (5), *Lobophora* (14), *Padina* (4), *Spatoglossum* (1) and *Styopodium* (1) (Table 1; Fig. 2). The molecular work carried out on the genus *Lobophora* by Vieira, Camacho et al. (2016; 2017), at the Indo-Pacific scale, extends the known diversity to more than 14 taxa in FP, including two new species, *L. pacifica* and *L. obscura*, and 12 undescribed species (Table 1). Molecular analyses also identified three *Dictyota* species in FP: *D. ceylanica*, *D. hamifera*, and *D. friabilis* (Tronholm, Steen et al., 2010; Tronholm, Sansón, Afonso-Carillo, Verbruggen, De Clerck, 2010). Except for *Lobophora* and *Dictyota*, none of the other Dictyotaceae genera have been re-assessed using molecular data, and the French Polynesian Dictyotaceae diversity is probably largely underestimated.

Compared to other archipelagos, the Society Islands have been the subject of more detailed studies, and 11 Dictyotaceae species have been recorded (Table 1). Between November 2017 and September 2018, we collected a total of 49 specimens of Dictyotaceae at three sites in Tahiti (Arue, Faa'a, and Punaauia). The methods are detailed in the [Supplementary Material S2](#). The resulting species list is presented in Table 2 and includes, in particular, the new species *L. pacifica* described by [Vieira, Camacho et al. \(2016\)](#). This species was previously recorded as *L. variegata*, which, as a result of the revision, is now geographically restricted to the Caribbean region. Our observations confirmed the presence of most of the species listed by [N'Yeurt and Payri \(2006\)](#), except *Dictyopteris repens*. The molecular analyses carried out on our samples also revealed the presence of species previously unrecorded from Tahiti, as well as previous misidentifications. This is the case of two *Padina* species that were previously overlooked in FP: *P. boergesii* (previously misidentified in FP as *P. pavonica*, a widely distributed Atlantic and Mediterranean species; [Gómez Garreta, Rull, & Ribera Siguán, 2007](#)) and *P. minor* (previously subsumed in FP under *P. boryana*) (Table 2).



3. Ecological dynamics of Dictyotaceae in Tahiti

To better understand the ecological dynamics of the Dictyotaceae species around Tahiti Island, we conducted several surveys during a period of one year (March 2018 to March 2019) at two sites, on the north coast (Arue 17.51°S-149.54°W) and on the west coast (Punaauia 17.66°S-149.60°W). Methods are detailed in the [supplementary material S2](#). This section updates the previous knowledge on the ecology of these species using data obtained during this monitoring (percent cover, water temperature, swell, and nutrients). A bibliographical synthesis of the biotic factors that influence these populations is also presented. Finally, we discuss the risk of Dictyotaceae proliferation in FP.

3.1 Abundance, seasonality, and habitat of Dictyotaceae in Tahiti

All species, genera, and sites included, the percent cover of Dictyotales varied from $3.39 \pm 9.68\%$ in October to $14.55 \pm 5.16\%$ in March 2018 (Table S2). The maximum abundances were observed on reefs of Punaauia. We provide the results for each genus in Table 3 and discuss them below.

Lobophora. *Lobophora* species were found in a wide diversity of habitats. Because of limited morphological differences between *Lobophora* species,

Table 2 Dictyotaceae species collected at different sites around Tahiti Island during previous studies.

Species	Afaahiti	Arue	Faa'a	Paea	Papeari	Punaauia	Tata'a	Markers used
<i>Dictyopteris repens</i> (Okamura)Børgesen	+					+		–
<i>Dictyota bartayresiana</i> J.V.Lamouroux		*	*		+	+/*		cox3/psbA
<i>Dictyota ceylanica</i> Kützting		*	◇			+/*		cox3/psbA/cox1/26S
<i>Dictyota friabilis</i> Setchell		+/*/◇				+/*	+	psbA
<i>Dictyota hamifera</i> Setchell	+/◇	+/*	◇	+		+/*		psbA/cox1/cox3/nad1
<i>Lobophora pacifica</i> (Setch.) C.W.Vieira, De Clerck & Payri	+		◇			+/◇		cox3/rbcL
<i>Padina boryana</i> Thivy	+		*		+	+/*	+	cox3
<i>Padina boergesenii</i> Allender & Kraft						*		cox3
<i>Padina minor</i> Yamada			*			*		cox3/psbA
<i>Spatoglossum asperum</i> J.Agardh	+	+/*				+/*		psbA

(+): N'Yeurt & Payri, 2006; (◇): Vieira, Camacho et al., 2016, 2017; Tronholm, Sansón, Afonso-Carillo, Verbruggen, De Clerck, 2010; Tronholm, Steen et al., 2010; and (*) new collections between November 2017 and September 2018; the DNA markers used in each study are indicated.

Table 3 Percent cover (mean \pm sd) of Dictyotaceae species measured during our survey in 2018 at Arue and Punaauia (Tahiti Island).

	Arue			Punaauia		
	March	July	October	March	July	October
Dictyotaceae	4.48 \pm 4.18	5.22 \pm 10.82	3.39 \pm 9.68	14.55 \pm 5.16	7.42 \pm 8.80	6.43 \pm 6.53
<i>Dictyota bartayresiana</i>	3.84 \pm 2.69	2.53 \pm 2.22	1.72 \pm 1.45	6.63 \pm 4.82	2.59 \pm 2.43	1.68 \pm 1.46
<i>Dictyota hamifera</i>	1.53 \pm 1.43	1.40 \pm 1.89	2.04 \pm 1.48	—	—	1.26 \pm 1.53
<i>Dictyota friabilis</i>	0.62 \pm 0.52	0.27 \pm 0.10	—	0.57 \pm 0.50	0.50 \pm 0.38	0.34*
<i>Dictyota ceylanica</i>	0.83 \pm 0.54	—	—	—	—	0.60*
<i>Lobophora</i> spp.	2.13 \pm 1.91	4.20 \pm 6.68	3.18 \pm 3.99	0.29 \pm 0.22	1.71 \pm 1.44	1.57 \pm 1.45
<i>Padina</i> spp.	2.03 \pm 3.36	0.63 \pm 0.41	1.16 \pm 1.54	11.80 \pm 13.36	5.15 \pm 4.57	5.37 \pm 7.76
<i>Spatoglossum asperum</i>	—	—	—	3.24 \pm 2.44	4.96 \pm 5.01	2.63 \pm 2.15

(—) Species absent; (*) Species found only once.

identification in the field is difficult. This was a limiting factor for our monitoring, and we only recorded them as *Lobophora* spp. At all sites surveyed, *Lobophora* spp. cover was low and ranged from $0.29 \pm 0.22\%$ (March) to $4.20 \pm 6.68\%$ (July) (Table 3). The highest abundances were observed during the austral winter (July) at both sites. While these results tend to suggest that *Lobophora* species are not abundant on Tahitian reefs, they do not account for the cryptic biomass growing under the canopy of other seaweeds (e.g., *Sargassum*, *Turbinaria*), or on the underside of rocks and crevices.

Dictyota. *Dictyota* species can grow on various substrates and can epiphytize numerous organisms (Beach et al., 2003; Herren, Walters, & Beach, 2006). During our survey, *Dictyota bartayresiana* was found growing in dense patches or balls of up to 15 cm in diameter, on coral rubbles, dead corals, and pavement. Sometimes this species was epiphytic on corals, sponges, and other benthic organisms. The most abundant *Dictyota* species was *D. bartayresiana*; although its percent cover was under 10% (Table 3). Monthly surveys found a similar seasonality at both Arue and Punaauia, with the highest abundance occurring in March ($3.84 \pm 2.69\%$ and $6.63 \pm 4.82\%$, respectively) and the lowest abundance in October ($1.72 \pm 1.45\%$ and

1.68 ± 1.46%, respectively) (Table 3). *Dictyota hamifera* was growing mainly as an epiphyte on *Sargassum pacificum* or *Turbinaria ornata*. This species is easy to recognize and distinguish from other species in the genus thanks to its branchlets bearing hooks. At Punaauia, *D. hamifera* was rare and only found in October 2018 (Table 3). At Arue, this species was found throughout the year within *Sargassum* beds on the algal crest, with the highest abundant observed on October 2018 (2.04 ± 1.48%) (Table 3). The species *D. friabilis* and *D. ceylanica* were found in low abundances (<1% cover) in all habitats and at both sites (Table 3).

***Padina*.** The most common *Padina* species found in Tahiti was *P. bor-yana*. *Padina* species were found throughout the year at Arue and Punaauia mostly on coral rubbles in sandy habitats or located at the base of dead corals. The abundance of *Padina* was much larger at Punaauia (5–12%) in comparison to Arue (1–2%) (Table 3), probably because more sandy sites were surveyed at Punaauia. The abundance of *Padina* was the lowest during the austral winter (July; 0.63 ± 0.41% at Arue, and 5.15 ± 4.57% at Punaauia) and reached its maximum during the austral summer (March; 2.03 ± 3.36% at Arue and 11.80 ± 13.36% at Punaauia) (Table 3).

***Spatoglossum*.** *Spatoglossum asperum* was commonly found at the base of massive coral colonies (such as *Porites*) in the lagoon (0.5–2 m deep) or forming large beds at depths of 15–20 m on the outer slope of Taharaa and Punaauia. This species was also found in large patches at 100 m deep outside of Papeete harbor (Payri, com.pers.). In lagoons, older plants can reach large sizes (50 cm) and are heavily epiphytized by crustose coralline algae and turf. During our survey, *S. asperum* was only found on the reef of Punaauia, where its abundance increased from the beginning of the year to reach a maximum in July (4.96 ± 5.01%), and then declined to reach a minimum abundance in October (2.63 ± 2.15%) (Table 3).

3.2 Main factors controlling the abundance of Dictyotaceae species

The combination of bottom-up (e.g., nutrient supply, light availability) and top-down control (e.g., herbivory) usually maintains macroalgal abundance and prevents macroalgal proliferation (Lapointe, Littler, & Littler, 1997; Littler, Littler, & Brooks, 2006; Smith, Hunter, & Smith, 2010). The loss of this ecosystem balance can lead to a proliferation of macroalgae, and in the long-term to ecological phase-shifts (Fong, Frazier, Tompkins-Cook, Muthukrishnan, & Fong, 2016; Hughes, 1994; Hughes, Graham, Jackson,

Mumby, & Steneck, 2010; Rasher, Hoey, & Hay, 2013). Dictyotales species including members of the genera *Lobophora*, *Dictyota*, and *Styopodium* have been reported to proliferate in several regions of the world (Barott et al., 2011; Bonaldo & Hay, 2014; Hughes et al., 2010; Longo & Hay, 2015; 2017; Rasher et al., 2013). Following reef degradation, damaged corals are initially overgrown by small ephemeral algae, which are quickly replaced by longer-lived taxa, notably *Sargassum*, *Lobophora*, *Dictyota* and *Padina*, some of which could represent a threat to coral reefs (Brown et al., 2018; Fong & Paul, 2011, pp. 241–272; Ho & Carpenter, 2017; Mumby, Steneck, Adjeroud, & Arnold, 2016; Paul et al., 2011). In the following paragraphs, we discuss some of the main ecological processes known to control the abundance and distribution of Dictyotaceae species globally.

3.2.1 Abiotic factors

3.2.1.1 Nutrients

Macroalgae need macronutrients (e.g., carbon, nitrogen, and phosphorus), micronutrients (e.g., iron, zinc, etc.), and vitamins (e.g., vitamin B12) to grow (Lobban & Harrison, 1994, p. 366). An excess of nutrients can favor the overgrowth of certain species of macroalgae (Zubia, Depetris, Flores, Turquet, & Cuet, 2018). As a bottom-up factor, nutrification can lead to coral reef degradation (Fabricius, 2005; Lapointe, 1997). Several sources of nutrients have been described including groundwater flow, terrestrial runoff (Camoin, Gautret, Montagioni, & Cabioch, 1999), upwelling (Camoin et al., 2006), and dissolved organic matter (DOM) derived from reef organisms (Heindel et al., 2012). In Tahiti, during our surveys, nitrogen concentration reached a maximum during the hot and rainy season (November to March; $>1 \mu\text{mol.L}^{-1}$) and a minimum during the cold and dry season (April to October; $<1 \mu\text{mol.L}^{-1}$, Fig. S2). In Tahiti, annual precipitations can reach up to 10,000 mm/year (Pheulpin, Recking, Sichoix, & Barriot, 2016). Therefore, the riverine input is particularly significant during the rainy season (November to March), during which large amounts of sediments are released into the lagoon, increasing nutrient concentrations (Pheulpin, Sichoix, Barriot, & Recking, 2014). In our study, the abundance of *D. bartayresiana* appeared to follow nitrogen concentrations, with the highest percent cover occurring during the rainy/hot season (Table 3; Fig. S2). In Moorea, Clausing and Fong (2016) also reported a higher growth rate in *D. bartayresiana* after a rainy period followed by high light intensity. These observations tend to support the hypothesis that nutrient

inputs enhance the growth of *D. bartayresiana*. Besides, experiments in the Caribbean reefs have demonstrated that the growth and proliferation of *Dictyota* spp. were influenced mainly by nutrient enrichment and herbivore exclusion (Sotka & Hay, 2009).

3.2.1.2 Water temperature

Water temperature has a direct effect on metabolic and photosynthetic rates, which control growth, reproduction, and decay of seaweeds (Lüning & Tom Dieck, 1989). It is considered a key driver of seasonal fluctuations of algal biomass (Fulton et al., 2014). During our survey, the minimum sea surface temperature (SST) was recorded at Arue in September 2018 (26.4 °C) and the highest in May 2019 (31.9 °C) (Fig. S3). The cover of *Dictyota bartayresiana* and *Spatoglossum asperum* seemed to follow SST fluctuations in different ways over the survey period (Table 3). During the warm season (November to April), *S. asperum* was less abundant, and thalli started to deteriorate, while this was the period when *D. bartayresiana* was the most abundant. These observations illustrate the different thermal preferences of *S. asperum* and *D. bartayresiana*, and, therefore, their distinct seasonality.

3.2.1.3 Swell

Swell is a determinant factor which regulates algal abundance in coral reefs by ripping macroalgae off the reef and exporting them to other coral reefs (Herren et al., 2006). For example, strong swells can rip off macroalgae and contribute to the formation of drifting rafts (Goldberg & Kendrick, 2004; Zubia et al., 2014). The eastern and northern coasts of Tahiti are exposed to swell mostly during the hot season (October to April), while south swell is almost constant throughout the year (Laurent, Maamaatuaiahutapu, Maiiau, & Varney, 2004). Swells generated by hurricanes and lows, between December and April, may also come from the west (Andréfouët & Adjéroud, 2019). Data collected during our surveys follow these general patterns (Fig. S3). The swell energy at Punaauia was high during the cold season (May to October), especially in June, September, and October ($>30 \text{ kW}\cdot\text{m}^{-1}$), which also coincided with lower abundances of *D. bartayresiana* ($1.68 \pm 1.46\%$) (Table 3; Fig. S3). *Spatoglossum asperum* was more abundant in July ($4.96 \pm 5.01\%$) when the swell energy was the highest at Punaauia (Table 3; Fig. S3). *Spatoglossum asperum* appeared less influenced by the swell, probably because it occurs far from the reef crest and is protected by massive coral colonies at the base of which it grows.

3.2.2 Biotic factors

3.2.2.1 Herbivory

Herbivory is one of the critical factors that control macroalgal abundance. The lack of grazing due to overfishing, for example, can favor the proliferation of macroalgal species, sometimes leading to phase-shifts where macroalgae-dominated reefs replace coral-dominated reefs (Done, 1992). Macroalgae are also known to naturally produce allelopathic compounds that deter herbivores (Hay, 1997; Rasher & Hay, 2014; Sotka, Bell, Lowry, & Poore, 2017). Some herbivores have adapted to tolerate these defenses, but intense grazing pressure can favor macroalgae with a wide range of chemical defenses (Sotka, Bell, Lowry, & Poore, 2017).

Herbivore assemblages in Moorea, an island of the Society Archipelago near Tahiti, are mainly composed of species that belong to the families Acanthuridae, Scaridae, and Pomacanthidae with six fish species responsible for over 80% of the total macroalgae biomass consumption: *Ctenochaetus striatus*, *Scarus psittacus*, *Chlorurus spilurus*, *Acanthurus nigrofuscus*, *Zebrasoma scopas*, and *Naso lituratus* (Holbrook, Schmitt, Adam, & Brooks, 2016). According to Holbrook et al. (2016), sea urchins and other invertebrates contribute little to macroalgal herbivory in Moorea, although Zizka (2012) showed that *Dictyota bartayresiana* is the most consumed species by the sea urchins *Echinometra*. Fong (2015) and Fong et al. (2016) reported that grazing is an effective biomass regulator for *Dictyota bartayresiana* in Moorea, especially by large grazers when there is little influence of nutrients. *Dictyota bartayresiana* was also rapidly consumed by herbivorous fish species in Fiji (up to 86–100% after 48 h; Rasher et al., 2013). The efficiency of *Dictyota* chemical defenses varies depending on herbivorous species (Sotka, Bell, Lowry, & Poore, 2017). For example, *Dictyota pfaflii* showed significant activity against generalist herbivorous fishes and the sea urchin *Lytechinus variegatus*, while no effect was observed against the crab *Pachygrapsus transversus* (Barbosa et al., 2004). Pereira, Cavalcanti, & Texeira, 2000; Sotka, Bell, Lowry, & Poore (2017) report that herbivores highly appreciate *Dictyota* species despite their high level of secondary metabolites.

Grazing is a critical top-down process to maintain low *Lobophora* cover as illustrated by the shift in assemblages that occurred following herbivore die-offs in the Caribbean (Van Steveninck & Breeman, 1987) and the Canary Islands (Sangil, Sansón, Clemente, Afonso-Carrillo, & Hernández, 2014). In Palau, Mumby et al. (2016) showed that the primary grazers of *Lobophora* were Acanthuridae. Vieira, Stenger, Moleana, De Clerck, and Payri (2019) demonstrated limited variation in grazing sensitivity in *Lobophora* species by

the sea-urchin *Diadema setosum* and the rabbitfish *Siganus lineatus*. These authors concluded that spatial and associational refuges are primary defense strategies against herbivores. For instance, in Tahiti, *Lobophora* spp. are commonly found growing under the canopy of *Sargassum* and *Turbinaria* or encrusting reef crevices.

Padina species are calcifying macroalgae that consistently rank low in herbivorous fish preference (Hay, 1991). They are chemically defended by secondary metabolites (Renaud, Hay, & Schmitt, 1990). For instance, unlike parrotfish species, Siganidae species actively avoid calcified macroalgae such as *Padina* due to the high acidity of their stomachs, (Mantyka & Bellwood, 2007; Schupp & Paul, 1994). Herbivory also plays an essential role in controlling the morphology of some *Padina* species. For instance, *Padina sanctae-crucis* and *P. boergesenii* can shift from a vegetative turf morphology (*Vaughaniella* stage) to a foliose and fan-shaped morphology when grazing pressure is low, allowing them to persist in habitats subject to various grazing pressures (Diaz-Pulido, Villamil, & Almanza, 2007; Lewis, Norris, & Searles, 1987). No data is currently available on the effect of grazing on *Padina* and *Spatoglossum* species in FP.

3.2.2.2 Interactions with corals

While little is known about the coral reef health in Tahiti due to the absence of surveys, in the neighboring island of Moorea, located 25 km from Tahiti, the situation is better informed. Since 1979, severe degradations of the coral reefs of Moorea have been observed, and several human and natural disturbances have been incriminated. These include organic and chemical pollution, terrestrial runoff, dredging, coral exploitation, microbial diseases, coral bleaching, and *Acanthaster planci* infestations (Faure, 1989; Gleason & Wellington, 1993; Kayal et al., 2012; Trapon, Pratchett, & Penin, 2011). These disturbances are not only affecting coral species abundance and assemblages (i.e., the decline in *Acropora* and increasing prevalence of *Pocillopora* and *Porites*; Trapon et al., 2011), but they also impact macroalgal assemblages and cover (e.g., *Turbinaria ornata*; Bittick, Clausing, Fong, Scoma, & Fong, 2019). As corals decline and macroalgae proliferate, their interactions intensify and potentially affect the survival, growth, reproduction, and recruitment of coral larvae (e.g., Diaz-Pulido, Harii, McCook, & Hoegh-Guldberg, 2010; Ritson-Williams, Arnold, Fogarty, Steneck, et al., 2009). Macroalgae then directly or indirectly impact coral health through shading, abrasion, transmitting coral diseases or microbes, and allelochemicals (Hughes et al., 2007; McCook, Jompa, & Diaz-Pulido, 2001; Nugues,

Smith, Van Hooindonk, Seabra, & Bak, 2004; Vieira, Engelen et al., 2016). However, macroalgae–coral interactions are known to be species-specific, which means that different coral species will not be equally sensitive and affected by the same macroalgal species. The genus *Lobophora* is known for its ability to outcompete corals through direct contact and associated microbiome carrying coral pathogens leading to coral bleaching and death (Vieira, Payri, & De Clerck, 2015; Vieira, Camacho et al., 2016; Vieira, Engelen et al., 2016). The situation is similar for the genus *Dictyota* which can induce coral bleaching and death through abrasion and the effect of their associated microbiomes (Barott et al., 2011; Rasher & Hay, 2010, 2011), and inhibit larval settlement (Diaz-Pulido et al., 2010; Paul et al., 2011). For instance, in Moorea, Longo and Hay (2017) showed that *D. bartayresiana* lipid-soluble extract could decrease the photochemical efficiency of *Pocillopora verrucosa* by 20–30%. Similarly, *Padina* species have been shown to impact the settlement and metamorphosis of *Pocillopora damicornis* larvae in the Philippines (Maypa & Raymundo, 2004), and Kaullysing et al. (2016) suggested that *Padina boryana* overgrowth is potentially stressful to the *Acropora muricata* colonies. To the best of our knowledge, there is no study reporting negative or positive interactions between *Spatoglossum* and corals.

3.3 Is there a risk for further macroalgae proliferation in Tahiti?

The coral reefs of FP have experienced repeated macroalgal blooms over the last decades. These events mainly involved two species of Sargassaceae (Fucales): *Sargassum pacificum* and *Turbinaria ornata*, which also happen to be the most prevalent species in terms of biomass in normal conditions (Payri & Stiger, 2001; Stiger & Payri, 1999a, 1999b). These proliferation events have prompted intense efforts in fundamental and applied research on macroalgae in the region. Recently, however, these proliferations have occurred with a higher frequency, and they now seem to involve additional species of the family Dictyotaceae. Indeed, over the past decade, two species of the family Dictyotaceae (*Dictyota bartayresiana* and *Spatoglossum asperum*) have become increasingly abundant in the lagoons of Tahiti (Zubia, pers. obs.). However, the percent cover measured during our survey is low at both sites (<10%) and does not currently support the hypothesis of an ongoing proliferation of these species. In the absence of previous baseline data, it is not possible to tell whether the abundance of these species has indeed significantly increased over the past decade. In the neighboring island of Moorea, Adam et al. (2011) and Holbrook et al. (2016) have demonstrated that

intense grazing could prevent the establishment and proliferation of macroalgae. Although this biotic factor was not assessed during our surveys, we recommend that it is included in further studies and monitoring in Tahiti, where inhabitants and environmental pressures are high in comparison to other islands in FP (Andréfouët & Adjéroud, 2019). With increasing global ocean acidification, this is particularly worrying because naturally acidified reefs tend to host Dictyotaceae species such as *Dictyota* (Del Monaco, Hay, Gartrell, Mumby, et al., 2017), *Lobophora* (Bouraké, New Caledonia; Payri, com. Pers.), and *Spatoglossum* species (Enochs et al., 2015). For instance, Enochs et al. (2015) observed a clear shift from coral to fleshy macroalgae ecosystems at low pH with *Spatoglossum stipitatum* covering more than 50% of the substrate.



4. Potential for the development of biotechnological applications

Through evolution, macroalgae have adapted to external pressures (e.g., desiccation, UV radiations, infections, grazing) and to mitigate these pressures some species are producing a wide array of bioactive metabolites (Bischof et al., 2006; Duffy & Harvilicz, 2001; Steinberg & De Nys, 2002). With more than 1500 metabolites described, the class Phaeophyceae (brown algae) represents a rich source of natural products that belong to several chemical families such as terpenoids, phenols, fatty acids derivatives, and polysaccharides among others. Within the brown algae, the families Dictyotaceae and Sargassaceae, in particular, are recognized for the production of phenolics (mainly phlorotannins) and terpenoids (mainly sesquiterpenes, diterpenes and meroterpenes) (Carroll, Copp, Davis, Keyzers, & Prinsep, 2019; and previous reports in the series) which are widely used in the industry. Here, we review the metabolites known for the species of Dictyotaceae recorded in FP.

4.1 Chemodiversity & biological activities

Dictyotaceae species are well-known for their outstanding richness in terpenoids (De Paula, Vallim, & Teixeira, 2011; Vieira et al., 2017), which represents more than 33% of all the specialized metabolites described from the class Phaeophyceae (Carroll et al., 2019; and previous reports in the series). More specifically, several Dictyotaceae species can biosynthesize a wide array of sesquiterpenes (e.g., *Dictyopteris* and *Taonia* spp.), cyclic diterpenes (e.g., *Dictyota* and *Spatoglossum* spp.) or meroterpenes, also called terpenoids of

mixed biogenesis (e.g., *Dictyopteris* and *Stypopodium* spp.). Over 200 diterpenes have been isolated from 35 species of Dictyotaceae worldwide, mainly from the genus *Dictyota* (Chen et al., 2018; Vallim, De Paula, Pereira, & Teixeira, 2005). Besides their use in taxonomic determination and biogeographic markers, these molecules have been found to exhibit interesting biological activities. Table 4 provides an overview of the compounds and biological activities recorded in the literature for Dictyotaceae species recorded in Tahiti.

Dictyopteris. Aside from two studies on the content of sulfuric acid and inorganic ions of Dictyotaceae species (Sasaki, Kataoka, Kamiya, & Kawai, 1999; Sasaki, Kataoka, Murakami, & Kawai, 2004) and on the antineoplastic activity of algae where its extracts were found to be inactive (Kashiwagi, Mynderse, Moore, & Norton, 1980), no comprehensive work has been published on the chemical characterization of the species *Dictyopteris repens*. This lack of information is unexpected as *Dictyopteris* spp. are known to biosynthesize a broad array of specific compounds such as C₁₁ hydrocarbons, sesquiterpenes, merosesquiterpenes or sulfur containing derivatives (Philippus et al., 2018; Zatelli, Philippus, & Falkenberg, 2018).

Dictyota. Species of the genus *Dictyota* are mostly known for their ability to produce a wide range of cyclic diterpenes (Chen et al., 2018; Hay, 1997; Kelecom & Teixeira, 1986; Teixeira & Kelecom, 1988; Vallim et al., 2005). Cyclic diterpenes found in Dictyotaceae can be divided into three structural groups (Fig. 3). Group I includes compounds obtained through a first C-1/C-10 cyclization from geranylgeranylpyrophosphate (GGPP) including the prenylated guaiane subgroup among others. Group II contains diterpenes formed from GGPP through a first C-1/C-11 cyclization, belonging mainly to the dolabellane subgroup among others. Finally, group III contains compounds derived from a first C-2/C-10 cyclization of the GGPP precursor belonging to the crenulane, xeniane, and dichotomane families subgroups among others (Chen et al., 2018). Among the *Dictyota* species found in FP, *Dictyota bartayresiana* appeared as the most studied with several diterpenes isolated (Table 4, Fig. 4). *Dictyota bartayresiana* was also investigated for its fatty acids (Gosch, Paul, De Nys, & Magnusson, 2015) and lipid hydroperoxydes contents (Kumari, Singh, Bijo, Reddy, & Jha, 2012), and it was found to be rich in cellulose which could be interesting for further economic applications (Siddhanta et al., 2009). Several extracts of these species have been assayed for their antibacterial activity (Antonysamy, Velayutham, Mani, Thangaiah, & Irullappan, 2015; Parmar et al., 2016) and their antiviral properties against *Vaccinia* virus (Kamat et al., 1992). In

Table 4 Overview of the biological activities recorded in the literature for Dictyotaceae species present in French Polynesia with indications of the type of molecules reported and the type of extraction used.

Taxa	Molecules reported	Extraction methods	Biological activities	Location	References
Dictyotaceae	Dictyols (diterpenes)	—	—	Worldwide	Hay, 1997
Dictyotaceae	Diterpenes	—	Herbivory deterrent & use in chemotaxonomy	Worldwide	Kelecom & Teixeira, 1986
<i>Dictyopteris</i>	C11-hydrocarbons, sulfur compounds, terpenes, meroditerpenes, halogenated compounds and sterols	—	Therapeutic and ecological activities	Worldwide	Zatelli et al., 2018
<i>Dictyopteris</i>	No compound could be identified in the extracts	DCM:MeOH (2:1)	—	São Paulo, Brazil	Philippus et al., 2018
<i>Dictyopteris repens</i>	—	—	No Antineoplastic activity	Palau, Western Caroline Islands	Kashiwagi et al., 1980
<i>Dictyopteris repens</i>	Sulfuric acid and inorganic ions content	Crude extract distilled water	—	Ishigaki Island, Okinawa	Sasaki et al., 1999
<i>Dictyopteris repens</i>	Sulfuric acid and inorganic ions content	Crude extract distilled water	—	Ishigaki Island, Okinawa	Sasaki et al., 2004
<i>Dictyota bartayresiana</i>	—	Ethanol extract	Antiviral (<i>Vaccinia virus</i>)	Gujarat, India	Kamat et al., 1992
<i>Dictyota bartayresiana</i>	A known dolastane, five known dolabellanes and five new diterpenes	DCM:MeOH (3:1)	—	Mannar, India	Bheemasankara Rao et al., 1994

<i>Dictyota bartayresiana</i>	—	Acetone, ethanol and water extracts	Ichtyotoxic activity	Mexico	De Lara-Isassi et al., 2000
<i>Dictyota bartayresiana</i>	A known dolastane, five known dolabellane, five new compounds (3 dolabellanes, 2 dolastanes)	—	—	Mannar, India	Sarma, Krishna, & Kawai, 2006
<i>Dictyota bartayresiana</i>	Cellulose rich	Methanol extract	—	India	Siddhanta et al., 2009
<i>Dictyota bartayresiana</i>	—	Methanol extract	Antioxidant activities	India	Palanisamy et al., 2010
<i>Dictyota bartayresiana</i>	Terpenes	Methanol extract	Coral bleaching	Viti Levu, Fiji	Rasher, Stout, Engel, Kubanek, & Hay, 2011
<i>Dictyota bartayresiana</i>	Fatty acids and lipid hydroperoxydes contents	Chloroform:MeOH (1:2)	—	Saurashtra coast, Gujarat, India	Kumari et al., 2012
<i>Dictyota bartayresiana</i>	Synthesize silver nanoparticles (Ag-NPs)	Methanol extract	Antifungal activity	Tamilnadu, India	Kumar & Sudha, 2013
<i>Dictyota bartayresiana</i>	—	Methanol extract	Highest antidiatom and antifouling	Mannar, India	Deepa et al., 2014
<i>Dictyota bartayresiana</i>	—	Methanol extract	No haemogglutinin activity (blood cell agglutination)	Manoli island	Mangaiyarkarasi, Kanna, Girija, & Gnanamurthy, 2014

(Continued)

Table 4 Overview of the biological activities recorded in the literature for Dictyotaceae species present in French Polynesia with indications of the type of molecules reported and the type of extraction used.—cont'd

Taxa	Molecules reported	Extraction methods	Biological activities	Location	References
<i>Dictyota bartayresiana</i>	—	Methanol extract	<i>In vivo</i> lethality test <i>Artemia salina</i> (shrimp)	Tamilnadu, India	Antonyamy, Thangiah et al., 2015
<i>Dictyota bartayresiana</i>	—	Methanol extract	Larvicidal effect on <i>Culex quinquefasciatus</i>	Tamilnadu, India	Antonyamy et al., 2015a
<i>Dictyota bartayresiana</i>	—	Methanol extract	Antibacterial screening	Tamilnadu, India	Antonyamy, Velayutham et al., 2015
<i>Dictyota bartayresiana</i>	—	Aqueous extract	Cytotoxicity and anticancer potential	Tamilnadu, India	Antonyamy, Thangiah et al., 2015
<i>Dictyota bartayresiana</i>	—	Crude extract	Antibacterial (<i>Staphylococcus aureus</i> and <i>Escherichia coli</i>) and antifungal (<i>Candida</i> <i>albicans</i>) activity	Mtwapa, Kenya	Kaaria et al., 2015
<i>Dictyota bartayresiana</i>	—	Ethanol extract	low antibacterial	Gujarat, India	Parmar et al., 2016
<i>Dictyota bartayresiana</i>	Lipid soluble extracts	Methanol extract	Coral bleaching of <i>Porites</i> spp.	Votua Reef, Viti Levu, Fiji	Rasher & Hay, 2010
<i>Dictyota bartayresii</i>	Diterpenoids	Crude extract	Antifungal activity	Belize	Norris & Fenical, 1982

<i>Dictyota bartayresii</i>	Pachydictyol-A	DCM:MeOH (3:1)	Host and herbivory test	Belize and Bahamas	Hay, Duffy & Fenical, 1990
<i>Dictyota bartayresii</i>	β -dimethylsulfonio-propionate content	25% NaOH (w/v) and DMS: acrylic acid (1:1)	—	Meixia, China	Bischoff et al., 1994
<i>Dictyota bartayresii</i>	Fatty acids content	Trans-esterification method	—	North Queensland, Australia	Gosh, Paul, De Nys, & Magnusson, 2015
<i>Dictyota ceylanica</i>	Phenolic concentrations	Methanol extract	—	Thevenard island, Western Australia	Van Hees et al., 2017
<i>Dictyota friabilis</i>	Dolabelladienetriol	CH ₂ Cl ₂ extract	Strong potential against HIV-1 in cervical tissue explants	Atol das Rocas reef, Rio Grande do Norte State, Brazil	Stephen et al., 2017
<i>Dictyota friabilis</i>	Phlorotannins	Methanol extract	Prevent melanosis and extend shelf-life of <i>Litopenaeus vannamei</i> shrimps	Iran	Sharifian, Shabanpour, Taheri, & Kordjazi, 2019
<i>Dictyota pfaffii</i>	10,18-diacetoxy-8-hydroxy-2,6-dolabelladiene, 10-acetoxy-8,18_dihydroxy-2,6-dolabelladiene, 8,10,48-trihydroxy-2,6-dolabelladiene	MeOH:DCM (3:7), MeOH extracts	Antiviral (HIV) and anti-herpes virus activities	Rio Grande, Brazil	Barbosa et al., 2004
<i>Dictyota pfaffii</i>	Dolabellane diterpene: 10,18-diacetoxy-8-hydroxy-2,6-dolabelladiene	CH ₂ Cl ₂ : MeOH 7:3 and MeOH (100%)	Herbivory deterrent against sea-urchins and fish	Atol das Rocas reef, Rio Grande do Norte State, Brazil	Barbosa, Teixeira, Villaça, Pereira, et al., 2003

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Table 4 Overview of the biological activities recorded in the literature for Dictyotaceae species present in French Polynesia with indications of the type of molecules reported and the type of extraction used.—cont'd

Taxa	Molecules reported	Extraction methods	Biological activities	Location	References
<i>Dictyota pfaffii</i>	Dolabellane diterpene	Crude extract	Herbivore deterrent against the sea-urchin <i>Lytechinus variegatus</i> , generalist fishes and not against crab <i>Pachygrapsus transversus</i>	Atol das Rocas reef, Rio Grande do Norte State, Brazil	Barbosa et al., 2004
<i>Dictyota pfaffii</i>	Diterpene	Hexane extract	Strong antifouling activity against the mussel <i>Perna perna</i>	Niterói, Rio de Janeiro, Brazil	Barbosa, Fleury, Da Gama, Teixeira, & Pereira, 2007
<i>Dictyota pfaffii</i>	Three new dolabellane diterpenes: Dolabelladienols A–C	CH ₂ Cl ₂ extract	Antiviral activity (HIV) and low cytotoxic against MT-2 lymphocyte tumor cells	Atol das Rocas reef, Rio Grande do Norte State, Brazil	Pardo-Vargas et al., 2014
<i>Dictyota pfaffii</i>	Dolabelladienetriol	CH ₂ Cl ₂ extract	Potential against HIV-1 on infected female mice	Atol das Rocas reef, Rio Grande do Norte State, Brazil	Garrido et al., 2017
<i>Dictyota pfaffii</i>	Dolabelladienetriol	CH ₂ Cl ₂ extract	Low activity potential against HIV-1 on infected female mice	Atol das Rocas reef, Rio Grande do Norte State, Brazil	Garrido et al., 2011
<i>Dictyota pfaffii</i>	Dolabelladienetriol	—	Inhibition of HIV-1 replication in human primary cells	Brazil	Cirne-Santos et al., 2006
<i>Dictyota pfaffii</i>	Dolabelladienetriol	Dolabelladienetriol	Inhibition of HIV-1 on peripheral blood mononuclear cells	Brazil	Cirne-Santos et al., 2008

<i>Dictyota pfaffii</i>	Dolabelladienetriol	Two diterpenes	Inhibition of HSV-1 infection in Vero cells	Brazil	Abrantes et al., 2010
<i>Dictyota pfaffii</i>	Dolabelladienetriol	Dolabelladienetriol	Inhibit Leishmania in macrophages	Brazil	Soares et al., 2012
<i>Dictyota</i> spp.	Dictyoepoxide, pachydictyol-A, pachydictyol-A epoxide, acetals 2a and 2b, dictyolactone, acetyl dictyolal, dictyoxide, dictyol B acetate	CH ₂ Cl ₂ extract and Trimethylpentane	Inhibition of vasopressin binding to pig kidney	Bahia, Los Angeles	Patil et al., 1993
<i>Dictyota</i> spp.	pachydictyol-A acetals 2a and 2b, dictyolactone	CH ₂ Cl ₂ extract and Trimethylpentane	Vasopressin antagonists	Bahia, Los Angeles	Patil et al., 1993
<i>Dictyota</i> spp.	Diterpene alcohol-A, pachydictyol A and dictyol E	Lipid-soluble extract	Inhibit invertebrate larvae settlement	North Carolina, USA	Schmitt, Hay, & Lindquist, 1995
<i>Dictyota</i> spp.	—	—	Inhibit invertebrate larvae settlement	Hawai'i	Walters, Ruban, & Horton, 1996
<i>Dictyota</i> spp.	Rich in terpenoid	—	Defenses against generalist herbivores	Worldwide	Hay, 1996
<i>Dictyota</i> spp.	Lipid-soluble chemical	—	Defenses that deter feeding by reef herbivores	Worldwide	Hay, 1997
<i>Dictyota</i> spp.	Rich in terpenoid	—	Defenses against generalist herbivores	Worldwide	Fong & Paul, 2011
<i>Dictyota</i> spp.	Dictyols	—	Herbivory deterrent	Worldwide	Paul & Puglisi, 2004

(Continued)

Table 4 Overview of the biological activities recorded in the literature for Dictyotaceae species present in French Polynesia with indications of the type of molecules reported and the type of extraction used.—cont'd

Taxa	Molecules reported	Extraction methods	Biological activities	Location	References
<i>Dictyota</i> spp.	Rich in terpenoid	—	Defenses against generalist herbivores	Tropical Atlantic American region	Vallim et al., 2005
<i>Dictyota</i> spp.	—	—	Increased mortality rates of coral recruits	Long Key, Florida	Kuffner et al., 2006
<i>Dictyota</i> spp.	93 diterpenes and 15 skeletal classes	—	Herbivory deterrent & use in chemotaxonomy	Worldwide	Kelecom & Teixeira, 1986
<i>Dictyota</i> spp.	Over 90 diterpenes and 17 skeletal classes	—	Chemotaxonomy	Worldwide	Teixeira & Kelecom, 1988
<i>Dictyota</i> spp.	233 diterpenes	—	—	Worldwide	Chen et al., 2018
<i>Padina boergesenii</i>	Squalene	N-hexane defatted methanol (99.5%) crude extract	Antioxidant and anti-inflammatory	Gulf of Mannar, India	Rajamani et al., 2018
<i>Padina boergesenii</i>	Triterpene	Methanol extract	Enzyme inhibitory activities	Gulf of Oman	Ali et al., 2017
<i>Padina boryana</i>	Fucose, galactose, mannose, glucose and uronic acid residues	Sulfated and Acetylated fraction	Anticancer activity <i>in vitro</i>	Nhatrang Bay, Vietnam	Usoltseva et al. 2018
<i>Padina boryana</i>	Polysaccharides especially galactofucans	Aqueous EtOH (70%) with added NaHCO ₃	Non-toxic and antitumor activity <i>in vitro</i> against DLD-1 human colon carcinoma cells	Vietnam	Shevchenko et al., 2017
<i>Padina boryana</i>	High productivity of lipids and fatty acid methyl esters	DCM:MeOH (2:1) with added NaCl	Candidate for investigation of biodiesel production	Red Sea at Jeddah Corniche, Saudi Arabia	Abomohra et al., 2018

<i>Padina boryana</i>	Polyphenolic and flavonoid contents	Ethanol, acetone, and hexane extract	Antimicrobial activity against Gram-negative and positive strains and a pathogen fungus	Red Sea in Al-Leith Provence, Saudi Arabia	Sameeh et al., 2016
<i>Padina boryana</i>	Biochemical composition	—	Antioxidant activity and potential food uses	Abu Qir Bay, Egypt	Ismail et al., 2017
<i>Padina boryana</i>	Lipid soluble extract	Methanol extract	Allelopathic effect on coral <i>Porites porites</i>	Votua Reef, Viti Levu, Fiji	Rasher & Hay, 2010
<i>Padina minor</i>	β -dimethylsulfonyl-propionate content	25% NaOH (w/v) and DMS: acrylic acid (1:1)	—	Ximaozhu, China	Bischoff et al., 1994
<i>Padina pavonica</i>	—	Methanol extract	Antibiotic activities against <i>Bacillus subtilis</i> , (<i>B. cereus</i> and <i>Staphylococcus aureus</i> / Reported as inactive for antimicrobial activities in previous Indian and Mediterranean studies	Yucatan, Mexico	Salvador, Gómez Garreta, Lavelli, & Ribera, 2007
<i>Padina pavonica</i>	Chemical composition (total phenolic, flavonoid, tannin, lipid and sterol profiles)	Acetone extract	Anti-proliferative and pro-apoptotic activity on human osteosarcoma cells and antioxidant activity	Moorea, French Polynesia	Bernardini et al., 2018

(Continued)

Table 4 Overview of the biological activities recorded in the literature for Dictyotaceae species present in French Polynesia with indications of the type of molecules reported and the type of extraction used.—cont'd

Taxa	Molecules reported	Extraction methods	Biological activities	Location	References
<i>Padina</i> sp.	Contained additional non-polyphenolic non-polar secondary metabolites	Aqueous methanol extract	Herbivory deterrent	Australia	Steinberg & Paul, 1990
<i>Spatoglossum asperum</i>	—	Ethanol extract	Cytotoxic activity on <i>Artemia salina</i> (Brine shrimp)	Karachi, Pakistan	Ara et al., 1999
<i>Spatoglossum asperum</i>	—	Ethanol extract	Hypolipidaemic activity, effect on cardiac and liver enzymes	Karachi, Pakistan	Ara et al., 2002
<i>Spatoglossum asperum</i>	Polyunsaturated fatty acids	Chloroform:MeOH (1:2)	Nutritional significance	Gujarat, India	Kumari, Kumar, Gupta, Reddy, & Jha, 2010
<i>Spatoglossum asperum</i>	Polyphenols	Methanol extract	Antioxidant activity (relatively high DPPH activity)	Maharashtra, India	Vinayak et al., 2011
<i>Spatoglossum asperum</i>	Polyphenols	Methanol extract	Cytotoxic activity (highly toxic and caused the death of the brine shrimp)	Maharashtra, India	Vinayak et al., 2011
<i>Spatoglossum asperum</i>	Fatty acids and lipid hydroperoxydes contents	Chloroform:MeOH (1:2)	—	Saurashtra coast, Gujarat, India	Kumari et al., 2012

<i>Spatoglossum asperum</i>	—	Ethanol extract	Hypolipidemic activities/decreases in the serum total cholesterol	—	Gade et al., 2013
<i>Spatoglossum asperum</i>	—	Methanol extract	No antidiatom/antifouling activity	Mannar, India	Deepa et al., 2014
<i>Spatoglossum asperum</i>	—	Chloroform:MeOH (1:1)	Maximum activity against <i>V.cholera</i> and <i>K.pneumonia</i>	Tamilnadu, India	Sivakumar & Vignesh, 2014
<i>Spatoglossum asperum</i>	—	Methanol extract	Free radical scavenging activity	Tamilnadu, India	Pandithurai & Murugesan, 2014
<i>Spatoglossum asperum</i>	Polyphenols	Sequential extraction: hexane, dichloromethane, ethyl acetate, and methanol	antitumor activity against pancreatic cancer	India	Aravindan et al., 2015
<i>Spatoglossum asperum</i>	—	Crude extract	Antibacterial (<i>Staphylococcus aureus</i> and <i>Escherichia coli</i>) and antifungal (<i>Candida albicans</i>) activity	Mkomani, Kenya	Kaaria et al., 2015
<i>Spatoglossum asperum</i>	Synthesis of silver nanoparticules (Ag-NPs), terpenoids and phenols	Chloroform:MeOH (1:1)	Antimicrobial activity against plant diseases	Mannar, India	Jothirethinam, Prathilba, Shanti, & Arunkumar, 2015
<i>Spatoglossum asperum</i>	—	Methanol extract	Antimicrobial activity, antibacterial activity against <i>S. aureus</i>	Mandapam coast, India	Pandithurai et al., 2015

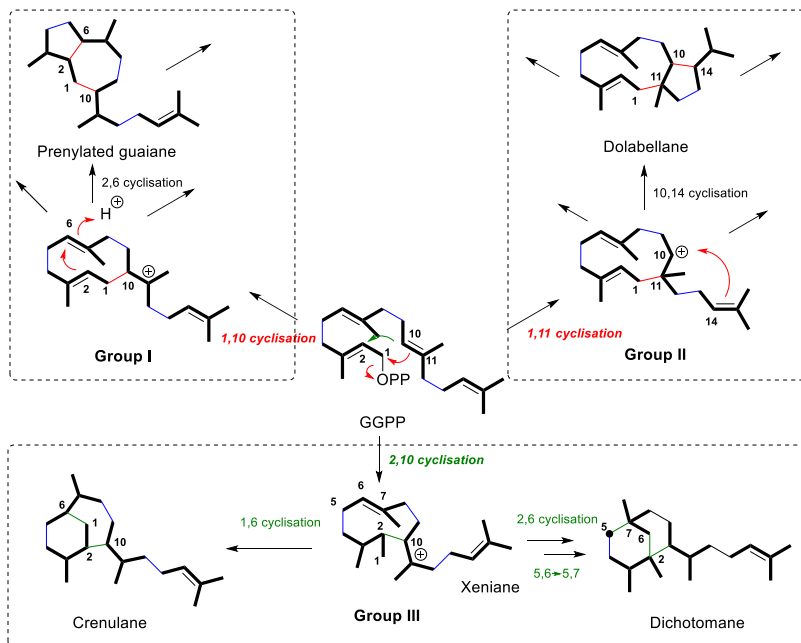


Fig. 3 Biosynthetic pathways of the three main groups of diterpenes isolated from various Dictyotaceae species.

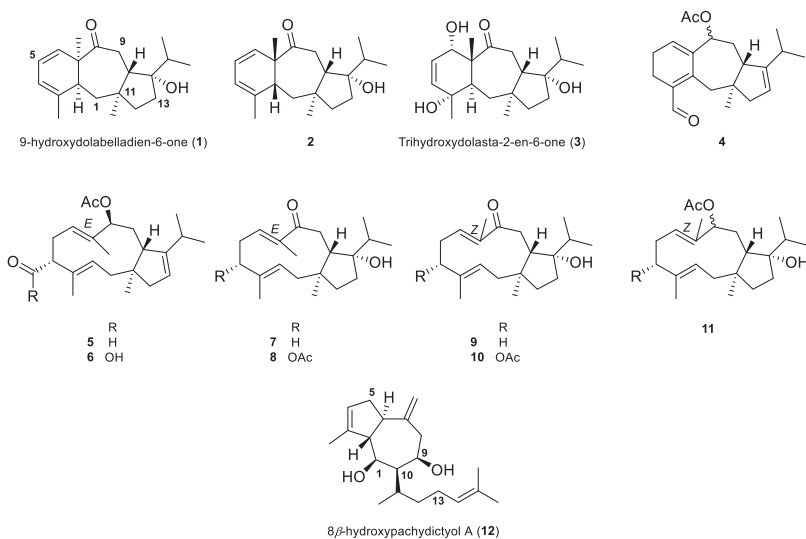


Fig. 4 Structures of diterpenoids isolated from *Dictyota bartayresiana*.

addition, *D. bartayresiana* extracts have shown a lethal activity against *Artemia salina* and *Culex quinquefasciatus* larvae (Antonymsamy, Velayutham et al., 2015; Antonymsamy, Thangiah, & Irulappan, 2015), an ichthyotoxic effect against the fish *Carassius auratus* (De Lara-Isassi, Álvarez-Hernández, & Collado-Vides, 2000), and antifouling properties against the diatom *Navicula subinflata* (Deepa, Srikumar, & Padmakumar, 2014). It was also suggested that *D. bartayresiana* could be used as a natural healing drug and for general good health as some of its extracts were active against cancer cell lines (Antonymsamy, Thangiah et al., 2015) and showed antioxidant activity (Palanisamy, Sellappa, & Stella, 2010).

In the specific case of *Dictyota ceylanica*, only the phenolic contents (Van Hees, Olsen, Wernberg, Van Alstyne, & Kendrick, 2017) and overall biochemical composition (total carbohydrates, total proteins, pigments, vitamins) (Chakraborty & Santra, 2008) have been described. For *Dictyota friabilis* (previously known as *Dictyota pfaffii*), analyses of Brazilian specimens allowed the isolation of several dolabellane diterpenes displaying a broad range of biological activities (antiviral, cytotoxic, antifouling, etc.) (Table 4, Fig. 5). More specifically, the known dolabellane diterpene (group II) (1R*, 2E, 4R*, 6E, 8S*, 10S*, 11S*, 12R*)-10,18-diacetoxy-8-hydroxy-2,6-dolabelladiene was the first compound described (Fig. 5) as the main component of the organic extract (Barbosa, Teixeira, Villaça, Pereira, et al., 2003). Further studies on this species allowed to isolate four new dolabellanes (1R*, 2E, 4R*, 6E, 8S*, 10S*, 11S*, 12R*-10-acetoxy-

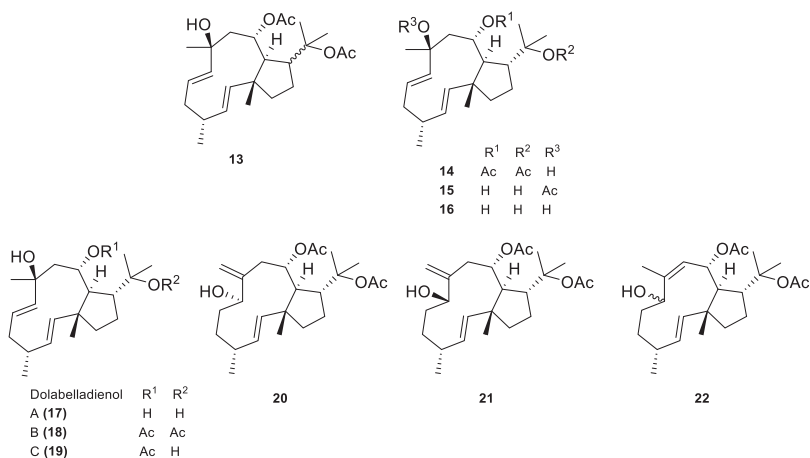


Fig. 5 Structures of diterpenoids isolated from *Dictyota friabilis* (syn. *Dictyota pfaffii*).

8,18-dihydroxy-2,6-dolabelladiene, Dolabelladienol A, B, and C) as well as the known Dolabelladienetriol, and previously described from the digestive gland of *Dolabella californica* (Ireland & Faulkner, 1977; Barbosa et al., 2004; Pardo-Vargas et al., 2014) (Fig. 5). Dolabelladienetriol, 10-acetoxy-8,18-dihydroxy-2,6-dolabelladiene, and 10,18-diacetoxy-8-hydroxy-2,6-dolabelladiene showed potent *in vitro* antiviral activity against HIV-1, but Dolabelladienetriol was the only compound which inhibited the reverse transcriptase enzyme of the virus. The antiviral properties of Dolabelladienetriol were then deeply investigated (Abrantes et al., 2010; Cirne-Santos, Teixeira, Castello-Branco, Frugulhetti, & Bou-Habib, 2006; Cirne-Santos et al., 2008; Garrido et al., 2017; Garrido et al., 2011; Stephens et al., 2017) and this diterpene was also shown to significantly inhibit the growth of *Leishmania* in macrophages (Soares et al., 2012). More recently, Dolabelladienols A and B were evaluated in the antiviral test against HIV-1 and were seen to be more active than Dolabelladienetriol (Pardo-Vargas et al., 2014). In another field of application, *D. friabilis* phlorotannins were assessed for their capacity to prevent the melanosis, quality changes and to prolong the shelf-life of iced Pacific white shrimps (*Litopenaeus vannamei*) (Sharifian, Shabanpour, Taheri, & Kordjazi, 2019). Regarding *Dictyota hamifera*, we found no studies dedicated to chemodiversity or biological properties.

Lobophora. There are no studies dedicated to the evaluation of the phytochemical content and the subsequent biological properties of *Lobophora pacifica*. Considering the vast array of bioactivities exhibited by *Lobophora* spp. metabolites in general (Gaubert, Greff, Thomas, & Payri, 2019; Vieira et al., 2015), it would be extremely relevant to investigate the chemodiversity associated to the species *Lobophora* in FP.

Padina. A minimal number of studies have isolated specialized metabolites from *Padina*. Fucoïdians extracted from Vietnamese samples of *Padina boryana* were evaluated for their anticancer properties against colorectal carcinoma cells (Shevchenko et al., 2017; Usoltseva et al., 2018). Samples of *Padina boryana* from the Red Sea have been assessed for their potential in biodiesel production (Abomohra, El-Nagggar, & Baeshen, 2018) polyphenolic contents, and antimicrobial activity (Sameeh, Mohamed, & Elazzazy, 2016), but also to determine their gross biochemical composition and their antioxidant properties (Ismail, El Zokm, & El-Sayed, 2017). Rasher and Hay (2010) assessed the allelopathic effects of the lipid-soluble fraction of the methanolic extract of *P. boryana* against the coral *Porites porites*. An

antioxidant and anti-inflammatory compound identified as squalene was isolated from *Padina boergesenii* samples collected in the Gulf of Mannar (India) (Rajamani, Balasubramanian, & Thirugnanasambandan, 2018), while a new triterpene with several enzyme-inhibitory activities was described in samples of the same species from Oman (Ali et al., 2017). Many other studies were dedicated to the evaluation of a large number of biological activities (antioxidant, antidiabetic, hepatoprotective, etc.) of the extracts of *P. boergesenii*, mainly from samples from Mannar (Table 4). Dimethylsulfoniopropionate (DMSP) content was evaluated from Chinese samples of *Padina minor* (Bischoff et al., 1994), while several studies dealt with the biological properties of extracts coming from various collecting sites (Table 4). In Moorea, *Padina pavonica* (not recorded from Tahiti during our survey) was collected and tested for its pro-apoptotic activity on human osteosarcoma cells, a rare bone cancer condition (Bernardini, Minetti, Polizzotto, Biazzo, & Santucci, 2018). The chemical composition of this species revealed interesting pharmacological and health-protecting activities and a great richness in flavonoids (Bernardini et al., 2018).

***Spatoglossum*.** *Spatoglossum asperum* has been studied in the Indian Ocean exclusively (Pakistan, India, and Kenya) (Table 4). Ara, Sultana, Ehteshamul-Haque, Qasim, and Ahmad (1999) showed a positive response to the cytotoxic activity of *S. asperum* from Pakistan. This cytotoxicity was confirmed by Vinayak, Sabu, and Chatterji (2011) on brine shrimps. Ara, Sultana, Qasim, and Ahmad (2002) showed a hypolipidaemic effect and effects on cardiac and liver enzymes. *Spatoglossum asperum* has numerous other interesting biological activities including antibacterial activity against *Staphylococcus aureus* (Pandithurai, Murugesan, & Sivamurugan, 2015), *Escherichia coli* (Kaaria, Wakibia, Matiru, Ndung'u, & Bii, 2015), *Bacillus cereus*, *Bacillus subtilis*, *Klebsiella pneumonia*, *Pseudomonas aeruginosa*, and *Salmonella typhi* (Pandithurai et al., 2015; Sivakumar & Vignesh, 2014), antifouling activities (Deepa et al., 2014), and antioxidant activities (Pandithurai & Murugesan, 2014; Vinayak et al., 2011). Antimicrobial activities have been tested against plant diseases for agricultural uses (Jothirethinam, Prathilba, Shanti, & Arunkumar, 2015). In 2015, *S. asperum* extracts revealed positive antitumoral effects (Aravindan, Ramraj, Somasundaram, Herman, & Aravindan, 2015). Among the publications listed in Table 4, none gives precise chemical compositions of *S. asperum*. Vinayak et al. (2011) and Aravindan et al. (2015) believe that polyphenols are responsible for the cytotoxic and anti-tumoral activities; however, they did not refer to isolated molecules.

4.2 Applications

4.2.1 Human consumption

The consumption of algae as food is the most significant market, representing about eighty percent of the world's algal production (FAO, 2016). According to a review by Zubia and Mattio (2019), four Dictyotaceae genera are used for food, mainly in the South Pacific Islands, including *Dictyota*, *Dictyopteris* (*Dictyopteris plagiogramma* “limu lipoa”; Hart, Ticktin, Kelman, Wright, & Tabandera, 2014), *Padina*, and *Spatoglossum*. Other Dictyotaceae such as *Padina* and *Dictyota* are used for their medicinal properties and as a source of food in many Pacific Islands (Abbott, 1984; Conte & Payri, 2002; Novaczek, 2001, pp. 1–48; South, 1993). *Dictyota* is eaten in various ways (seasoning, soup, etc.), and is also recognized as preventive medicine for heart diseases, stroke (algin compounds), and goiter (iodine content) (Novaczek, 2001, pp. 1–48). *Padina* is used to add flavor to dishes and is a good source of calcium (Novaczek, 2001, pp. 1–48). *Dictyopteris plagiogramma* is consumed traditionally in Hawaii (Abbott, 1984) and has a particularly strong and distinctive fragrance (due to dictyoterpenes; Moore, 1974), but this species is disappearing from the coast due to pollution (Hart et al., 2014).

In FP, seaweeds are still consumed today, particularly in the Marquesas and Austral islands with 11 species recorded (Conte & Payri, 2002, 2006; De Gaillande, Payri, Remoissenet, & Zubia, 2017), six of them belonging to the genus *Caulerpa*. In most of the Islands, this tradition has been lost, except in the Marquesas and the Austral archipelagos where *Caulerpa chemnitzia* (= *C. racemosa* var. *turbinata*) known as sea grapes (“remu” or “imu topua” in polynesian language) is consumed regularly (De Gaillande et al., 2017). In recent years, seaweed consumption has become more popular, and the French Polynesian Government wants to diversify the offer through the development of seaweed farming for *Caulerpa* spp. and a few red algae (*Gracilaria* spp., *Gelidiella acerosa*, *Acanthophora spicifera*). The development of Dictyotaceae species consumption like *Dictyota*, *Padina* or *Spatoglossum* could also be an exciting option to diversify the market.

4.2.2 Animal nutrition

A large proportion of methane emitted into the atmosphere derives from agriculture and specifically ruminant enteric fermentation which contributes approximately to 28% of global anthropogenic CH₄ emissions (Beauchemin, Kreuzer, O'Mara, & McAllister, 2008). Feed management and

additives such as high-quality forages, grains, ionophores, fats, yeasts, enzymes, microbes, plant extracts, and algae have the potential for CH₄ abatement (Beauchemin, Mc Allister, & McGinn, 2009). Algae products can improve ruminant health and productivity, increase feed quality, and inhibit methanogenesis (Holdt & Kraan, 2011; Kinley, De Nys, Vucko, Machado, & Tomkins, 2016). Kinley et al. (2016) showed that *Asparagopsis* induces near elimination of methane *in vitro*, and Machado, Magnusson, Paul, De Nys, and Tomkins (2014) found that the brown algae *Dictyota* spp. can reduce methane production by over 92% compared to controls.

Many experiments are currently underway in the field of aquaculture, for the incorporation of algae in shrimp and fish feeds (Nelson, Glenn, Conn, Walsh, & Akutagawa, 2001; Reverter, Bontemps, Lecchini, Banaigs, & Sasal, 2014). These algae or seaweed extracts are used either to replace proteins of animal origin either for their probiotic or antimicrobial effects, usually in the context of Integrated Multi-Trophic Aquaculture (IMTA) projects. In FP, emerging *Platax orbicularis* (orbicular batfish) aquaculture is affected by bacterial infections causing severe mortality episodes. Effective solutions are investigated to find natural bioactive compounds to counteract the infections caused principally by *Tenacibaculum maritimum* and *Vibrio harveyi*, and Reverter et al. (2016) demonstrated the promising results obtained with the Rhodophyta *Asparagopsis taxiformis*. Due to their antiviral and antimicrobial activities, their abundance, availability, and accessibility, Dictyotaceae species represent an equally interesting group to consider. Our research unit in Tahiti (UMR-EIO) is currently investigating the efficiency of French Polynesian *Dictyota bartayresiana*, *Dictyota hamifera*, and *Spatoglossum asperum* extracts against the pathogens *V. harveyi* and *T. maritimum*.

4.2.3 Health care, medicinal, pharmaceutical, and cosmetic properties

The use of macroalgae in cosmetics is quickly expanding as they represent a natural and active environmental resource. Several species are already used by several cosmetic industries in hair care, skin whitening, anti-aging, moisturizers, or in sunscreens (Ariede et al., 2017), but there is no reference on the use of tropical species for cosmetics in the literature. As previously discussed in section 4.1 and presented in Table 4, Dictyotaceae species synthesize a wide range of molecules with specific biological activities that could be used as active ingredients in cosmetics or health industries. For instance, Fayad et al. (2017) highlighted the promising activity of *Padina pavonica*

for the inhibition of hyaluronidase activity, which is expected to delay skin aging. *Spatoglossum asperum* also showed hypolipidic effects interesting against cholesterol disease (Gade, Tulasi, & Bhai, 2013). Other species of Dictyotaceae could be relevant for the health industry for their antiviral, antimicrobial, antioxidant, anti-inflammatory, and anti-cancer activities (Table 4), which are significant medical research challenges. According to our literature review, it is clear that the Dictyotaceae species of FP are a potential source of new exciting and potentially unique molecules that could be extremely useful for the cosmetic and health industry. However, although the potentials are high, only limited research is available that has explored specifically the diversity of the French Polynesian Dictyotaceae molecules and their associated biological potential.

4.2.4 Agriculture

Seaweeds can be used for many agricultural applications including bio-fertilizers, soil conditioners, and enhancers because of their high quantities of micro- and macronutrients, vitamins, amino acids, and growth regulators (Arioli, Mattner, & Winberg, 2015; Kumar & Sahoo, 2011; N'Yeurt & Iese, 2015a). Seaweed extracts represent a major opportunity to significantly enhance crop production and resistance to stress and disease (Arioli et al., 2015). Brown algae are particularly useful fertilizers (Arioli et al., 2015). Experiments in Fiji have demonstrated the potential of both *Sargassum polycystum* and *Gracilaria edulis* as excellent liquid fertilizers for a variety of common Pacific crops (unpublished results, N'Yeurt, pers. com.). Brown-algae based fertilizers contain alginates and sulfated polysaccharides, their chelating properties combined with metal ions in the soil form chelates that absorb moisture and improve the growth of soil bacteria (Cardozo et al., 2007; Khan et al., 2009). In FP, agronomical enrichment trials were conducted using drifting brown algae (*S. pacificum* and *T. ornata*) as organic additives (Zubia et al., 2014). This study demonstrated that low supplements of drift algae (1 and 3%) to plant compost significantly improved maize growth (stems length, aerial plants dry mass, and roots dry mass). In Tuvalu, farmers successfully use additives made of dried *Sargassum polycystum* on their crops (N'Yeurt & Iese, 2015b). Although we did not find studies on potential uses of Dictyotaceae species for agricultural purposes during our review, they could represent good candidates to develop eco-friendly fertilizer and additives of farming practices, in particular, to fight against phytopathogens due to their strong antimicrobial activities (Table 4).



5. Scope for future research

This paper represents the first detailed assessment of the Dictyotaceae family in FP. It reviews and supplements the existing knowledge on the diversity, ecology, chemodiversity, and potential economic applications of these species. Molecular analyses of the different genera are underway and will undoubtedly increase the known diversity of the Dictyotaceae family (44 species across all archipelagos to date). These results will be crucial for a better understanding of the diversity patterns in FP, and biogeographical studies in the Indo-Pacific, which are currently constrained by overlooked cryptic diversity (Vieira et al., 2017). Our research project was motivated by the observation of increasing amounts of Dictyotaceae species (especially *Dictyota bartayresiana* and *Spatoglossum asperum*) on the reefs of Tahiti Island over the past decade. However, our results do not indicate the occurrence of proliferation events, as the abundances we measured were relatively low (cover <10%) on all reefs surveyed throughout the year. Despite this result, and in light of our review, we argue here that monitoring Dictyotaceae species should be continued because of the potential negative impact they may have on coral health, particularly during periods of intense bleaching (see Section 3.2.2). Proliferations events were mainly triggered by increased temperatures, nutrients, and/or pH or biotic factors such as a decrease in herbivores which negatively impacted coral cover and favored the more resistant and opportunistic Dictyotaceae species (see Section 3). As Tahiti's coral reefs are subject to significant anthropogenic and environmental pressures (Andréfouët & Adjeroud, 2019), we believe that further studies are needed to better characterize the ecological dynamics of Dictyotaceae, particularly biotic factors. These data will be critical to design appropriate management policies and avoid future additional proliferations on the reefs of Tahiti. Finally, Dictyotaceae species represent promising resources for many biotechnological applications (human and animal nutrition, agriculture, health, cosmetic), most of which could be developed in FP. However, further studies are needed to characterize the chemodiversity of local populations and assess which economic sectors would be most suited for FP.

Acknowledgments

This work is part of the Ph.D. thesis of Tohei Theophilus. We are very thankful to the University of French Polynesia and the Délégation à la Recherche de Polynésie française for their financial support without which the research program DIVECOBAL would not have been possible.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/bs.abr.2019.12.001>.

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