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The section Digitatae of the genus *Laminaria* (Phaeophyta) in the northern and southern Atlantic: crossing experiments and temperature responses

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Abstract. Hybridization experiments between seven north and south Atlantic *Laminaria* species were carried out. Morphologically normal F_1 sporophytes developed from the following crosses among south Atlantic species: *L. pallida* × *L. schinzii*, *L. pallida* × *L. abyssalis* and *L. schinzii* × *L. abyssalis*. Normal F_1 sporophytes also resulted from the crosses *L. digitata* (north Atlantic) × *L. pallida* (south Atlantic) and *L. digitata* (north Atlantic) × *L. abyssalis* (south Atlantic). Hybrids between north Atlantic *L. ochroleuca* and south Atlantic *L. pallida*, *L. schinzii* and *L. abyssalis* and between north Atlantic *L. digitata* and south Atlantic *L. schinzii* initially developed as normal sporophytes but became deformed later on and further development was retarded. No hybrids resulted from attempted crosses between northeastern Atlantic *L. saccharina* and *L. abyssalis* from Brazil. Temperature tolerance, relative growth rates and temperature demands for gametogenesis revealed the existence of a warm temperate group within the digitate *Laminaria* species consisting of *L. ochroleuca*, *L. pallida*, *L. schinzii* and *L. abyssalis*. Hybridization experiments and temperature responses suggest that north Atlantic *L. digitata* and *L. ochroleuca* are still similar to south Atlantic *Laminaria* species, confirming the speculation that a transequatorial migration of a warm-temperate *L. ochroleuca*-like ancestor may have taken place.

Introduction

The digitate section of the genus *Laminaria* Lamouroux comprises eight species with a branched holdfast and *L. yezoensis* Miyabe with a discoid holdfast. In addition there are several species with an uncertain taxonomic position (Petrov and Vozzhinskaja 1970, Kain 1979). *L. setchellii* Silva and *L. bongardiana* Postels and Ruprecht (= *L. groenlandica* Rosenvinge *sensu* Druehl 1968; see Lüning and tom Dieck 1990) are confined to the north Pacific, *L. digitata* (Hudson) Lamouroux to the northern, western and eastern north Atlantic, while *L. hyperborea* (Gunnerus) Foslie and *L. ochroleuca* De la Pylaie grow only in the eastern north Atlantic with deep water populations of *L. ochroleuca* also occurring in the Mediterranean.

In the south Atlantic *Laminaria pallida* (Greville). J. Agardh and *L. schinzii* Foslie are present along the South African and Namibian coastline. Two species of *Laminaria* were reported in the western south Atlantic: *L. brasiliensis* Joly and Oliveira Filho with a divided blade and *L. abyssalis* Joly and Oliveira Filho with a simple blade. Both are restricted to an area off Rio de Janeiro and Espirito Santo provinces, at depths of 40 to 100 m (Oliveira and Quége 1978).

The north Atlantic species with the most southerly distribution limit, *Laminaria ochroleuca*, was originally considered to be conspecific with the South African *L. pallida* due to a rather similar morphology (Bornet 1892). Both have a stiff stipe, the blade is of a pale colour and no constriction between old and new blades exist. Van den Hoek (1982) hypothesized that *L. pallida* and *L. ochroleuca* are warm temperate sister species with an amphiequatorial distribution. *L. schinzii* is very similar to *L. pallida*, differing mainly from the latter by its hollow stipe (Foslie 1893) and by its more northerly distribution. Whereas *L. schinzii* is found up to Rocky Point (18°50′S) in Namibia (Anderson and Bolton 1985), the northernmost location for *L. pallida* is recorded at approximately 30°S (Bright 1938, Lüning 1990). The two species are difficult to distinguish in areas where they occur sympatrically (Bolton personal communication).

In the present investigation, hybridization studies between north and south Atlantic digitate *Laminaria* species were performed and the temperature demands for growth, survival and gametogenesis determined in order to obtain more parameters to characterize these species, which may also faciliate a future analysis of their ancestry.

Materials and methods

Few-celled gametophyte fragments of filamentous red-light grown gametophytes of the investigated *Laminaria* species (Table 1) were newly isolated and propagated. Techniques of gametophyte and sporophyte cultivation, hybridization, determination of relative growth rates, temperature tolerances of the sporophytes and rates of fertility of female gametophytes have been described elsewhere (tom Dieck 1992). All crosses were tested at least three times.

Table 1. *Laminaria* spp. Origin of *Laminaria* spp. gametophyte cultures used in the present investigation

Species	Code	Sex	Location	Culture number
L. abyssalis	ABY	m	Espirito Santo, Brazil	1291
		f		1292
L. digitata	DIG	m	Helgoland, Germany	1003
		f		1004
L. hyperborea	HYP	m	Helgoland, Germany	1001
		f		1002
L. ochroleuca	OCH	m	Roscoff, France	1262
		f		1263
L. pallida	PAL	m	Oudekraal, South Africa	1266
		f		1267
L. saccharina	SAC	m	Helgoland, Germany	1005
		f		1006
L. schinzii	SCH	m	Lamberts Bay, South	1264
		f	Africa	1265

Results

Hybridization

The results of attempted crossings between seven north Atlantic and south Atlantic *Laminaria* species, their maximum age and size of the F_1 sporophytes are given in Table 2.

Successful reciprocal crosses grown up to morphologically normal F_1 sporophytes were obtained between all three south Atlantic species, *Laminaria abyssalis*, *L. pallida* and *L. schinzii* (Figs. 1, 2).

Normal F_1 hybrid sporophytes were also obtained in reciprocal crosses of *Laminaria digitata* × *L. abyssalis* as well as in the crossing *L. pallida* male × *L. digitata* female (Fig. 3). The crossing *L. digitata* male × *L. pallida* female produced morphologically normal hybrid sporophytes up to an age of 4 mo and a size of 4 to 7 cm. Later on the blades lost their smoothness and their planar structure forming longitudinal thickenings, and the holdfast showed poor development in comparison to other species although these plants did not stop their blade growth.

The F_1 hybrid sporophytes which were formed by reciprocal crosses between *Laminaria digitata* and *L. schinzii*, *L. ochroleuca* and *L. pallida*, *L. ochroleuca* and *L. schinzii* as well as *L. ochroleuca* and *L. abyssalis* showed a normal development of the submacroscopic and early macroscopic sporophytic stage. After several

Table 2. *Laminaria* spp. Hybridization within seven species of *Laminaria* and the development of the F_1 sporophytes indicated as maximum age, maximum size and general morphology which was achieved during cultivation. ABY: *L. abyssalis*; DIG: *L. digitata*; HYP: *L. hyperborea*; OCH: *L. ochroleuca*; PAL: *L. pallida*; SCH: *L. schinzii*; SAC: *L. saccharina*. –: no development of normal microscopic and macroscopic sporophytes; S!: sori were formed; NT: crossing not tested; *: published in tom Dieck (1992)

Female	Male						
	ABY	DIG	HYP	OCH	PAL	SCH	SAC
ABY	6 mo 20 cm normal	9 mo 13 cm normal	–	3 mo 5 cm deformed	3 mo 5–10 cm normal	24 mo 60–90 cm normal	–
DIG	28 mo 40–80 cm normal	24 mo* 40–80 cm normal, S!	–*	–*	9 mo 30–40 cm normal	6 mo 10–30 cm normal	–*
HYP	–	3.5 mo 1–3 cm stunted	18 mo* 20 cm normal	–*	6 mo 1–3 cm stunted	6 mo 1–3 cm stunted	–*
OCH	2 mo 3 cm deformed	–*	–*	18 mo 40–50 cm normal	4 mo 10 cm deformed	4 mo 5–7 cm deformed	NT
PAL	22 mo 40 cm normal	9 mo 20 cm normal – deformed	6 mo 3–8 cm deformed	4 mo 5 cm deformed	21 mo 50 cm normal	21 mo 50 cm normal	NT
SCH	22 mo 40–60 cm cm	9 mo 10–20 cm deformed – normal	6 mo 3–7 cm stunted	4 mo 3–5 cm deformed	21 mo 50 cm normal	26 mo 50–70 cm normal	NT
SAC	–	–*	–*	NT	NT	NT	2 mo 2–3 cm normal

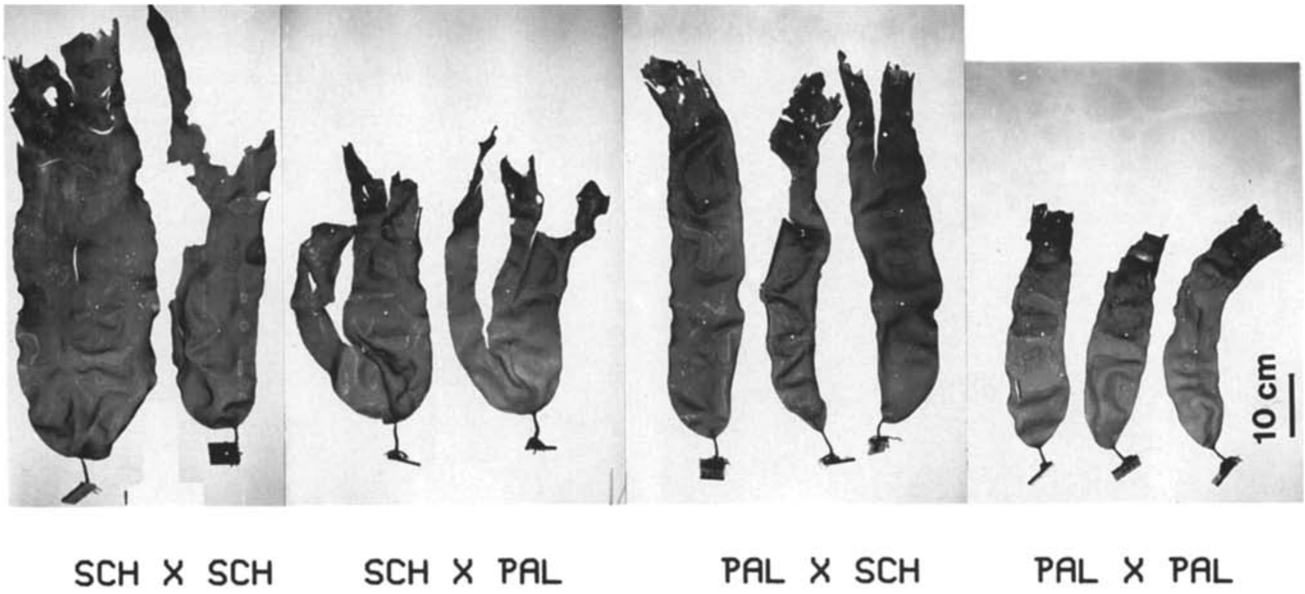

Fig. 1. *Laminaria pallida* and *L. schinzii*. 8-mo old single species and hybrid sporophytes resulting from crosses between *L. pallida* (PAL) and *L. schinzii* (SCH). First code denotes male parent

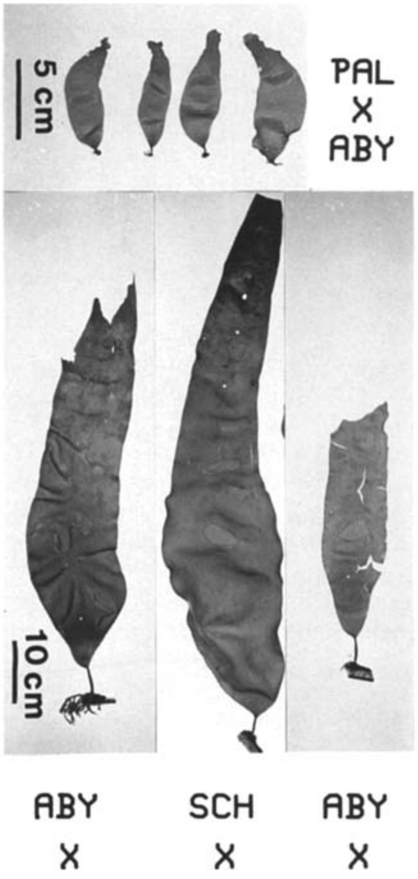

Fig. 2. *Laminaria abyssalis*, *L. pallida* and *L. schinzii*. Hybrid sporophytes resulting from crosses between *L. abyssalis* (ABY) and *L. pallida* (PAL) and *L. schinzii* (SCH). Upper row: 3-mo old sporophytes; lower row: 10-mo to 1-yr old sporophytes. First code denotes male parent

months the development of these hybrid sporophytes clearly differed from that of the respective single species sporophytes. Reduced growth was observed simultaneously with morphological changes such as the formation of thickened longitudinal or transverse bands on the blade or a thickening of the meristematic zone. These characteristics were not exhibited by either parthenogenetic sporophytes or single species sporophytes of the same age or older (Fig. 4).

Reciprocal crosses of *Laminaria hyperborea* with south Atlantic *L. abyssalis* were unsuccessful, and only stunted hybrid plants developed between *L. hyperborea* and *L. pallida* as well as *L. schinzii* after an initially normal development (Table 2). Attempted hybridization between the northeastern Atlantic *L. saccharina* (Linnaeus) Lamouroux and the single bladed Brazilian *L. abyssalis* were also unsuccessful (Table 2). Single species sporophytes of all investigated species however developed normally up to an age of 6 to 26 mo (Table 2).

All sporophytes obtained during this investigation (except *Laminaria digitata*; see tom Dieck 1992) never formed sori, either in continuous long day conditions or after a transfer to short day conditions. Thus no further generations were obtained.

Herbarium specimen of different developmental stages of all cultivated single species or hybrid sporophytes are kept at the Biologische Anstalt Helgoland, Hamburg in ItD's herbarium.

Observations on the morphology of the investigated species

None of the species studied developed a split blade during culture, even after several years of growth. In a few cases the blades were torn distally thereby creating splits.

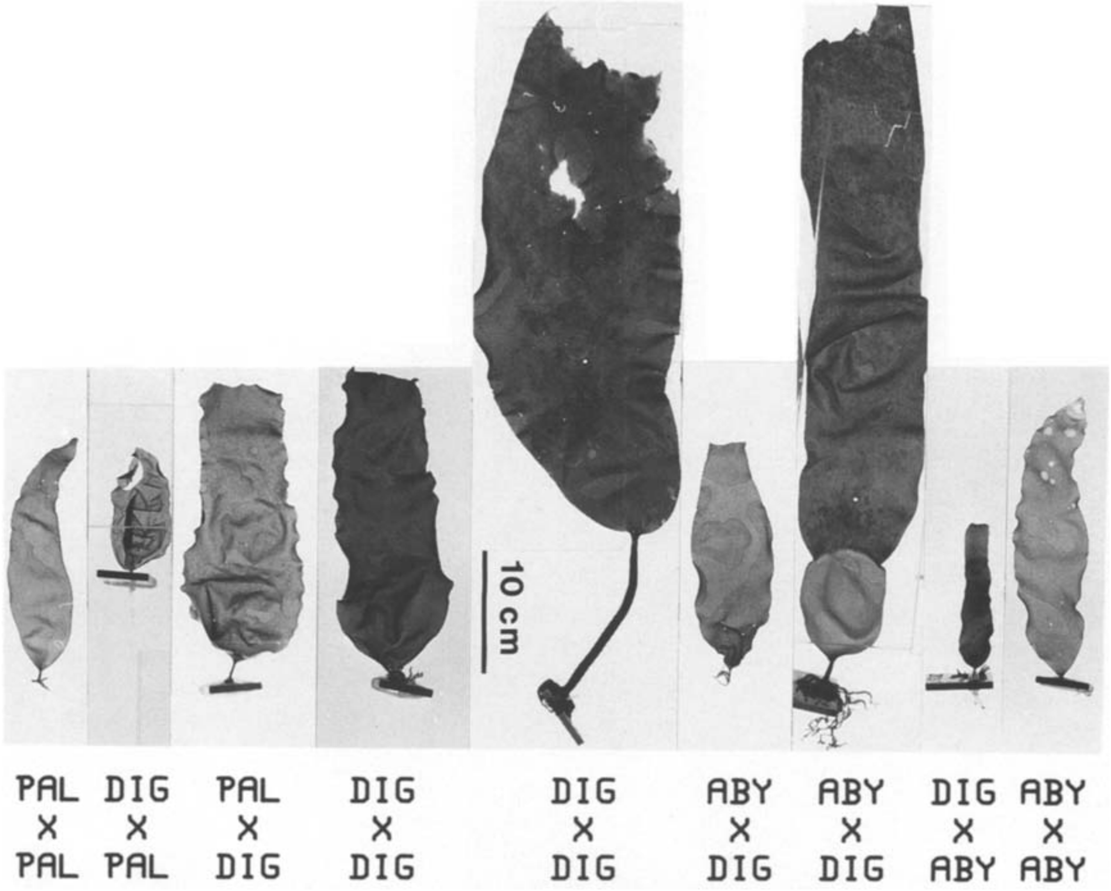

Fig. 3. *Laminaria pallida, L. digitata* and *L. abyssalis*. 6-mo old (small plants) and 2-yr old (big plants) single species and hybrid sporophytes resulting from crosses between *L. pallida* (PAL), *L. digitata* (DIG) and *L. abyssalis* (ABY). First code denotes male parent

Young sporophytes of *Laminaria abyssalis* of several cm length had a light brown colour and readily developed holdfasts. The base of the blade was cuneate in the submacroscopic, as well as in the juvenile macroscopic state.

The blade and stipe of *Laminaria pallida* and *L. schinzii* always had a light brown colour, even at an older age. Sometimes a thin colourless skin was shed from the stipe and the lower meristematic blade zone. The stipes and basal blades were thus always smooth and without epiphytes. The stipe of both species became stiff during the course of development. *L. schinzii* and *L. pallida* were in general of very similar appearance. The main difference was that *L. schinzii* grew larger and faster than *L. pallida*.

Observations on *Laminaria ochroleuca* and *L. hyperborea* are described elsewhere (tom Dieck 1992).

Relative growth rate and temperature tolerance of sporophytes

The relative growth rates of *Laminaria pallida, L. schinzii* and *L. abyssalis* and of hybrids between them are shown in Fig. 5 A to F. The upper (and lower) survival temperatures of single species sporophytes, hybrid sporophytes and parthenogenetic sporophytes are shown in Table 3. The temperature responses of the north Atlantic digitate species *L. ochroleuca, L. digitata* and *L. hyperborea* are given elsewhere (tom Dieck 1992).

The southern Atlantic species *Laminaria schinzii, L. pallida* and *L. abyssalis* grew well at temperatures up to 22 °C, optimally either between 15 and 20 °C (*L. abyssalis*) or between 10 and 15 °C (*L. schinzii* and *L. pallida*) and exhibited almost no growth at 0 °C (Fig. 5A to C). *L. abyssalis* did not even survive 0 °C for 2 wk and grew rather slowly at 5 °C (Fig. 5C). The upper survival temperature of these three species ranged between 22 and 24 °C.

The hybrid sporophytes from reciprocal crosses between *Laminaria abyssalis* and *L. schinzii* (Fig. 5 E), and from the crosses *L. pallida* male × *L. abyssalis* female (Fig. 5 F) and *L. ochroleuca* male × *L. abyssalis* female (Fig. 5 G) showed a wider temperature range for optimum growth and better temperature tolerance than the respective single species sporophytes. Hybrid sporophytes resulting from reciprocal crosses of *L. schinzii* and *L. abyssalis* survived 0 °C for 2 wk, a characteristic of *L. schinzii*. The range of optimum growth was 10 to 20 °C, increased by 5 °C in comparison to the single species sporophytes. The hybrids grew well at 22 °C and survived 24 °C, a characteristic of *L. abyssalis*. An increased growth optimum of 10 to 20 (22) °C and a maximum survival temperature of 24 °C in the crosses *L. pallida* male × *L. abyssalis* female and *L. ochroleuca* male × *L.*

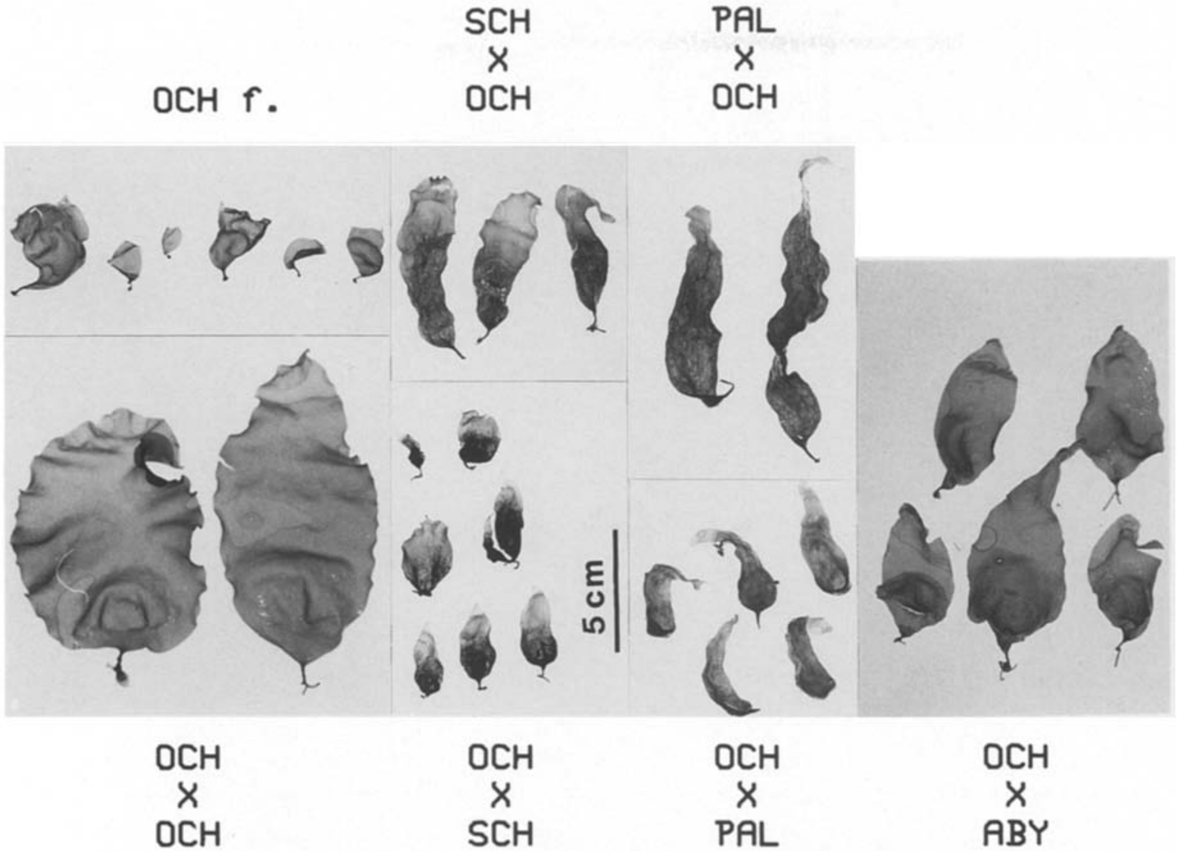

Fig. 4. *Laminaria ochroleuca*. 3- to 4-mo old parthenogenetic, single species and hybrid sporophytes. OCH f: parthenogenetically derived sporophytes of *L. ochroleuca*; OCH: *L. ochroleuca*; SCH: *L. schinzii*; PAL: *L. pallida*; ABY: *L. abyssalis*. First code denotes male parent

Table 3. *Laminaria* spp. Temperature tolerance of *Laminaria* spp. sporophytes determined after 2 wk exposure to the given temperatures. UST: upper survival temperature (°C); ABY: *L. abyssalis*; PAL: *L. pallida*; SCH: *L. schinzii*; OCH: *L. ochroleuca*; X: Plants alive; 1R–5R: One to five out of five experimental plants regenerated in post-cultivation conditions; –: plants dead

Male × female	0 °C	20 °C	21 °C	22 °C	23 °C	24 °C	25 °C	UST
ABY × ABY	–			X	X	X	–	24
PAL × PAL		X	X	5R	–	–		22
	–	X		1R	–	–		
SCH × SCH	5R	X		X	–	–		22/23
	5R	X		X	5R	–		
PAL × ABY	–	X		X	X	5R	–	24
SCH × ABY	–	X		X	5R	5R	–	24
	5R	X		X	X	5R	–	
ABY × SCH	X			X	X	5R	–	24
PAL × SCH	2R	X		5R	–	–		22
	–	X		X	–	–		
SCH × PAL	–	X		X	5R	–		23
	–	X		X	X	–		
OCH × ABY	–			X	5R	–		23
ABY female		X		5R	–	–	–	22

abyssalis female also implied an influence of *L. abyssalis*. The hybrids from reciprocal crosses between *L. pallida* and *L. schinzii* showed an increased growth optimum (Fig. 5 D) in comparison to the single species sporophytes (Fig. 5 A and B), but no differences in temperature tolerance (Table 3).

The upper temperature tolerance of parthenosporophytes of *Laminaria abyssalis* was reduced by 2 °C in comparison to the single species sporophytes (Table 3).

The relative growth rates of north Atlantic *Laminaria digitata*, *L. ochroleuca* and *L. hyperborea* have been described in tom Dieck (1992).

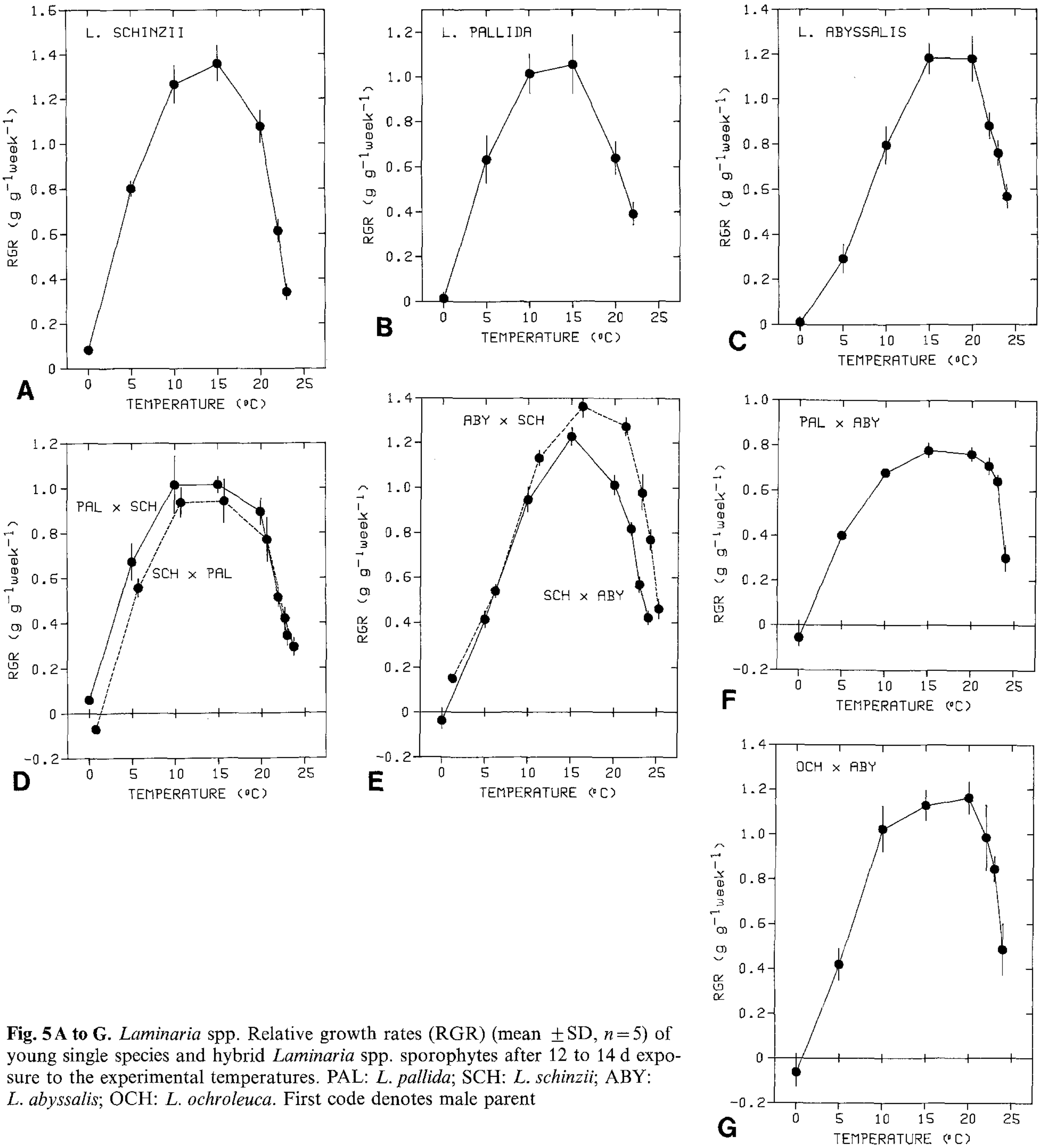

Fig. 5A to G. *Laminaria* spp. Relative growth rates (RGR) (mean ±SD, $n=5$) of young single species and hybrid *Laminaria* spp. sporophytes after 12 to 14 d exposure to the experimental temperatures. PAL: *L. pallida*; SCH: *L. schinzii*; ABY: *L. abyssalis*; OCH: *L. ochroleuca*. First code denotes male parent

Fertility of gametophytes

The fertility of filamentous female gametophytes of *Laminaria pallida*, *L. schinzii* and *L. abyssalis* at four different temperatures and six different photon fluence rates, respectively, is shown in Fig. 6.

Laminaria pallida easily became fertile at 5, 11 and 17 °C, but not at 21 °C. Maximum rates of fertility of 85 to 100% were obtained at 11 °C at a photon fluence rate of 9 to 93 µmol m^{-2} s^{-1} and at 17 °C at a photon fluence rate of 9 to 41 µmol m^{-2} s^{-1}.

Laminaria schinzii showed maximum fertility of 82 to 100% at 11 °C at a photon fluence rate of 2 to 93 µmol m^{-2} s^{-1} and at 17 °C at a photon fluence rate of 4.5 to 41 µmol m^{-2} s^{-1}. At 5 and 21 °C the fertility was reduced considerably, and no sporophytes were formed at 21 °C.

Laminaria abyssalis did not become fertile at 5 °C and only at a reduced rate at 21 °C. No sporophytes were formed at 21 °C. Maximum fertility of 98% occurred at 17 °C at a photon fluence rate of 19 µmol m^{-2} s^{-1}.

All gametophytes were either damaged or killed in high photon fluence rates of 93 (to 19) µmol m^{-2} s^{-1}, depending on the temperature applied (Fig. 6).

The temperature and light dependency of gametophyte fertility of *Laminaria digitata*, *L. hyperborea* and *L.*

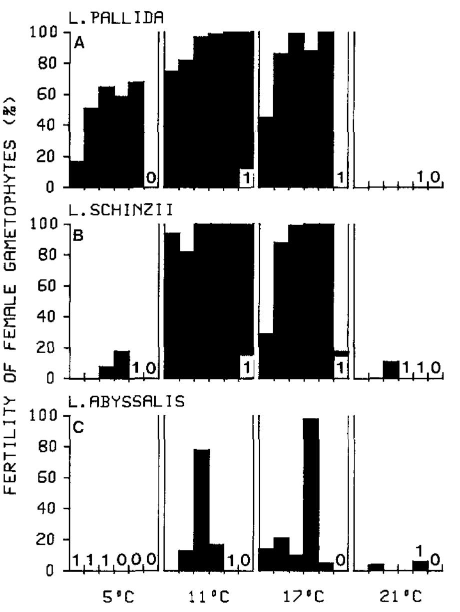

Fig. 6. *Laminaria pallida*, *L. schinzii* and *L. abyssalis*. Fertility of female gametophytes of three *Laminaria* species at four temperatures and six photon fluence rates after 4 wk. Photon fluence rates at each temperature are 2, 4.5, 9, 19, 41, 93 µmol m^{-2} s^{-1} (from left to right). 0: dead; 1: many gametophytes damaged

ochroleuca has been described elsewhere in comparison to related north Pacific species (tom Dieck 1992).

Discussion

Successful hybridization up to the F$_1$ sporophyte generation of the three south Atlantic *Laminaria* species and of north Atlantic *L. digitata* with south Atlantic *L. abyssalis* and *L. pallida* indicate that there is still a close genetic relationship among them in this characteristic. Partial hybridization was also possible between north Atlantic *L. ochroleuca* and south Atlantic *L. pallida*, *L. schinzii* and *L. abyssalis*, which initially formed normal hybrid sporophytes that became slightly abnormal after several months.

This hybridization success between north and south Atlantic species is in contrast to crossing experiments which were carried out between north Atlantic and north Pacific digitate *Laminaria* species. None of the possible combinations between north Pacific *L. setchellii*, *L. bongardiana* (= *L. groenlandica sensu* Druehl 1968; see Lüning and tom Dieck 1990), and north Atlantic *L. hyperborea*, *L. digitata* and *L. ochroleuca* provided a viable hybrid sporophytes (tom Dieck 1992). This again was astonishing, as in the section Simplices of the genus *Laminaria* successful crossbreeding resulted in adult F$_1$ hybrid sporophytes between north Atlantic and north Pacific *L. saccharina* (L.) Lamouroux and between north Atlantic *L. longicruris* Bach. Pylaie and *L. ochotensis* Miyabe from Japan (Bolton et al. 1983).

The interpretation of the hybridization experiments of the present study mainly relies on the definition of more or less normal hybrid sporophytes. Clear evidence of interfertility is only obtained when the sporophytes are cultured to fertility and a meiosis is checked, at best in nature. To avoid contamination of the North Sea with foreign species the sporophytes of this investigation were not cultured in the sea at the Helgoland marine biological station, but rather under controlled laboratory conditions. Induction of sori of *Laminaria* spp. in culture, however, is only possible in *L. saccharina* and in *L. setchellii* (Lüning 1988, tom Dieck 1991) and not yet in the other investigated *Laminaria* species. Therefore the morphological criterion of 'normal hybrid sporophytes' was used to evaluate the hybridizational success. 'Normal' in this context means that the hybrid sporophytes developed a blade, stipe and holdfast morphologically similar to the cultured single species sporophytes and different from parthenogenic sporophytes, i.e., with a smooth blade surface, a plane meristematic region and continuous growth at least during the first year. All crosses were initiated under conditions that were good for the respective species, i.e., optimum temperature and light intensity for gametogenesis and high nutrient supply (tom Dieck 1992). To judge the hybridizational success the early development of single species-, hybrid- and parthenogenetic sporophytes was simultaneously observed. In all successful crosses the morphological and chronological development was similar to the single species sporophytes. An extreme example of disturbance of hybrid sporophyte development that was different from the development of parthenogenetic sporophytes and thus was regarded as unsuccessful hybridization was shown by tom Dieck (1992) for hybrids resulting from crosses between north Atlantic *L. hyperborea* and north Pacific *L. setchellii*. These hybrid sporophytes initially developed normally but subsequently became stunted showing no further increase in length.

The survival time under culture conditions as indicated in Table 2 is additional evidence of hybridizational success. In all attempted crosses which were unsuccessful the hybrid sporophytes survived a much shorter time than the respective single species sporophytes and showed abnormal morphology. In all attempted crosses which were successful, however, the hybrids had similar survival rates than the respective single species sporophytes with exception of *Laminaria abyssalis*. The low survival rate of *L. abyssalis* seems to be a result of inappropriate culture conditions in the tank system. The initial development of *L. abyssalis* in unialgal culture conditions was, however, normal and comparable to the other single species sporophytes and to hybrid sporophytes. The same is valid for *L. saccharina*.

In general, interfertility among related brown algae should only be used with care for species delimitation. It was shown in several cases that crossability is not an all-or-nothing criterion (e.g. Saito 1972, Stache 1990, tom Dieck 1992), and F$_1$ hybrids were also obtained between well defined morphological species or genera (e.g. Sanbonsuga and Neushul 1978, Mathieson et al. 1981, Coyer et al. 1992). Perhaps this paradox in brown algae could be resolved if the phylogenetic species concept instead of the biological species concept were applied. Cracraft (1989) demonstrated the empirical consequences of alternative species concepts. He emphasized that hybridization among taxa does not necessarily imply that they are sister species. According to Cracraft hybridization may take place among taxa separated by at least two speciation events.

The results of the crossing experiments in *Laminaria* spp. presented here in combination with the temperature responses and distribution data of the species may have implications for the taxonomy of the genus. In the case of the species pair *L. ochroleuca*/*L. pallida* the results do not provide sufficient evidence for assuming that *L. ochroleuca* is an amphiequatorial species (van den Hoek 1982) comprising the South African *L. pallida*. The reduced hybridization capacity of *L. ochroleuca* with *L. pallida* (Table 2) and the distinct growth responses (Fig. 5 B present study and tom Dieck 1992) and temperature range of gametogenesis (Fig. 6 present study and tom Dieck 1992) add to the morphological and ecological differences in addition to the geographical disjunction. *L. pallida* gametophytes easily become fertile at 5 °C while *L. ochroleuca* gametogenesis is inhibited at 5 °C and gametophytes only survive at low photon fluence rates at this temperature. The growth optimum of *L. pallida* is at 10 to 15 °C, but that of *L. ochroleuca* at 15 to 20 °C. The growth at 5 °C is very slow in *L. ochroleuca* in contrast to *L. pallida.* Both species, however, have the same temperature tolerance: sporophytes died at 0 and 23 °C (Table 3 present study and tom Dieck 1992) and gametophytes at 25 °C (tom Dieck 1989).

The distinction between *Laminaria pallida* and *L. schinzii*, two morphologically similar, partly sympatric species, is not so clear. The two species hybridize easily and F_1 sporophytes were cultivated up to an age of 21 mo (Table 2). Furthermore, the relative growth rate and morphology of both species in culture is very similar (Figs. 5 A, B). Both have a stiff stipe, a yellowish-brown colour of the blade and stipe, and show an epidermal shedding of the stipe and proximal blade. The main difference of the two isolates is the faster growth rate of *L. schinzii* in contrast to *L. pallida* resulting in longer and broader plants of *L. schinzii* after the same cultivation time and in the same cultivation conditions (Fig. 1). Another difference is the slightly higher temperature tolerance of *L. schinzii* (Table 3). But as only one isolate of each species was tested, these differences may be ecotypic attributes. In nature, adult plants of *L. schinzii* have a hollow stipe in contrast to *L. pallida* (Foslie 1893). However, at some places along the western coast of South Africa hollow-stiped plants and solid-stiped plants grow side by side and are outwardly indistinguishable (J. Bolton personal communication). It is therefore likely that *L. pallida* and *L. schinzii* are conspecific. Further studies are required to determine the taxonomic importance of the hollow-stipe criterion in these species. In the section Simplices, north Atlantic *L. longicruris* and *L. saccharina* are mainly distinguished by the presence or absence of hollow stipes. Chapman (1973, 1974) found a clinal relationship with the occurrence of long, hollow stipes increasing with decreasing exposure. Furthermore *L. saccharina* and *L. longicruris* proved to be interfertile (Chapman 1974, Lüning et al. 1978, Bolton et al. 1983), both results suggesting conspecifity. A similar situation may exist in *L. pallida* and *L. schinzii.*

Laminaria abyssalis was originally described as a Simplices species (Joly and Oliveira 1967), but is included in the Digitatae section in the present publication for the following reasons: (1) *L. abyssalis* hybridized with *L. pallida, L. schinzii, L. digitata* and partly with *L. ochroleuca*, all digitate species, but not with northeastern Atlantic *L. saccharina* of the Simplices section. (2) The shape of young, several mm long blades cannot be used to discriminate the two Brazilian species as proposed by Yoneshigue and Oliveira (1987). According to these authors young blades of *L. brasiliensis* are cuneate, but cordate in *L. abyssalis*. The *L. abyssalis* gametophytes used in the present investigation originally were isolated from a plant with blades which were not split. But young sporophytes of this isolate always developed a cuneate base (microscopic and macroscopic young plants) during this investigation (Fig.3), whereas young *L. brasiliensis* plants described by Oliveira (1978) had a cuneate to cordate base of the blade. This variability either indicates that blade base morphology of young plants is not a good characteristic or that the two Brazilian species are a single species. (3) According to preliminary biometric measurements of digitate and non-digitate plants within the Brazilian distribution area, it was not possible to discriminate two *Laminaria* species (Quége 1988). Therefore it is probable that *L. abyssalis* and *L. brasiliensis* are conspecific. A re-definition of the Digitatae section, including species that do not obligatorily form digits in the blade as *L. abyssalis*, is however not meaningful until the conspecifity of the two Brazilian species is demonstrated beyond doubt.

There are only a few examples where hybrid or parthenogenic sporophytes within the Laminariales were investigated physiologically in comparison to the single species sporophytes. In the present investigation the relative growth rates of the hybrid sporophytes had a broader optimum growth range (ca. 5 °C) than the respective single species sporophytes (Fig. 5). The temperature tolerance of the hybrids was either equivalent to the more tolerant parent or intermediate to both parents. In contrast, parthenogenic sporophytes of *Laminaria abyssalis* (present study), *L. digitata*, *L. ochroleuca* and *L. setchellii* (tom Dieck 1992) had a 1 to 2 °C lower temperature tolerance than the single species sporophytes. Hybrids between *L. schinzii* and *L. abyssalis* had a 1 to 2 °C broader survival range than both parents. In all other cases the survival range of the hybrids was equivalent to the more tolerant parent. This was even true for the hybrids resulting from crosses between *L. ochroleuca* male × *L. abyssalis* female, which became morphologically deformed during their further development. This indicates that temperature tolerance is not linked to sex. A comparable growth characteristic is known from single species and hybrid sporophytes of *Ecklonia maxima* (Osbeck) Papenfuss and *E. biruncinata* (Bory) Papenfuss (Bolton and Anderson 1987). *E. biruncinata* and the hybrids survived 26 °C in contrast to *E. maxima*. The optimum range of growth was not increased but slightly narrower with intermediate optimum temperatures. A similar effect was observed in hybrids of different *Ectocarpus siliculosus* (Dillw.) Lyngbye strains (Bolton 1983).

The relative growth rates, temperature tolerances and in part also the temperature range of gametogenesis of the north Atlantic *Laminaria ochroleuca* (tom Dieck 1992) and of the three south Atlantic species (Fig. 5 A to C, Fig. 6, Table 3) all show a warm temperate character with sporophytic survival temperatures of 22 to 24 °C, optimum growth temperatures of 10 to 20 °C and little growth or mortality at 0 °C. Upper survival temperatures of the gametophytes are even 2 to 3 °C higher than of sporophytes (tom Dieck 1989), and gametogenesis is greatly inhibited at 5 °C with the exception of *L. pallida.* This temperature characteristic is in accordance with the speculation of van den Hoek (1982) that a warm temperate *L. ochroleuca*-like species probably crossed the equator during times of glaciation when the warm equatorial belt was small. The fact that *L. digitata* demonstrates a better hybridization capability with the south Atlantic species than *L. ochroleuca,* but is less adapted to warm conditions, should not be used to infer evolutionary relationships as the ability to interbreed is considered to be a plesiomorphic condition (Rosen 1979, Lindström 1987). The conjecture resulting from the present investigation that either a more warm-adapted ancestor of *L. digitata* or a common ancestor of *L. ochroleuca* and *L. digitata* might have crossed the equator is not in accordance with the radiation scenario and the calculated divergence time from single-copy DNA-DNA hybridization for *L. digitata, L. hyperborea, L. ochroleuca, L. saccharina* and *L. rodriguezii* Bornet (Stam et al. 1988). These authors suggest that a radiational burst of the five north Atlantic and Mediterranean *Laminaria* species took place in the north Pacific from their most recent common ancestor about 15 to 19 × 10^6 yr ago. Their hypothesis implies that all five species should have close relatives in the north Pacific from which they diverged after entering the north Atlantic during times of the first inundation of the Bering land bridge (3.5 × 10^6 yr ago). Incidently it is not possible to identify a morphologically and ecophysiologically related species to *L. ochroleuca* in the north Pacific (tom Dieck 1992). Thus, this species either became extinct, or the radiational burst of the *Laminaria* species investigated by Stam et al. (1988) took place more recently in the north Atlantic. Stam et al. (1988) pointed out that the interpretation of actual divergence times must be considered as a working hypothesis until there is more knowledge about the reliability of the molecular clock.

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