

Distinctive morphological features, life-cycle phases and seasonal variations in subtropical populations of *Dictyota dichotoma* (Dictyotales, Phaeophyceae)

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Abstract

Although it has been suggested that the distribution of *Dictyota dichotoma* is probably restricted to the European Atlantic Ocean and the Mediterranean Sea, its occurrence in the Canary Islands (new southernmost distribution limit) is confirmed by nuclear ribosomal sequence data (LSU rDNA). Even though *D. dichotoma* has been described and illustrated prominently in early studies of brown algae, the species remains difficult to characterize due to considerable morphological plasticity. An exhaustive analysis of several quantitative characters confirms significant morphological variation both seasonally and between life-cycle phases. The species may be characterized in the Canary Islands only by the following qualitative features: erect thallus attached by a single holdfast, subdichotomous branches always of similar width, straight terminal segments and smooth margins and an entirely unilayered medulla. In the Canary Islands, *D. dichotoma* is an aseasonal annual with at least three overlapping generations in which sporophytes and gametophytes grow simultaneously. Thallus life span seems to be less than 3 months. The species occurs throughout the year, but as cryptic microthalli in autumn. Two abundance peaks were detected with the maximum value in February (6.2 thalli m⁻²). The optimum reproductive stage (88.3% fertile specimens) occurred in winter and the maximum vegetative stage (maximum thallus length: 18.6 cm) in summer. Sporophytes outnumbered gametophytes throughout the year, with ratios decreasing from 13.2±1.1 in winter to 1.9±0.2 in summer. Gametophytes made up to 25% of the population and fertile thalli were always dominant. The populations from the Canaries exhibited a temporal displacement compared to northern populations with the favorable period in the coldest season (winter) and the resting period in the warmest season (autumn).

Keywords: Canary Islands; *Dictyota dichotoma*; morphology; nuclear ribosomal sequence data (LSU rDNA); phenology; seasonal variation.

Introduction

The genus *Dictyota* Lamouroux comprises species widely reported from tropical and subtropical shores around the world (De Clerck et al. 2006). The type species, *Dictyota dichotoma* (Hudson) Lamouroux, was originally described from Walney Island, United Kingdom (Hudson 1762, Silva et al. 1996) and reported later from numerous localities in the Atlantic, Indian and Pacific Oceans (see Guiry and Guiry 2007). Nevertheless, karyological studies (chromosome counts) and crossing experiments carried out by Schnetter et al. (1987) suggested that the distribution of *D. dichotoma* was probably restricted to European Atlantic coasts and the Mediterranean Sea. In agreement with Schnetter's beliefs, De Clerck (2003) concluded that *D. dichotoma* was most probably absent in the Indian Ocean, despite numerous previous reports. Records from the Pacific Ocean have also been questioned (South and Skelton 2003, Tsuda 2004). The presence of *D. dichotoma* along European and Mediterranean shores is undisputed, but it is much less clear how far south the range of this species extends. Assessing the geographic distribution of *D. dichotoma*, however, is problematic due to considerable morphological plasticity. Although this species has been described and figured prominently in early studies of brown algae and phycological manuals (e.g., Thuret 1855, Newton 1931, Hamel 1939, Smith 1955, Bold and Wynne 1978), there is no diagnostic characterization of the species based on modern criteria. Currently, a combination of high morphological variability and a lack of distinctive characters makes an accurate and concise description difficult (De Clerck 2003). An unequivocal identification of the specimens from extra-European or Mediterranean shores (e.g., Canary Islands) must be based on a comparison with DNA sequences from the genuine European *D. dichotoma*. The first aim of this study was to confirm the identity of specimens named *D. dichotoma* from the Canary Islands using nuclear ribosomal sequence data (LSU rDNA) and to present a detailed account of its vegetative and reproductive morphology, analyzing the plasticity of the species.

As in other Dictyotales, *Dictyota dichotoma* has a diplohaplontic life cycle with macroscopic sporophytes alternating with morphologically similar gametophytes (van den Hoek et al. 1995). However, little is known about the life history processes in natural populations of *Dictyota* species (Peckol 1982, King and Farrant 1987, Phillips 1988, Hwang et al. 2005). Populations apparently survive less favorable seasons as small germlings, which form new populations when favorable conditions return. Occurrence of microthalli (resting stages) has been reported in *Dictyota menstrualis* (Hoyt) Schnetter, Hörnig et Weber-Peukert (Richardson 1979, as *D. dichotoma*)

from the western Atlantic Ocean. According to the scarce information available, *D. dichotoma* seems to have a varying phenology through its latitudinal range. It is widely known that *D. dichotoma* is not visible to the unaided eye from approximately October to March along temperate Atlantic European coasts (Hamel 1939, Stegenga and Mol 1983). The Mediterranean populations occur from February to August, being largely absent in autumn and early winter (Feldmann 1937, O. De Clerck personal observations). However, preliminary observations of Canary Islands populations still suggest a different phenology. Essential information about lifespan of the individual thalli, number of generations per year and sporophyte/gametophyte ratio is not available. The second aim of the present study was to test a possible temporal displacement of favorable and resting periods across the distribution range of the species and to provide phenological data on population dynamics in a subtropical locality.

Materials and methods

Sampling was carried out monthly from April 2003 to March 2004 at Punta del Hidalgo, north Tenerife, Canary Islands (28°35' N, 16°20' W). All specimens from a sublittoral area of 25 m² were counted monthly for a density value. A minimum of 10 individuals was randomly collected from adjoining areas each month and preserved in 4–10% formalin in seawater. For morphometric analyses and descriptive purposes, thalli were scored for 14 vegetative characters. In addition, sporophytes were scored for 2 additional characters and gametophytes for 12 (male) and 6 (female) characters.

For each specimen, thallus length, number of branches arising from main axes, lengths and widths of interdichotomies and apical width were measured. The angle between two branches (branching angle) was measured in the median and proximal parts of the thallus. Lengths and widths of cortical and medullary cells were measured in surface view at an interdichotomy situated well below the apex, while their height was measured in transverse section. The number of medullary cells with cell wall thickenings per mm² was counted in surface view at the second interdichotomy below the apex. Mature parts of each individual were selected for reproductive features. Number, widths and lengths of rows of antheridia, lengths and widths of central antheridia and tiers per antheridium, number of oogonia per sorus and diameters of central oogonia were obtained in surface view. Heights of paraphyses, antheridia, oogonia and stalk cells, and number of loculi per tier of antheridia were measured in transverse section. For each character, minimum and maximum sizes and the 95% confidence limits were determined. Micrographs were taken using a Nikon Coolpix 4600 digital camera (Nikon, Tokyo, Japan) attached to a ZEISS standard microscope (Zeiss, Berlin, Germany). Specimens examined were deposited in herbarium TFC (Departamento de Biología Vegetal, Universidad de La Laguna, Canary Islands).

Data were analyzed using parametric statistical methods, following Sokal and Rohlf (1995). Levene's test was

applied to test the various data for homogeneity of variances. For studying the effects of season, data from 3 months were used per season (spring: March, April and May; summer: June, July and August; autumn: September, October and November; winter: December, January and February). One-way analysis of variance was used to detect temporal variation between seasons and between life-cycle phases (autumn was not considered because the number of specimens was very low). Student-Newman-Keuls (SNK) or Scheffé multiple range tests were used to segregate groups means. All statistical analyses were performed using the SPSS system for Windows v.12.0. (SPSS, Chicago, IL, USA).

LSU rDNA sequences of Canary Islands specimens were generated and compared with sequences from genuine *Dictyota dichotoma* from continental Europe, as well as from additional species that share a similar morphology, or which are known to occur in the Macaronesian region (Table 1). Although a rather conservative phylogenetic marker, the LSU gene has several regions that are highly variable and species specific. Most notably, the C-helix (De Rijk et al. 2003) possesses several loop regions that have sufficient variation at the species level. DNA extraction, amplification, sequencing and alignment of the LSU sequences based on secondary structure were carried out according to De Clerck et al. (2006). Two-dimensional drawings of helices were produced using RnaViz2 (De Rijk et al. 2003).

Results

Molecular identification

Partial LSU rDNA sequences of the *Dictyota* population at Punta Hidalgo, Tenerife were generated and compared to a variety of existing *Dictyota* sequences of morphologically similar species and sequences generated from additional *Dictyota* species growing in the Canary Islands. The sequence of the presumed *Dictyota dichotoma* from Tenerife differed at two positions (uncorrected distance=0.2%) from two sequences known to belong to *D. dichotoma* from Atlantic France based on an alignment containing 1373 positions. Uncorrected distances among the other species ranged from 1.5% to 4%. Furthermore, no sequence differences were observed between *D. dichotoma* from the Canary Islands and the specimens from Roscoff and Audresselles in the C-helix (Figure 1). The latter region of the LSU is highly variable within the Dictyotales, displaying a huge variation in secondary structure among the genera. Species level comparison typically reveals several point mutations and indels that appear to be species specific.

Vegetative and reproductive morphological characteristics

Thalli of *Dictyota dichotoma* are erect, (3.7–)8.7–9.4(–18.6) cm long, often supple but occasionally with stiff basal parts, attached by rhizoids that usually form a discoid holdfast (Figures 2–4). *In vivo*, thalli have a brightly blue-greenish iridescence, while dry specimens are pale yellowish brown. Widths are similar through the

Table 1 Species used for molecular analysis.

Species	Collecting data	GenBank accession no.
<i>Dictyota dichotoma</i> (Hudson) Lamouroux	Punta Hidalgo, Tenerife, Canary Islands (A. Tronholm, M. Sansón and J. Afonso-Carrillo, 21/12/2005, TFC Phyc 13158)	AM981190
<i>Dictyota dichotoma</i> (Hudson) Lamouroux	Point du Nid de Corbet, Audresselles, Atlantic France, (O. De Clerck, 16/10/2004, ODC 1027)	DQ472105
<i>Dictyota dichotoma</i> (Hudson) Lamouroux	Ile Verte, Roscoff, Brittany, Atlantic France (E. Coppejans, 22/07/2005, HEC 15613)	AM981191
<i>Dictyota pulchella</i> Hörnig et Schnetter	East side of airport causeway, St. George, Bermuda (C.E. Lane and C.W. Schneider, 02/04/2003, CLO 30101)	DQ472113
<i>Dictyota ceylanica</i> Kützing	Faaa, Tahiti (H. Verbruggen, 21/05/2002, HV 214a)	DQ472122
<i>Dictyota ciliolata</i> Sonder ex Kützing	Punta Hidalgo, Tenerife, Canary Islands (A. Tronholm, M. Sansón and J. Afonso-Carrillo, 21/12/2005, TFC Phyc 13159)	AM981192
<i>Dictyota crenulata</i> J. Agardh	Bermuda (C.E. Lane and C.W. Schneider, CLO 31302)	AM981193
<i>Dictyota fasciola</i> Howe	Ile de Frioul, Marseille, Mediterranean France (O. De Clerck, 23/09/2004, ODC 1029)	DQ472126
<i>Dictyota liturata</i> Kützing	The Bluff, Treasure Beach, Durban, South Africa (O. De Clerck and F. Leliaert, 15/06/2003, KZN2282)	AM981194

whole thallus, with interdichotomies (3–)7.5–7.8(–15) mm long and (1.5–)3.2–3.3(–6) mm wide, and apices rounded to obtuse, (0.25–)1.1–1.2(–3) mm wide (Figure 5). Thalli branch subdichotomously, with a distinct main axis to (6–)13–14(–25) times branched. The branching angles are acute in the apical portions of the thallus, (6–)19–21(–45)°, whereas they are wider in the middle and basal segments, (27–)58–61(–130)°. Margins and surface are smooth, although proliferations arising perpendicularly from the surface are occasionally formed at basal segments. Hair tufts are common, except on the margins. The cortex is unilayered, and consists of cortical cells that are elongate and rectangular in surface view, (16–)40–42(–69) µm long and (7–)15–16(–31) µm wide, and nearly square in transverse section, (9–)16–17(–29) µm high, with numerous discoid plastids arranged along the cell periphery. The medulla is unilayered and occasionally multilayered in damaged parts of the thallus. Medullary cells are hyaline, rectangular in surface view and transverse section, (47–)93–96(–190) µm long, (45–)60–62(–105) µm wide and (42–)80–82(–136) µm high. In transverse section, there are 4–5 cortical cells per medullary cell. Nearly 5% of medullary cells have conspicuously thickened cell walls, with (1–)9–12(–46) cells thickened per mm². Thickenings form a molding-like structure filling 2–4 angles between the outer and inner cell walls of the medullary cells. In surface view, thickenings are L-, U-, or frame-shaped, bright structures located below the layer of cortical cells and reaching up to 10 µm (Figure 6). Thickenings are restricted to a single wall parallel to the thallus surface, and in transverse section, less than half of the cell height is thickened (Figure 7).

Sporophytes bear sporangia scattered on both thallus surfaces; they are restricted to the central part of the thallus (Figures 8 and 9). Sporangia are dark brown, sub-spherical, (52–)112–115(–160) µm in diameter, without an involucre and are borne on single stalk cells that are (9–)17–18(–33) µm high (Figure 10). Mature divided sporangia have rarely been observed on the thallus. Presumably, they divide only immediately prior to release. After spores are released, the sporangial wall persists (Figure 10).

Male gametophytes form whitish, blister-like sori over the whole thallus surface, often merging with adjacent sori to form large, irregular patches (Figure 11). In surface view, antheridial sori are ellipsoidal, (270–)477–510(–720) µm long and (195–)296–319(–570) µm wide, each surrounded by a ring of (1–)3(–4) rows of pigmented paraphyses (Figure 12). Antheridia are arranged in regular rows, each row (5–)10–11(–21) µm wide and (195–)391–426(–645) µm long, with central mature antheridia (19–)31–34(–64) µm long, (16–)25–28(–38) µm wide, and with (4–)33–40(–112) tiers per antheridium. In transverse section, antheridia are subcylindrical, (52–)83–88(–136) µm high and contain (4–)20–24(–36) loculi per tier, each borne on a single stalk cell that is (9–)15–16(–24) µm high (Figure 13). Paraphyses are unicellular, subclavate (64–)90–95(–124) µm high, and persist as a ring after the sperms are released and antheridia are detached (Figure 14). After male gametes have been shed, the inner paraphyses in the persistent ring of senescent sori elongate and divide to 2–4 cells long, curving inwards (Figure 15).

Sori of dark brown oogonia are spread over the whole thallus surface (Figure 16). In surface view, oogonial sori are rounded to oval, (180–)320–347(–540) µm long and (90–)227–248(–405) µm wide, with (9–)32–36(–60) oogonia per sorus (Figure 17). Mature oogonia are (26–)55–61(–93) µm in diameter. In transverse section, oogonia are subclavate to pyriform, (30–)82–89(–136) µm high, each borne on a single stalk cell that is (11–)16–18(–43) µm high (Figure 18).

Occurrence, abundance and seasonal variation

Individuals of *Dictyota dichotoma* grow scattered and epilithically in shallow sublittoral habitats together with other Dictyotales, such as *Lobophora variegata* (Lamouroux) Oliveira, *Taonia atomaria* (Woodward) J. Agardh, *Zonaria tournefortii* (Lamouroux) Montagne, *Padina pavonica* (Linnaeus) Thivy, other *Dictyota* species, and articulate coralline algae (*Jania adhaerens* Lamouroux and *Corallina elongata* Ellis et Solander).

Specimens of *Dictyota dichotoma* were observed throughout the year (except in October), though in very

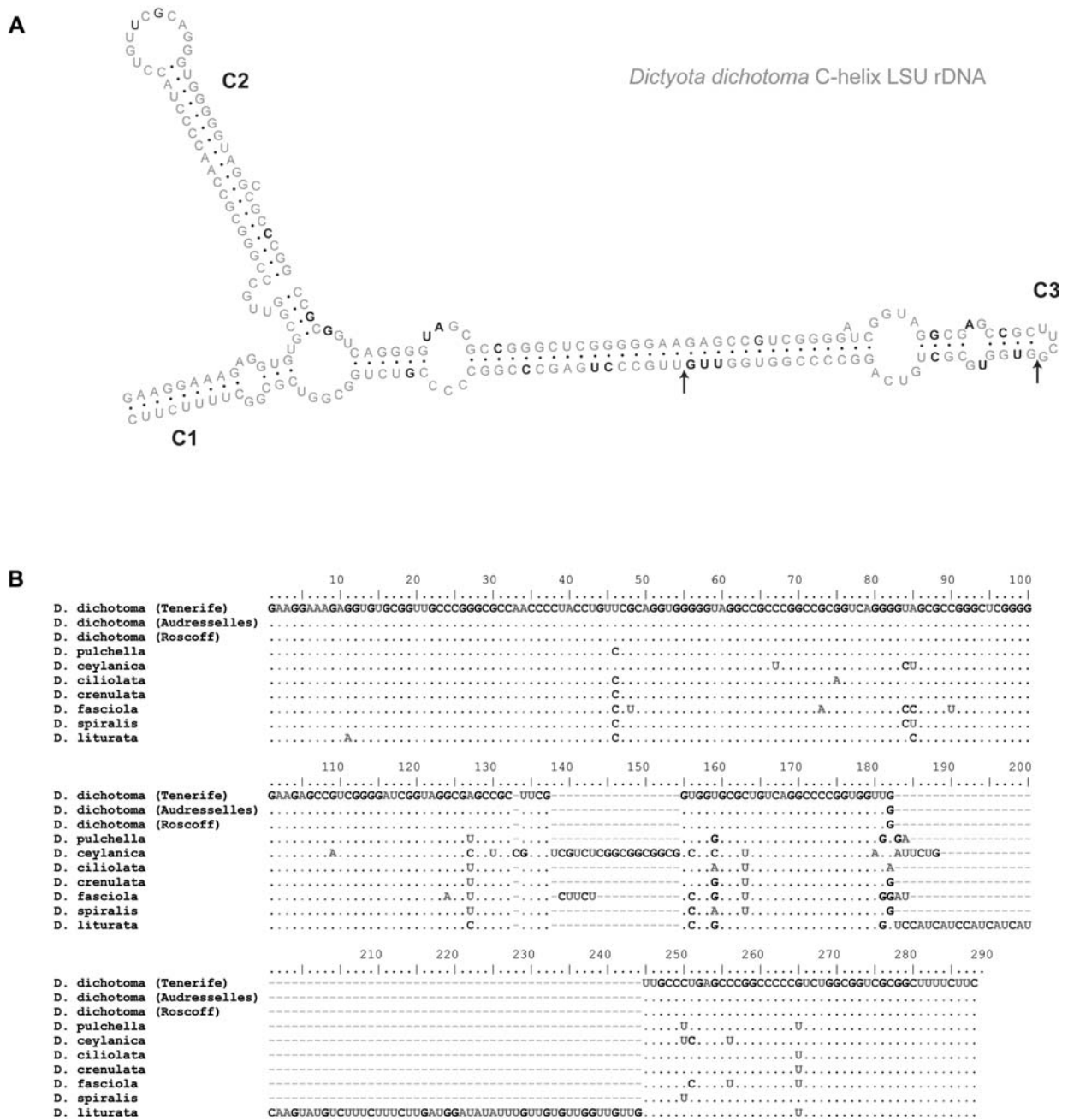


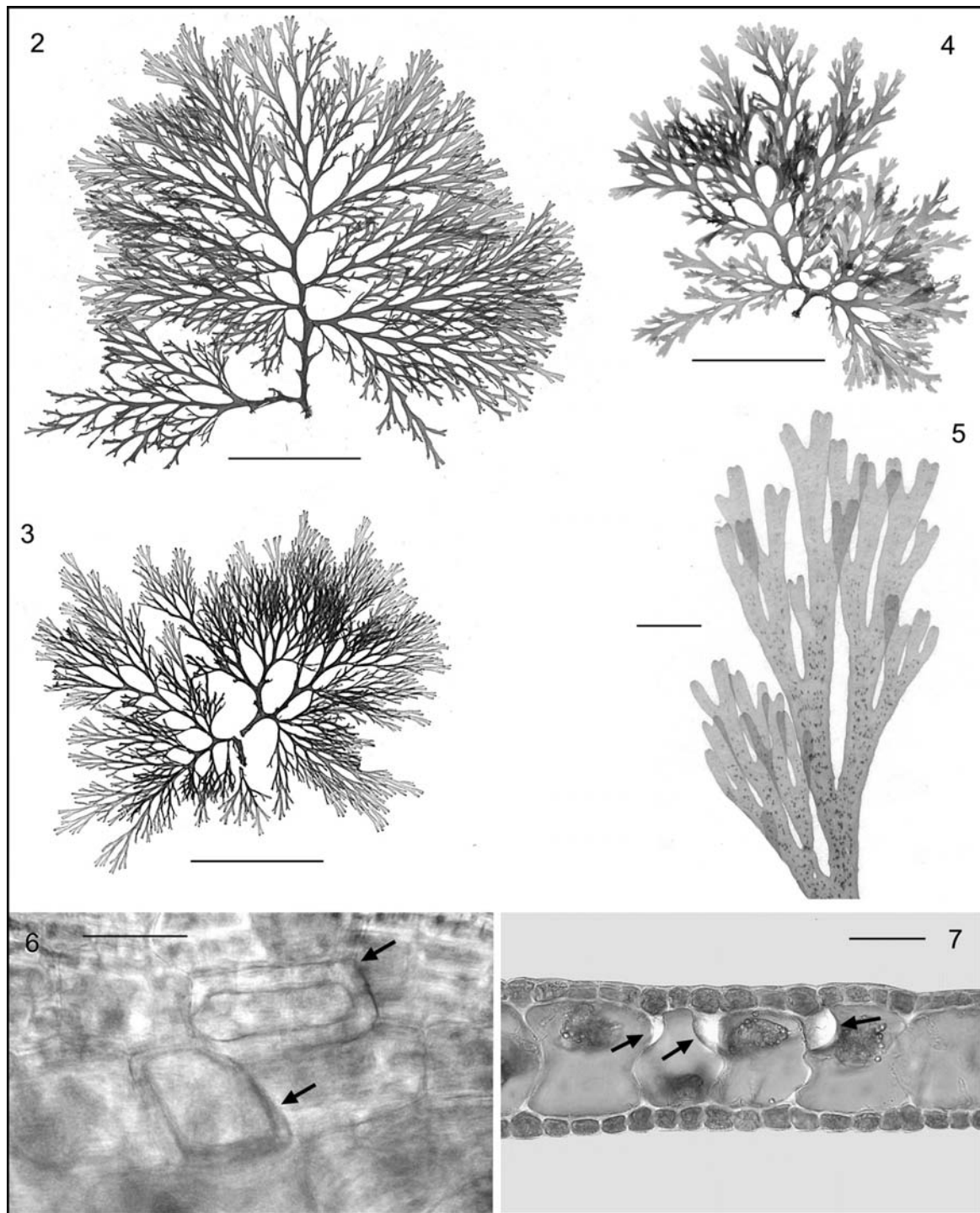
Figure 1 *Dictyota dichotoma*: comparison of the LSU rDNA C-helix between *D. dichotoma* and a selection of species occurring in the North East Atlantic Ocean and Mediterranean Sea. (A) Secondary structure of C-helix of *D. dichotoma* with indication of nucleotides displaying variation (bold) and positions where inserts have been detected (arrows) among the species compared. (B) Condensed alignment of the LSU rDNA C-helix.

low numbers in autumn. Fluctuations in monthly density value occurred in the study area; there was a bimodal distribution of density by time (Figure 19). The first peak occurred in May (3.2 individuals m⁻²) and the population density declined steadily towards autumn. After the minimum density value of autumn, the number of individuals per m² increased again to a maximum of 6.2 individuals m⁻² in February.

Higher densities during certain months can be attributed to variability in sporophyte occurrence. The number of gametophytes was low year-round and fluctuated little (Figure 19). Dominance of sporophytes over gametophytes reached a maximum in winter, with 13.2±1.1 spo-

rophytes for every gametophyte, and was rather lower in spring (2.5±0.6) and summer (1.9±0.2). Fertile thalli were always more abundant than non-fertile thalli, with ratios of 6.5±2.2 in winter, 4.3±1.6 in spring and 2.7±2.4 in summer. Gametophytes as well as non-fertile specimens were not found from September to November.

Thalli of different ages from juvenile to adult were present in each month, producing variable trends in habit parameters. In December, individuals had the lowest mean value in thallus length (6.1±1.0 cm) and number of branches (10.6±1.6), whereas the tallest (11.6±3.2 cm) and most branched (17.1±3.0) specimens were found in July. The greatest inequalities in both length (9.1±3.4 cm)

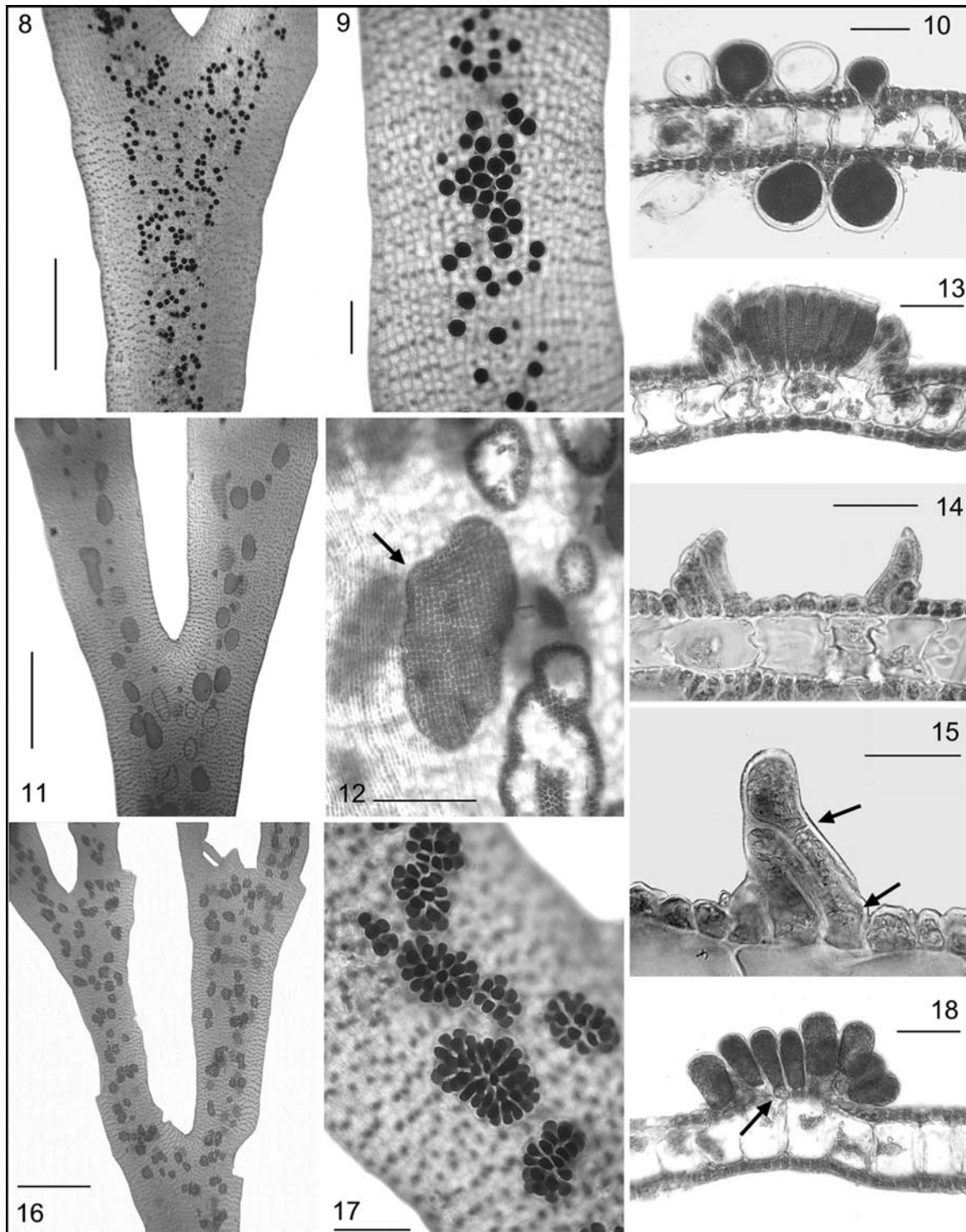


Figures 2–7 *Dictyota dichotoma*.

(2) Habit of a sporophyte (TFC Phyc 13083). (3) Habit of a male gametophyte (TFC Phyc 13084). (4) Habit of a female gametophyte (TFC Phyc 13085). (5) Detail of terminal portion of a female gametophyte showing subdichotomous branching, rounded obtuse apices and smooth margins (TFC Phyc 13086). (6) Surface view of a thallus showing two thickened frame-shaped medullary cells (arrows) (TFC Phyc 13087). (7) Transverse section of a thallus with unilayered cortex and medulla, with two thickened medullary cells (arrows) (TFC Phyc 13087). Scale bars: Figures 2–4=5 cm, Figure 5=5 mm, Figures 6–7=50 μm .

and number of branches (14.7 ± 5.0) between individuals were observed in August. In December, lengths of inter-dichotomies were at the lowest mean value (6.9 ± 2.7 mm), and the highest values (8.5 ± 1.8 mm) occurred in April, before thalli reached their maximal length. There was a different pattern in widths of inter-dichotomies, as thalli had the highest mean value (3.9 ± 0.8) in March and the lowest (2.7 ± 0.6) in May. In

August, thalli had the narrowest apices (0.8 ± 0.2 mm), while the widest (1.5 ± 0.5 mm) occurred in April. Finally, the apical parts of thalli had the highest mean branching angle in December ($23.1 \pm 7.7^\circ$) and the lowest ($16.6 \pm 6.3^\circ$) in March, whereas middle-basal parts of thalli had their highest mean branching angle ($76.3 \pm 24.3^\circ$) in August and lowest ($51.6 \pm 16.7^\circ$) in April (Figure 20).



Figures 8–18 *Dictyota dichotoma*.

(8–9) Details of sporophytes in surface view with scattered sporangia on the central part of thalli (TFC Phyc 13087, 13088). (10) Detail of transverse section of a thallus with sporangia and walls of empty sporangia on both thallus surfaces (TFC Phyc 13087). (11) Surface view of branches of a male gametophyte showing the arrangement of antheridial sori (TFC Phyc 13089). (12) Detail in surface view of a mature antheridial sorus (arrow) and senescent empty sori in which only the ring of rows of pigmented paraphyses persists (TFC Phyc 13089). (13) Transverse section of an antheridial sorus with subcylindrical antheridia surrounded by subclavate paraphyses (TFC Phyc 13089). (14) Transverse section of the paraphyses of a senescent antheridial sorus (TFC Phyc 13089). (15) Transverse section of the ring of paraphyses of an empty antheridial sorus, with the elongate inner paraphyses three cells long (arrows) (TFC Phyc 13089). (16) Surface view of branches of a female gametophyte showing the arrangement of oogonial sori (TFC Phyc 13090). (17) Detail of the thallus surface with rounded to oval oogonial sori. (18) Transverse section of an oogonial sorus with subclavate oogonia borne on a single stalk cell (arrow) (TFC Phyc 13090). Scale bars: Figures 8, 11, 16=2 mm, Figures 9, 12, 17=300 μm , Figures 10, 13, 14, 18=100 μm , Figure 15=50 μm .

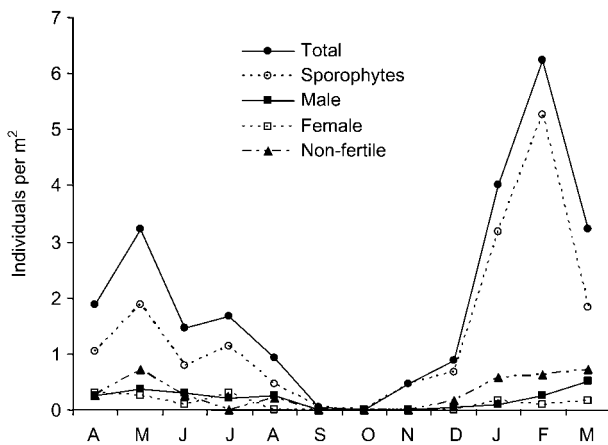


Figure 19 *Dictyota dichotoma*: temporal variations in density value of total individuals, sporophytes, male gametophytes, female gametophytes and non-fertile specimens through an annual cycle (from April 2003 to March 2004) in the study area of 25 m².

The different life-cycle phases had different patterns of temporal variation in thallus length (Figure 21). Sporophyte length increased in June–July (11.9 ± 3.1 cm), decreasing until September when macroscopic thalli almost disappeared. Sporophyte length increased again from December to February–March (11.4 ± 2.4 cm). Lengths of female gametophytes reached maximum mean values before and after the autumn resting period (13.1 ± 2.6 and 12.2 ± 1.5 cm, respectively), while the minimum value was observed in May (6.1 ± 1.7 cm). Although male gametophytes did not show seasonal variation in length, slight increases were observed in April, August and February. Non-fertile specimens varied less in length than fertile thalli throughout the year (Figure 21).

Significant seasonal variations were detected in most habit and anatomical parameters when different life-cycle stages were pooled. Interdichotomy widths (except for female gametophytes) and lengths and widths of cortical cells were the only features that did not vary through the year (Table 2).

Regardless of temporal variation, there were significant differences between the different life-cycle phases (Table 3). Non-fertile specimens were significantly shorter and less branched than fertile specimens. The height of medullary cells was the unique parameter which differed significantly between the three fertile phases, with the highest mean value in sporophytes, followed by female and male gametophytes in sequence. Sporophytes had thinner apices, longer cortical and medullary cells and wider cortical cells than gametophytes. Female gametophytes had broader and smaller interdichotomies than sporophytes and male gametophytes. Finally, male gametophytes had the narrowest apical angles, shortest cortical cells and the narrowest medullary cells (Table 3).

The reproductive parameters of *Dictyota dichotoma* varied significantly by season (Table 4). Sporangia had their widest diameters in winter. Oogonia had their maximum diameters and heights in spring, although the number per sorus was maximal in winter. Antheridial parameters did not vary significantly among seasons.

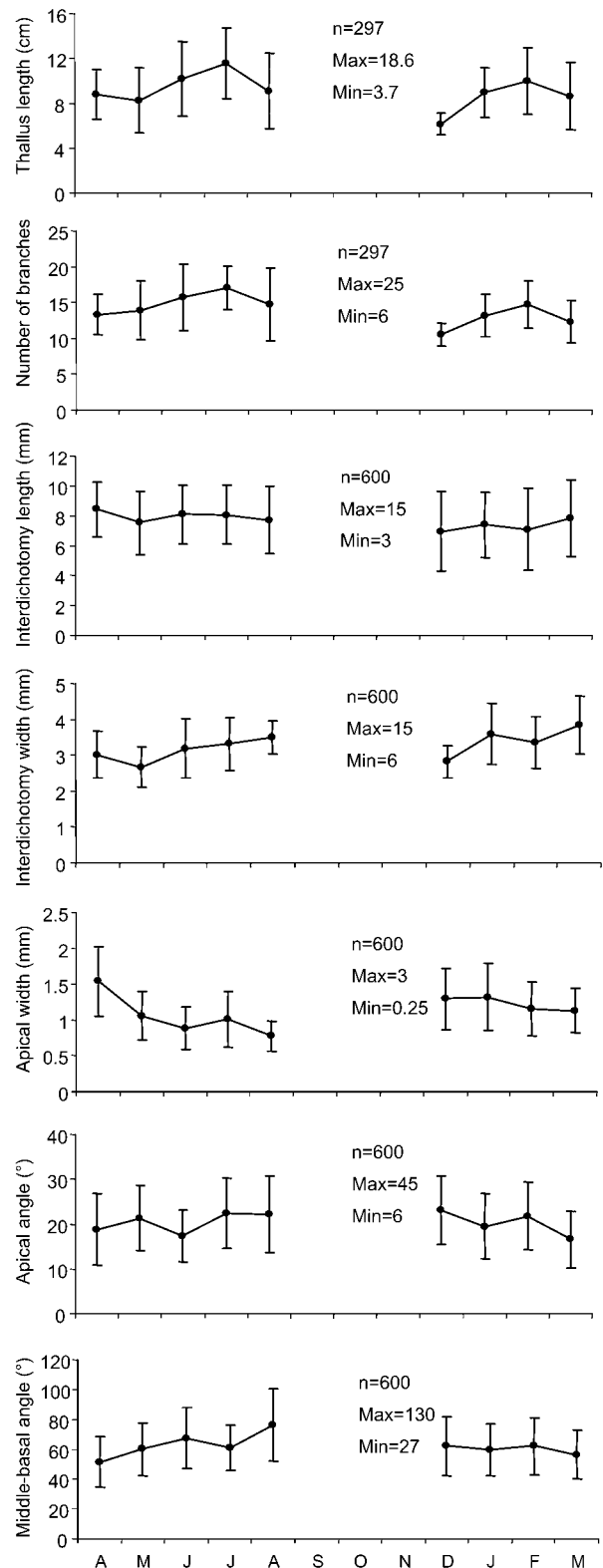


Figure 20 *Dictyota dichotoma*: temporal variations in habit parameters (mean \pm standard deviation) from April 2003 to March 2004.

n=sample size, Max=maximum value, Min=minimum value.

Discussion

Dictyota dichotoma has been referred to as a species that is notoriously difficult to identify because of its great morphological plasticity (e.g., Schnetter et al. 1987, Hwang et al. 2005). Species delimitation in *Dictyota* is

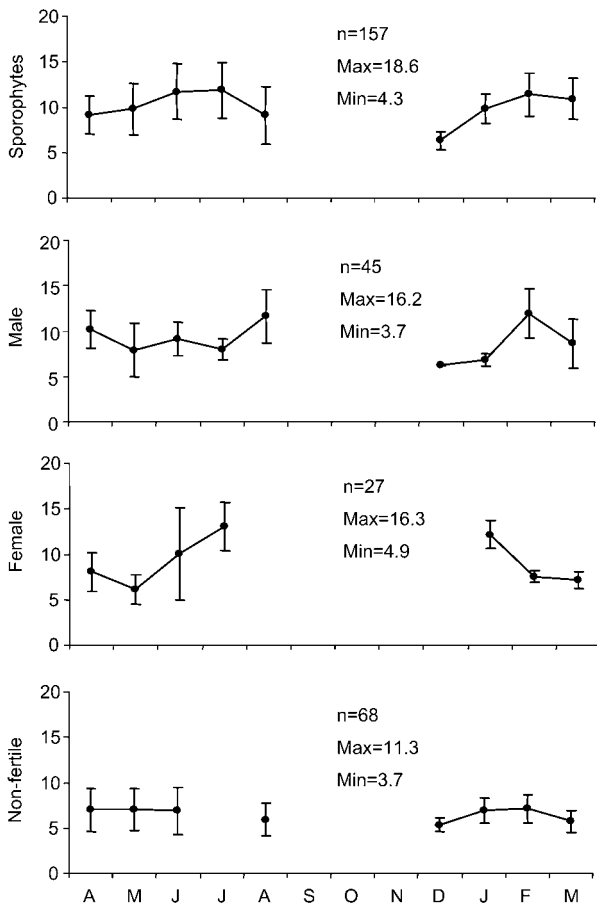


Figure 21 *Dictyota dichotoma*: temporal variations in thallus lengths of sporophytes, male gametophytes, female gametophytes and non-fertile specimens (mean \pm standard deviation) from April 2003 to March 2004. n=sample size, Max=maximum value, Min=minimum value.

mainly based on a combination of qualitative features (i.e., growth form, attachment, shape of the apical segments, branching pattern, margins, iridescence and reproductive structures) and quantitative features (i.e., interdichotomy size, branching angle, sizes of cortical and medullary cells and sizes of reproductive structures) (Weber-Peukert 1985, Hörnig et al. 1992a,b, De Clerck 2003). Our exhaustive analyses of variability in quantitative characters revealed that most of these characters showed significant variation by season and life-cycle phase. Some features (width of interdichotomies, lengths and widths of cortical cells, lengths of antheridial sori, number of rows per antheridium, lengths of antheridial rows, lengths and widths of central antheridia, heights of antheridia, numbers of tiers per antheridium, and lengths and widths of oogonial sori) were stable throughout the year, and other features (branching angle in the median and proximal parts of the thallus and the number of thickened medullary cells) were stable between life-cycle phases. However, simultaneous stability by season and life-cycle phase did not occur for any character.

Therefore, *Dictyota dichotoma* is characterized by a constant ensemble of qualitative features, while quantitative features could be useful for evaluating intra-population morphological variation (throughout the year and between the different life-cycle phases), and among pop-

ulations through the species' distribution area. Those quantitative features that varied significantly between sporophytes, male and female gametophytes (length and width of interdichotomies, branching angle and sizes of cortical and medullary cells) may be useful for determining the potential nature of non-fertile specimens. As characterized in this study, *D. dichotoma* has an erect thallus attached by a single holdfast, little width variation along the thallus, subdichotomous branching, straight terminal segments, smooth margins and an entirely unilayered medulla. Other few species, such as the Indian Ocean *D. dumosa* Børgesen and *D. rigida* De Clerck et Coppejans, and the Atlantic *D. liturata* J. Agardh and *D. menstrualis* (Hoyt) Schnetter, Hörnig et Weber-Peukert share this combination of characters (see Hörnig et al. 1992b, De Clerck and Coppejans 1999, De Clerck 2003).

Phylogenetic evidence shows that specimens examined in this study are genuine representatives of *Dictyota dichotoma*. Because of the diversity of the genus in the Canary Islands, where 14 species have been reported (Afonso-Carrillo and Sansón 1999), and the high morphological variability of the species, a molecular verification was essential. Nevertheless, our data indicate that specimens from Punta del Hidalgo (Canary Islands) differ somewhat in habit from populations of the same species growing in cooler environments. The Canarian thalli have maximum lengths of approximately 18 cm and maximal interdichotomy widths of 6 mm, while the Atlantic European thalli reach 30 cm high and 12 mm wide (Newton 1931). These morphological differences follow the general pattern that larger specimens occur in the coldest regions of the distribution area of a species (Lüning 1990), and the Canary Islands currently constitute the southernmost and warmest locality in the eastern Atlantic Ocean in which the occurrence of *D. dichotoma* has been confirmed.

In addition, specimens examined had two morphological features that had been previously overlooked. Firstly, thickened medullary cells were always present in all thalli examined. Although such thickenings are unknown in most species of *Dictyota*, they have been reported as occurring occasionally in *D. dichotoma* var. *intricata* from southern Australia and *D. stolonifera* Dawson from the Indo-Pacific Ocean (Womersley 1987, De Clerck and Coppejans 1999). The constant presence and distinctive shape of thickenings of Canarian thalli suggest that this could be a character with taxonomic value, but it needs to be tested in specimens of others populations through its distribution area. Secondly, antheridial sori are surrounded by pigmented unicellular paraphyses; the innermost row of paraphyses elongates and becomes multicellular after antheridia have been shed. Occurrence of both unicellular and multicellular paraphyses related to different developmental stages (as we have found in *D. dichotoma*) has not been previously reported in the genus. De Clerck et al. (2006) characterized *Dictyota* by its hyaline unicellular paraphyses, whereas *Canistrocarpus* De Paula et De Clerck has pigmented multicellular paraphyses. It now seems that this diagnostic character should be somewhat refined. During ontogenesis, the male sori paraphyses of *Dictyota* are unicellular, while they are 2–3-celled from the early developmental stages

Table 2 *Dictyota dichotoma*: one-way analyses of variance for effects of season on different vegetative parameters of pooled individuals, sporophytes, male and female gametophytes and non-fertile specimens (mean \pm standard deviation) at Punta del Hidalgo (Canary Islands), April 2003–March 2004.

Parameter	Spring	Summer	Winter	MS _{error}	F	p	SNK
Thallus length (cm)							
Total	8.56 \pm 2.74	10.47 \pm 3.37	8.88 \pm 2.78	0.175	F _{2,294} =10.857	<0.001	a)s, w; b)su
Sporophytes	9.95 \pm 2.45	11.24 \pm 3.21	9.58 \pm 2.70	0.226	F _{2,154} =4.714	0.010	a)w, s; b)su
Male	8.75 \pm 2.67	9.65 \pm 2.50	9.95 \pm 3.47	0.410	F _{2,42} =0.770	0.470	
Female	7.18 \pm 1.89	12.33 \pm 3.24	10.32 \pm 2.77	0.645	F _{2,24} =11.249	<0.001	a)s; b)w, su
Non-fertile	6.48 \pm 1.96	6.46 \pm 2.17	6.85 \pm 1.48	0.645	F _{2,65} =0.340	0.713	
Branches from main axes							
Total	13.17 \pm 3.44	16.03 \pm 4.24	13.37 \pm 3.28	0.221	F _{2,294} =16.729	<0.001	a)s, w; b)su
Sporophytes	14.03 \pm 3.36	16.50 \pm 4.11	13.85 \pm 2.86	0.287	F _{2,154} =8.795	<0.001	a)w, s; b)su
Male	14.27 \pm 3.68	16.47 \pm 3.36	15.38 \pm 4.34	0.558	F _{2,42} =1.582	0.218	
Female	12.93 \pm 2.40	17.88 \pm 4.29	17.60 \pm 1.82	0.731	F _{2,24} =8.747	0.001	a)s; b)w, su
Non-fertile	10.97 \pm 2.83	11.33 \pm 3.46	10.96 \pm 2.24	0.324	F _{2,65} =0.072	0.931	
Interdichotomies							
Length (mm)							
Total	7.92 \pm 2.24	8.04 \pm 1.99	7.19 \pm 2.50	0.094	F _{2,597} =8.071	<0.001	a)w; b)s, su
Sporophytes	8.17 \pm 2.24	7.84 \pm 1.95	7.75 \pm 2.61	0.126	F _{2,337} =1.120	0.327	
Male	8.89 \pm 2.32	7.83 \pm 2.10	6.82 \pm 2.33	0.210	F _{2,127} =9.352	<0.001	a)w; b)su; c)s
Female	6.70 \pm 1.62	8.83 \pm 1.80	5.95 \pm 1.77	0.176	F _{2,127} =25.617	<0.001	a)w, s; b)su
Total	3.21 \pm 0.86	3.30 \pm 0.75	3.33 \pm 0.79	0.033	F _{2,597} =1.292	0.275	
Sporophytes	3.19 \pm 0.90	3.16 \pm 0.75	3.28 \pm 0.67	0.043	F _{2,337} =0.626	0.535	
Male	3.46 \pm 0.82	3.17 \pm 0.71	3.14 \pm 0.54	0.061	F _{2,127} =2.824	0.063	
Female	3.10 \pm 0.74	3.83 \pm 0.53	3.75 \pm 1.16	0.080	F _{2,127} =10.446	<0.001	a)s; b)w, su
Apical width (mm)							
Total	1.23 \pm 0.42	0.94 \pm 0.35	1.26 \pm 0.43	0.018	F _{2,597} =31.245	<0.001	a)su; b)s, w
Sporophytes	1.21 \pm 0.51	0.86 \pm 0.36	1.19 \pm 0.38	0.025	F _{2,337} =18.448	<0.001	a)su; b)w, s
Male	1.24 \pm 0.33	0.94 \pm 0.16	1.45 \pm 0.48	0.036	F _{2,127} =21.494	<0.001	a)su; b)s; c)w
Female	1.25 \pm 0.25	1.13 \pm 0.43	1.25 \pm 0.46	0.033	F _{2,127} =1.370	0.258	
Branching angle							
Apical (°)							
Total	18.82 \pm 7.41	20.66 \pm 7.62	21.15 \pm 7.55	0.309	F _{2,597} =5.954	0.003	a)s; b)su, w
Sporophytes	19.38 \pm 7.35	20.55 \pm 7.59	20.78 \pm 7.41	0.403	F _{2,337} =1.297	0.275	
Male	14.93 \pm 4.57	21.60 \pm 7.91	18.58 \pm 6.91	0.622	F _{2,127} =10.157	<0.001	a)s; b)w; c)su
Female	20.12 \pm 8.31	19.70 \pm 7.43	25.50 \pm 7.05	0.710	F _{2,127} =7.071	0.001	a)su, s; b)w
Total	56.24 \pm 17.22	65.20 \pm 18.91	61.11 \pm 18.64	0.754	F _{2,597} =11.671	<0.001	a)s; b)w; c)su
Sporophytes	56.83 \pm 17.10	67.09 \pm 19.53	60.00 \pm 17.53	0.989	F _{2,337} =8.453	<0.001	a)s, w; b)su
Male	55.33 \pm 16.73	65.50 \pm 18.94	54.72 \pm 17.91	1.614	F _{2,127} =4.796	0.012	a)w, s; b)su
Female	55.47 \pm 18.06	59.77 \pm 16.63	72.45 \pm 18.25	1.680	F _{2,127} =11.150	<0.001	a)s, su; b)w

(Table 2 continued)

Parameter	Spring	Summer	Winter	MS _{error}	F	p	SNK
Cortical cells							
Length (μm)							
Total	41.03 \pm 10.37	41.59 \pm 9.98	40.48 \pm 9.35	0.405	$F_{2,597}=0.546$	0.580	
Sporophytes	44.64 \pm 9.53	44.57 \pm 9.95	42.92 \pm 9.15	0.515	$F_{2,337}=1.238$	0.291	
Male	37.90 \pm 9.40	37.19 \pm 6.48	37.08 \pm 8.59	0.721	$F_{2,127}=0.123$	0.885	
Female	34.67 \pm 9.21	39.51 \pm 11.40	37.43 \pm 8.84	0.857	$F_{2,127}=2.712$	0.070	
Total	15.78 \pm 3.41	15.85 \pm 3.43	16.06 \pm 3.09	0.135	$F_{2,597}=0.424$	0.655	
Sporophytes	16.15 \pm 3.35	16.18 \pm 3.62	16.94 \pm 3.28	0.185	$F_{2,337}=2.030$	0.133	
Male	15.11 \pm 3.87	15.47 \pm 3.41	14.42 \pm 2.22	0.279	$F_{2,127}=1.279$	0.282	
Female	15.35 \pm 3.17	15.47 \pm 2.91	15.47 \pm 2.41	0.252	$F_{2,127}=0.027$	0.973	
Total	17.87 \pm 3.65	16.34 \pm 2.77	14.56 \pm 2.35	0.137	$F_{2,597}=66.708$	<0.001	a)w; b)su; c)s
Sporophytes	18.33 \pm 3.60	17.08 \pm 2.83	14.88 \pm 2.47	0.185	$F_{2,337}=41.449$	<0.001	a)w; b)su; c)s
Male	16.30 \pm 3.87	15.17 \pm 2.13	13.80 \pm 2.04	0.257	$F_{2,127}=9.247$	<0.001	a)w; b)su, s
Female	17.85 \pm 3.38	15.95 \pm 2.81	14.58 \pm 2.17	0.284	$F_{2,127}=15.510$	<0.001	a)w; b)su; c)s
Medullary cells							
Length (μm)							
Total	96.91 \pm 22.30	88.73 \pm 18.89	95.56 \pm 22.05	0.883	$F_{2,597}=7.220$	<0.001	a)su; b)w; s
Sporophytes	99.42 \pm 24.07	90.20 \pm 21.04	99.88 \pm 22.15	1.247	$F_{2,337}=5.284$	0.006	a)su; b)s, w
Male	94.01 \pm 19.66	87.58 \pm 16.59	95.77 \pm 20.12	1.678	$F_{2,127}=2.208$	0.114	
Female	92.98 \pm 18.91	86.31 \pm 15.60	82.35 \pm 19.11	1.642	$F_{2,127}=4.264$	0.016	a)w, su; b)su, s
Total	62.75 \pm 11.06	58.40 \pm 6.68	61.43 \pm 12.10	0.477	$F_{2,597}=6.566$	0.002	a)su; b)w, s
Sporophytes	62.36 \pm 12.24	58.69 \pm 12.22	65.75 \pm 11.86	0.670	$F_{2,337}=8.267$	<0.001	a)su; b)s; c)w
Male	61.50 \pm 10.08	55.50 \pm 8.46	57.00 \pm 11.34	0.908	$F_{2,127}=3.840$	0.024	a)su, w; b)s
Female	64.50 \pm 8.42	61.50 \pm 13.27	54.00 \pm 7.44	0.918	$F_{2,127}=14.855$	<0.001	a)w; b)su, s
Total	82.16 \pm 16.62	75.00 \pm 14.42	82.64 \pm 12.57	0.616	$F_{2,597}=14.139$	<0.001	a)su; b)s; c)w
Sporophytes	82.50 \pm 19.20	77.62 \pm 14.06	87.43 \pm 10.63	0.859	$F_{2,337}=9.858$	<0.001	a)su; b)s; c)w
Male	83.30 \pm 9.35	62.77 \pm 9.33	77.11 \pm 14.42	1.244	$F_{2,127}=33.387$	<0.001	a)su; b)w; c)s
Female	80.60 \pm 13.71	84.33 \pm 9.92	75.21 \pm 8.64	1.046	$F_{2,127}=5.643$	0.004	a)w; b)s, su
Thickenings (number mm⁻²)							
Total	10.60 \pm 8.80	13.51 \pm 8.67	8.24 \pm 6.71	0.619	$F_{2,177}=5.577$	0.004	a)w, s; b)s, su
Sporophytes	9.12 \pm 9.26	12.17 \pm 6.15	7.53 \pm 5.16	0.739	$F_{2,99}=2.902$	0.060	
Male	18.08 \pm 7.39	11.83 \pm 5.62	7.27 \pm 3.67	1.138	$F_{2,36}=12.350$	<0.001	a)w; b)su; c)s
Female	9.06 \pm 5.84	19.33 \pm 14.62	11.58 \pm 11.69	1.729	$F_{2,36}=3.040$	0.060	

Groups include seasons (s=spring, su=summer and w=winter) that are not significantly different (SNK, $p<0.05$).

Table 3 *Dictyota dichotoma*: one-way analysis of variance on the effect of life-cycle phase on different vegetative parameters (mean±standard deviation) at Punta del Hidalgo (Canary Islands), April 2003–March 2004.

Parameter	Sporophytes	Male	Female	Non-fertile	MS _{error}	F	p	SNK
Thallus length (cm)	9.91±2.96	9.26±2.75	9.27±3.35	6.62±1.80	0.174	F _{3,303} =23.303	<0.001	a)nf; b)m, f, sp
Branches from main axes	14.43±3.67	15.20±3.75	15.26±3.80	11.01±2.67	0.218	F _{3,303} =20.066	<0.001	a)nf; b)sp, m, f
Interdichotomies								
Length (mm)	7.94±2.31	7.77±2.40	6.96±2.01		0.094	F _{2,597} =8.887	<0.001	a)f; b)m, sp
Width (mm)	3.21±0.79	3.25±0.70	3.47±0.92		0.033	F _{2,597} =4.924	0.008	a)sp, m; b)f
Apical width (mm)	1.12±0.46	1.23±0.41	1.22±0.37		0.018	F _{2,597} =4.566	0.011	a)sp; b)f, m
Branching angle								
Apical (°)	20.15±7.43	18.38±7.09	21.68±8.10		0.309	F _{2,597} =6.264	0.002	a)m; b)sp, f
Middle-basal (°)	60.36±18.23	58.22±18.40	61.68±19.15		0.754	F _{2,597} =1.177	0.309	
Cortical cells								
Length (µm)	44.02±9.50	37.37±8.22	36.63±9.77		0.405	F _{2,597} =42.113	<0.001	a)f, m; b)sp
Width (µm)	16.44±3.40	14.96±3.18	15.42±2.88		0.135	F _{2,597} =11.552	<0.001	a)m, f; b)sp
Height (µm)	16.81±3.41	14.99±2.93	16.40±3.24		0.137	F _{2,597} =14.589	<0.001	a)m; b)f, sp
Medullary cells								
Length (µm)	97.41±23.00	92.71±19.13	88.17±18.73		0.883	F _{2,597} =9.337	<0.001	a)f, m; b)sp
Width (µm)	62.69±12.36	57.92±10.36	60.58±10.47		0.477	F _{2,597} =8.245	<0.001	a)m; b)f, sp
Height (µm)	83.09±15.84	74.60±14.18	79.80±11.93		0.616	F _{2,597} =15.839	<0.001	a)m; b)f; c)sp
Thickenings (number mm ⁻²)	9.27±7.64	12.00±7.10	12.21±10.80		0.619	F _{2,177} =2.618	0.076	

Groups include life-cycle phases (sp=sporophytes, m=male gametophytes, f=female gametophytes, nf=non-fertile) that are not significantly different (SNK, $p < 0.05$).

onward in *Canistrocarpus*. It is only after gametes are shed that paraphyses divide in *Dictyota*, as some sort of secondary development (O. De Clerck and A. Tronholm unpublished results).

In Punta del Hidalgo, *Dictyota dichotoma* is present from winter to summer, with maximum abundance in the coldest part of the year. In autumn, the species disappears almost completely, but survives as microscopic resting stages. These observations may be correlated with the temperature range observed along the warm temperate northeastern Atlantic region, that varies between the winter isotherms of 10°C (north) and 20°C (south) (van den Hoek 1975, 1984). Both along continen-

tal European coasts and in the Canary Islands, maximal abundance occurs when seawater temperature is around 15°C. For northern populations, the favorable period is the warmest season and the resting period is a consequence of low winter temperatures (coldest season) (Hamel 1939, Stegenga and Mol 1983). In contrast, in the south, the favorable period is the coldest season and the resting period occurs during autumn (warmest season).

The bimodal distribution with two successive unequal peaks of abundance detected in the *Dictyota dichotoma* population studied may be correlated with at least three overlapping generations in which sporophytes and gametophytes are growing concurrently. The first gener-

Table 4 *Dictyota dichotoma*: one-way analysis of variance for effects of season on different reproductive parameters (mean±standard deviation) at Punta del Hidalgo (Canary Islands), April 2003–March 2004.

Parameter	Spring	Summer	Winter	MS _{error}	F	p	SNK
Sporangia							
Diameter (µm)	111.15±18.10	110.97±13.68	121.18±9.27	0.825	F _{2,337} =18.932	<0.001	a)su, s; b)w
Stalk cell height (µm)	20.04±4.22	18.12±4.54	15.67±3.47	0.242	F _{2,337} =37.695	<0.001	a)w; b)su; c)s
Male gametophytes							
Sori width (µm)	301.50±75.18	286.13±44.99	329.10±63.38	5.670	F _{2,127} =5.509	0.005	a)su, s; b)w
Sori length (µm)	480.75±107.79	480.38±81.84	513.60±87.39	8.180	F _{2,127} =1.959	0.145	
Rows of antheridia (number)	10.33±3.13	10.53±2.76	11.45±3.08	0.275	F _{2,117} =1.608	0.205	
Antheridia row length (µm)	403.13±109.50	399.38±87.71	423.00±89.43	8.747	F _{2,117} =0.699	0.499	
Antheridia row width (µm)	24.00±5.68	26.44±4.16	24.75±3.48	0.421	F _{2,117} =3.032	0.052	a)s, w; b)w, su
Central antheridia length (µm)	34.15±7.09	33.08±8.67	32.07±6.07	0.738	F _{2,97} =0.549	0.580	
Central antheridia width (µm)	25.23±5.54	26.42±5.33	27.01±5.43	0.540	F _{2,97} =0.725	0.487	
Antheridia height (µm)	84.07±14.82	84.37±14.04	87.29±13.90	1.298	F _{2,117} =0.620	0.540	
Antheridia stalk cell height (µm)	14.46±2.04	17.20±2.98	14.80±2.60	0.247	F _{2,127} =13.759	<0.001	a)s, w; b)su
Paraphyses height (µm)	97.22±12.18	87.64±10.21	91.92±14.16	1.133	F _{2,127} =5.951	0.003	a)su, w; b)w, s
Tiers (number)	32.10±25.26	36.20±16.55	40.60±20.02	1.920	F _{2,117} =1.652	0.196	
Loculi/tier (number)	19.55±8.16	23.55±7.01	24.50±3.43	0.777	F _{2,89} =3.939	0.023	a)s, su, w
Female gametophytes							
Sori width (µm)	237.00±45.61	229.00±72.31	243.38±70.48	5.303	F _{2,127} =0.481	0.619	
Sori length (µm)	337.25±67.28	318.00±100.92	338.25±72.21	6.797	F _{2,127} =0.741	0.479	
Oogonia/sorus (number)	29.33±11.46	30.17±7.33	42.80±7.12	0.980	F _{2,127} =27.181	<0.001	a)s, su; b)w
Central oogonia height (µm)	95.52±16.53	75.05±26.03	78.48±20.50	1.945	F _{2,127} =13.716	<0.001	a)su, w; b)s
Central oogonia diameter (µm)	62.20±16.93	53.79±15.66	52.28±16.79	1.560	F _{2,117} =4.638	0.012	a)w, su; b)s
Oogonia stalk cell height (µm)	16.40±4.31	16.07±2.02	20.12±8.47	0.555	F _{2,73} =3.152	0.049	a)su, s; b)w

Groups include seasons (s=spring, su=summer and w=winter) that are not significantly different (SNK, $p < 0.05$).

ation of macrothalli occurred in winter, when the population reached both maximum abundance and the highest number of fertile specimens (88.3%). The second and third generations grew throughout spring and summer, respectively. In summer, the species reached its optimum vegetative growth (maximum thallus length). Year-round overlapping generations have been observed also in *D. alternifida* J. Agardh and specimens attributed to *D. dichotoma* from South Australia by King and Farrant (1987). Temporal displacements in maximum abundance and thallus length have been reported also in other dictyotaleans, such as *Dictyopteris* Lamouroux, *Padina* Adanson and *Zonaria* Lamouroux species (King and Farrant 1987, Montañés et al. 2006). However, both peaks of abundance and thallus length occur simultaneously for specimens attributed to *D. dichotoma* from South Australia (in autumn–winter; King and Farrant 1987) and Korea (in summer; Hwang et al. 2005), and also for *Canistrocarpus cervicornis* (Kützinger) De Paula et De Clerck from the southern Red Sea (in winter; Ateweberhan et al. 2005, as *D. cervicornis*).

Dictyota dichotoma at Punta del Hidalgo (Canary Islands) is an aseasonal annual as defined by Lewis (1983). As indicated by the amplitude of successive waves in abundance of the species, lifespan of thalli seems to be less than 3 months, a consequence of seasonal changes in recruitment and mortality (Santos 1995, Arenas and Fernández 2000). In each month, sporophytes dominated the population, lending support to the hypothesis that reproduction in dictyotalean species is almost entirely by means of sporangia, with occasional sexual reproduction (Allender 1977, King and Farrant 1987, Womersley 1987, Phillips 1988, Mayhoub and Billard 1991, Hwang et al. 2005). Sporophytic dominance has been related to a direct development of apomeiotic tetraspores into new sporophytic thalli (apospory), non-random distribution patterns, greater longevity and vegetative reproduction of the sporophyte generation (Phillips 1988). However, life-cycle strategies (sexual vs. asexual cycle) vary among populations through the distribution area of a species. In *D. dichotoma sensu* Okamura from Korea, a dominant sexual life cycle occurs along the west coast, an exclusive asexual life cycle along the east coast, and both sexual and asexual reproduction occur on the south coast (Hwang et al. 2005). In the *D. dichotoma* population we studied, sexual reproduction has a relevant role, as gametophytes made up to 25% of the population. Additional studies are necessary to test whether changes in life-cycle patterns occur through the distribution area of *D. dichotoma* in the north Atlantic Ocean.

Most gametophytes collected near full and new moon had a high proportion of empty gametangia. The relation between gamete release and lunar cycle has been known for a considerable time in *Dictyota*. On European coasts, release occurs every fortnight (Williams 1905), monthly 6–7 days after full moon in North America (Hoyt 1927) and 11–12 days after full moon in southern Australia (Phillips 1988). Additional studies are necessary to determine whether specimens from the Canary Islands have the fortnightly behavior of the northernmost Atlantic populations.

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