

Temperature tolerance and survival in darkness of kelp gametophytes (Laminariales, Phaeophyta): ecological and biogeographical implications

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ABSTRACT: Filamentous red-light grown gametophytes of 47 species of the Laminariales, i.e. about 50% of all species of the order, were tested for upper survival temperature (UST; 2 wk exposure), and 42 of these species were tested for lower survival temperature (LST; 8 wk exposure). The lowest UST in the order is 19 to 20°C, encountered in the Arctic to cold-temperate species *Laminaria solidungula*, *Alaria esculenta* and *Agarum cribrosum*. The warm temperate Japanese species *Eisenia bicyclis* and *Undaria pinnatifida* have the highest UST of 28 to 30°C. The UST range in the order Laminariales, thus, spans about 10°C. This is about 5°C less than in the related order Desmarestiales which spans a range in UST of 15°C. The largest within-family variation in UST is found in the Alariaceae and Laminariaceae, the 2 families with most species and widest distribution. The Alariaceae span a range in UST of 10°C, the Laminariaceae of 7 to 8°C, the Lessoniaceae of 5 to 6°C, the Phyllariaceae of 4°C and the Chordaceae of 3 to 4°C. All gametophytes tested survive a temperature of 1°C for 8 wk. Eleven out of 42 species do not tolerate -1.5 and/or 0°C over 8 wk. Temperature tolerance of the gametophytes coincides with the large-scale distribution of the species, but is not crucial for distribution limits in most cases. In addition to the temperature tolerance, the dark tolerance of filamentous gametophytes of 12 kelp species was investigated. All but 3 species survived 18 mo of darkness.

INTRODUCTION

In recent years temperature tolerance and temperature responses of growth and reproduction have been experimentally determined in many marine macroalgal species (e.g. Lüning 1984, Cambridge et al. 1987, Guiry et al. 1987, Lüning & Freshwater 1988, Wiencke & tom Dieck 1989, 1990, Orfanidis 1991, Peters & Breeman 1992, 1993). The main purpose of these investigations was to answer questions in ecological and historical biogeography, as well as a general interest in autecology (e.g. van den Hoek 1982, Breeman 1988, van den Hoek & Breeman 1990).

During these investigations, thermal ecotypes have mostly been detected in species with a tropical to temperate distribution area but seldom in species with a temperate distribution area. Generally, temperature tolerance did not vary to the same extent as temperature effects on growth and reproduction (review: Breeman 1988). It was hypothesized that temperature

tolerance is a rather conservative character (Lüning & Freshwater 1988). As such, it is utilized in phylogenetic considerations.

Despite the large numbers of temperature tolerance studies the knowledge of the variation range of this parameter within algal orders is scarce. The purpose of this study was to test the upper survival temperature of as many species of the Laminariales as possible including those which grow in the most extreme temperature environments known for this order. Furthermore, it was to evaluate whether this character is as variable as the biogeographical distribution range from Arctic to warm temperate waters and the great morphological diversity of the order suggest.

MATERIAL AND METHODS

Temperature tolerance. The investigated Laminariales species are listed in Table 1. Temperature

Table 1. List of Laminariales gametophytes used in temperature tolerance and darkness survival tests. Locations: Aus = Victoria, Australia; Bam1, Bam2 = Bamfield, Canada; Bra = Espirito Santo, Brazil; Bri = Roscoff, Brittany, France; Cal = California, USA; Cal1 = Pillar Point, California, USA; Cal2 = Santa Barbara, California, USA; Chi1 = Mehuin, Valdivia, Chile; Chi2 = Mar Brava, Chiloé, Chile; Far = Faeroe Islands; Hok = Hokkaido, Japan; Hax = Halifax, Canada; Hel = Helgoland, North Sea, Germany; Icl = Tjórnes, Iceland; Iglo = Igloolik, Canada; IOM = Isle of Man; Irl = Ireland; Irl1 = Branock Isl., Ireland; Jap = Japan; NewZ = New Zealand; Nfl = Newfoundland, Canada; SAfr1 = Oudekraal, Cape Peninsula, South Africa; SAfr2 = Lamberts Bay, South Africa; Tasm1 = Tinderbox Bay, Tasmania, Australia; Tasm2 = Safety Cove, Tasmania, Australia. Culture numbers = male and female gametophyte respectively

Species		Location	Culture number
Laminariaceae, genus <i>Laminaria</i>			
<i>L. abyssalis</i>	Joly & Oliveira Filho	Bra	1291/1292
<i>L. angustata</i>	Kjellman	Hok	1035/1036
		Jap	1227/1228
<i>L. bongardiana</i> ^a	Postels & Ruprecht	Bam1	1204/1205
		Bam2	1109/1110
<i>L. coriacea</i>	Miyabe	Jap	1223/1224
<i>L. diabolica</i>	Miyabe	Jap	1225/1226
<i>L. digitata</i>	(Hudson) Lamouroux	Hel	1003/1004
<i>L. ephemera</i>	Setchell	Bam	1120
<i>L. farlowii</i>	Setchell	Cal2	1053/1054
<i>L. hyperborea</i>	(Gunnerus) Foslie	Hel	1001/1002
<i>L. japonica</i>	Areschoug	Hok	1029/1030
<i>L. longicuris</i>	Bach. Pylaie	Far	1145/1146
<i>L. longissima</i>	Miyabe	Hok	1037/1038
<i>L. ochroleuca</i>	De la Pylaie	Bri	1262/1263
<i>L. pallida</i>	(Greville) J. Agardh	SAfr1	1266/1267
<i>L. religiosa</i>	Miyabe	Jap	1231/1232
<i>L. saccharina</i>	(Linnaeus) Lamouroux	Hel	1005/1006
		IOM	1007/1008
<i>L. schinzii</i>	Foslie	SAfr2	1264/1265
<i>L. setchellii</i>	Silva	Bam	1212/1213
<i>L. sinclairii</i>	(Harvey ex Hooker f. & Harvey)	Cal1	1047/1048
	Farlow, Anderson & Eaton		
<i>L. solidungula</i>	J. Agardh	Iglo	1099/1100
Laminariaceae (except genus <i>Laminaria</i>)			
<i>Agarum cribrosum</i>	(Mertens) Bory	Iglo	1105/1106
<i>Costaria costata</i>	(Turner) Saunders	Jap	1239/1240
<i>Cymathere triplicata</i>	(Postels & Ruprecht) J. Agardh	Bam	1125/1126
<i>Kjellmaniella crassifolia</i>	Miyabe	Jap	1241/1242
<i>K. gyrate</i>	(Kjellman) Miyabe	Jap	1255/1256
<i>Pleurophycus gardneri</i>	Setchell & Saunders	Bam	1223/1224
Alariaceae			
<i>Alaria crassifolia</i>	Kjellman	Jap	1251/1252
<i>A. esculenta</i>	(Linnaeus) Greville	Icl	1019/1020
<i>A. marginata</i>	Postels & Ruprecht	Cal1	1049/1050
<i>Ecklonia radiata</i>	(C. Agardh) J. Agardh	Aus	1193/1194
		Tasm1	1253/1254
<i>Eisenia arborea</i>	Areschoug	Bam	1208/1209
<i>E. bicyclis</i>	(Kjellman) Setchell	Jap	1237/1238
<i>Pterygophora californica</i>	Ruprecht	Bam	1129/1130
<i>Undaria pinnatifida</i>	(Harvey) Suringar	Hok	1041/1042
Lessoniaceae			
<i>Dictyoneuropsis reticulata</i>	(Saunders) G. M. Smith	Cal	1163/1164
<i>Lessonia corrugata</i>	Lucas	Tasm2	1257/1258
<i>L. nigrescens</i>	Bory	Chi1	1245/1246
<i>L. trabeculata</i>	Villouta & Santelices	Chi2	1247/1248
<i>Macrocystis angustifolia</i>	Bory	Aus	1259/1260
<i>M. integrifolia</i>	Bory	Bam	1135/1136
		Cal	1155/1156
<i>M. pyrifera</i>	(Linnaeus) C. Agardh	Cal	1159/1160
		NewZ	1182/1183
<i>Nereocystis luetkeana</i>	(Mertens) Postels & Ruprecht	Cal	1206/1207
<i>Pelagophycus porra</i>	(Leman) Setchell	Cal	1161/1162
Chordaceae			
<i>Chorda filum</i>	(Linnaeus) Stackhouse	Irl	1195/1196
<i>C. tomentosa</i>	Lyngbye	Hel	1261
Phyllariaceae			
<i>Saccorhiza dermatodea</i>	(Bach. Pylaie) J. Agardh	Nfl	1190
<i>S. polyschides</i>	(Lightfoot) Batters	Irl1	1191/1192

^a*L. groenlandia* sensu Druehl (1968)

tolerance of filamentous red-light grown gametophytes was determined in glass tubes (55 mm high, 25 mm diameter) with plastic, nontransparent lids filled with 20 ml von-Stosch-enriched autoclaved seawater (VSES: modified after Guiry & Cunningham 1984, iodide enrichment after Tatewaki 1966). The glass tubes were immersed in temperature-controlled Haake D8-V water baths (variation $\pm 0.1^\circ\text{C}$) for 2 wk (upper temperature tolerance) or 8 wk (lower temperature tolerance). The upper temperature tolerance was determined in steps of 1°C and the tests were carried out 2 to 4 times. The lower temperature tolerance was tested at -1.5 , 0 and 1°C and the tests were usually repeated once. The gametophytes were inoculated in the test tubes without prior acclimatization to elevated or reduced temperatures. The gametophyte stock cultures were maintained at 10°C , except for *Laminaria solidungula*, *Saccorhiza dermatodea*, *Alaria esculenta* and *Agarum cribrosum* which were maintained at 1°C . A photon fluence rate of $30 \mu\text{mol m}^{-2} \text{s}^{-1}$ at the surface of the water baths was provided by fluorescent white light (Osram L 20W/19, Daylight de Luxe) for 12 h d^{-1} . The cultures received fresh prewarmed medium twice a week during the test period. The survival limits were determined after a postculture of 4 wk in Provasoli's enriched seawater (PES; Provasoli 1968) at 10°C and $16 \text{ h light d}^{-1}$ at photon fluence rates lower than $20 \mu\text{mol m}^{-2} \text{s}^{-1}$. The survival temperature was defined as that temperature at which living cells could be detected under the microscope after postcultivation. Part of the experiments was also conducted by using an automatic test system described by Lüning et al. (1987).

Dark tolerance. Dark tolerance of filamentous red-light grown gametophytes of 12 Laminariales species was qualitatively determined over a period of 18 mo. Similar amounts of thalli of female and male gametophytes of each species were inoculated in glass tubes (55 mm high, 25 mm diameter) with nontransparent plastic lids, filled with 20 ml PES and placed in darkness. The temperature was 0 or $8 (\pm 1)^\circ\text{C}$. Each month 1 tube of each species was transferred to white fluorescent light ($16 \text{ h light d}^{-1}$), while the remaining tubes were provided with fresh medium and then put back into darkness. Thus, the dark cultures were subjected to light once a month for about 10 min.

Survival was established after 1 or 2 mo in postcultivation conditions (Table 4). If the gametophytes were still vegetative after 1 mo they were further cultivated in most cases. Gametophytes were examined under the microscope. Resumed growth of gametophytes or formation of sporophytes was considered as recovery.

RESULTS

Temperature tolerance

The upper and lower temperature tolerance of filamentous gametophytes of 47 species of Laminariales after 2 wk exposure to the experimental temperatures is shown in Table 2. There was a difference in upper survival temperature (UST) of 10°C within all tested species of the order Laminariales. The lowest UST was 20°C (*Laminaria solidungula*, *Agarum cribrosum*, *Alaria esculenta*) while the highest UST was 30°C (*Eisenia bicyclis* from Japan). Of the Laminariaceae 26 species were tested, comprising about 50% of the species of this family. They exhibited a range in UST of 7°C , from 20 (*L. solidungula*) to 26 – 27°C (*L. japonica*, *Costaria costata*). Within the Alariaceae 8 species were tested, comprising about 25% of the species of this family. Their range in UST varied between 20 (*A. esculenta*) and 30°C (*E. bicyclis*), i.e. a 10°C difference as in the whole order Laminariales. The 2 species of the Chordaceae survived 24 to 25 (*Chorda tomentosa*) and 27 to 28°C (*C. filum*), i.e. a 3 to 4°C difference in the family. Within the Lessoniaceae 9 species were tested, which is about 55% of the species of the family. Their UST ranged from 22 to 23 (*Dictyonopsis reticulata*) to 26°C (*Macrocystis pyrifer*), a 4°C difference in upper temperature tolerance for this family. Two out of the 4 species of the Phyllariaceae were tested. Their UST were 21 (*Saccorhiza dermatodea*) and 24°C (*S. polyschides*).

Usually there was a difference in UST of 0 or 1°C between repetitive experiments of the same gametophyte stock culture (Table 2). In some cases this deviation was, however, 2°C . Differences in UST of male and female gametophytes of the same species were observed, but no general trend emerged. In 10 species the male gametophyte had a higher temperature tolerance than the female, in 7 cases it was vice versa and in all other tests male and female gametophytes exhibited the same UST.

The lower survival temperature (LST) of 42 tested Laminariales gametophytes varied only between -1.5 and 1°C under the specified conditions (Table 2). Male and female gametophytes of 25 species survived -1.5°C over 8 wk, while gametophytes of 11 species only survived 0 to 1°C and died at -1.5°C . Male and female gametophytes of 6 species showed different survival limits.

The change in UST of *Laminaria* gametophytes as a function of incubation time is shown for 2 species in Table 3. There was a 3 to 5°C difference in UST between 1 d and 8 wk exposure experiments. The most rapid decline in temperature tolerance was between 1 d and 1 wk experimental time. There was little

Table 2. Temperature tolerance of Laminariales gametophytes. Upper temperature tolerance (UST) and lower temperature tolerance (LST) were determined after 4 wk of postcultivation in 10°C after 2 or 8 wk exposure to the experimental temperatures, respectively. TR: no. of repeated treatments for UST. Underlining at UST indicates the most frequent survival temperature. Locations as in Table 1

Species	Location	Male		Female		TR
		LST	UST	LST	UST	
<i>Laminariaceae</i> , genus <i>Laminaria</i>						
<i>L. abyssalis</i>	Bra				24–26 ^a	3
		0–1	25	1	25	1
<i>L. angustata</i>	Hok	-1.5	23–25	-1.5	24–26	3
	Jap			-1.5	25–26	2
<i>L. bongardiana</i>	Bam1		20–22		19–21	3
	Bam2	-1.5	20–21	0	20	3
<i>L. coriacea</i>	Jap	-1.5	25	-1.5	24–25	2
<i>L. diabolica</i>	Jap	-1.5	25–26			2
<i>L. digitata</i>	Hel	-1.5	23	-1.5	23	3
	Hax		23–24		22–23	4
<i>L. ephemera</i>	Bam			-1.5 ^b	22–23 ^b	2
<i>L. farlowii</i>	Cal2	-1.5	23–24	-1.5	21–22–23	4
<i>L. hyperborea</i>	Hel	-1.5	22–23			3
				-1.5	22–23	2
<i>L. japonica</i>	Hok	-1.5	26–27	-1.5	25–26	2
<i>L. longicuris</i>	Far	-1.5	24	-1.5	24	3
<i>L. longissima</i>	Hok		24–25		24–25	3
<i>L. ochroleuca</i>	Bri	1	25	0–1	25	3
<i>L. pallida</i>	SAfr1	-1.5	23–25	1	25	3
<i>L. religiosa</i>	Jap	-1.5	24–26	-1.5	25–26	3
<i>L. saccharina</i>	Hel	-1.5	23–24	-1.5	23–25	2
	IOM		23–24		23–24	3
<i>L. schinzii</i>	SAfr2	-1.5–1	24–25	-1.5–1	25	3
<i>L. setchellii</i>	Bam	-1.5	23	-1.5	23	3
<i>L. sinclairii</i>	Cal1	-1.5	22–23	-1.5	23	3
<i>L. solidungula</i>	Iglo	-1.5	20	-1.5	19–20	2
<i>Laminariaceae</i> (except genus <i>Laminaria</i>)						
<i>Agarum cribrorum</i>	Iglo		20–21			3
<i>Costaria costata</i>	Jap	0	25–27	-1.5	26–27	3
<i>Cymathere triplicata</i>	Bam	-1.5	22			3
<i>Kjellmaniella crassifolia</i>	Jap	-1.5	25–26	-1.5	26	3
<i>K. gyrata</i>	Jap	-1.5	25–26			4
				0	25–26	3
<i>Pleurophycus gardneri</i>	Bam	0	22	0	22	2
<i>Alariaceae</i>						
<i>Alaria crassifolia</i>	Jap	-1.5	26	-1.5	24–26	3
<i>A. esculenta</i>	Icl	-1.5	19–20	-1.5	20–21	3
<i>A. marginata</i>	Cal1	-1.5	21–22	-1.5	22–23	3
<i>Ecklonia radiata</i>	Aus	1–>1	28	1–>1	27	2
	Tasm1		28		27–28	2
<i>Eisenia arborea</i>	Bam	0–1	25–27	1–>1	25–27	3
<i>E. bicyclis</i>	Jap	1	29–30	1	29	2
<i>Pterygophora californica</i>	Bam	-1.5	25	-1.5	24	2
<i>Undaria pinnatifida</i>	Hok	<0	28–29	<0	27–28–29	4
<i>Lessoniaceae</i>						
<i>Dictyoneuropsis reticulata</i>	Cal		23		22–23	2
<i>Lessonia corrugata</i>	Tasm2		23		23	2
<i>L. nigrescens</i>	Chi1		24		23–24	2
<i>L. trabeculata</i>	Chi2	0–1	23–25	>1	23–25	3
<i>Macrocystis angustifolia</i>	Aus	0	25	0–1	23–24	2
<i>M. integrifolia</i>	Bam	-1.5	24–25	1	24	2
	Cal	-1.5	24			2
<i>M. pyritera</i>	Cal	1	25–26	0–1	25	2
	NewZ				24	2
<i>Nereocystis luetkeana</i>	Cal	-1.5	23	-1.5	23	2
<i>Pelagophycus porra</i>	Cal	0–1	24–25	0–1	24	2
<i>Chordaceae</i>						
<i>Chorda filum</i>	Irl	-1.5	26–28	-1.5	27–28	3
<i>C. tomentosa</i>	Hel			-1.5 ^b	24–25 ^b	2
<i>Phyllariaceae</i>						
<i>Saccorhiza dermatodea</i>	Nfl			-1.5 ^b	21 ^b	2
<i>S. polyschides</i>	Irl1	1–>1	23–24	0–1	23–24	3

^aMale and female gametophytes were tested together. ^bSpecies is monoecious

Table 3. *Laminaria digitata* and *L. schinzii*. Upper survival temperature of *Laminaria* gametophytes exposed 1 d to 8 wk to the experimental temperatures. Results were obtained after 4 wk of postcultivation in 10°C. ×: all gametophytes survived; ·: gametophytes partly damaged, but regenerated; -: gametophytes dead, ?: no data

Species	Sex	Exposure time	Experimental temperatures (°C)								
			21	22	23	24	25	26	27	28	29
<i>L. digitata</i>	M	1 d				×	×	×	×	×	-
		2 d				×	×	×	-	-	-
		4 d			×	×	·	-	-	-	-
		1 wk		×	×	×	-	-	-	-	-
		2 wk		×	×	·	-	-	-	-	-
		4 wk		×	×	-	-	-	-	-	-
		8 wk	×	×	·	-	-	-	-	-	-
		F	1 d				×	×	×	·	-
	2 d					×	×	·	-	-	-
	4 d				×	×	·	-	-	-	-
	1 wk			×	×	·	-	-	-	-	-
	2 wk			×	×	?	-	-	-	-	-
	4 wk			×	·	-	-	-	-	-	-
	8 wk		×	·	·	-	-	-	-	-	-
<i>L. schinzii</i>	M		1 d					×	×	×	-
		2 d				×	×	×	-	-	-
		4 d				×	×	-	-	-	-
		1 wk			×	×	·	-	-	-	-
		2 wk			×	×	·	-	-	-	-
		4 wk		×	×	×	·	-	-	-	-
		8 wk	×	×	×	·	-	-	-	-	-
		F	1 d					×	×	·	·
	2 d					×	×	×	·	·	-
	4 d					×	×	-	-	-	-
	1 wk				×	×	×	-	-	-	-
	2 wk				×	×	·	-	-	-	-
	4 wk			×	×	·	-	-	-	-	-
	8 wk		×	×	·	-	-	-	-	-	-

8, indicating that the limit of long-term survival temperature was not yet reached after 8 wk for *Laminaria* gametophytes.

Dark tolerance

The development of filamentous gametophytes of 12 species of Laminariales after 6 to 18 mo in darkness is shown in Table 4. All survived a period of 16 mo in darkness while most species even survived 18 mo. Only *Laminaria bongardiana*, *L. hyperborea* and *L. saccharina* did not regenerate within 1 mo of postcultivation after 18 mo of darkness. The gametophytes of the 3 species that were cultivated at 0°C were in a good condition even after 18 mo of darkness, and the postcultivation confirmed this result. From Month 9 in darkness onwards gametophytes were often bleached when they were transferred to light. However, the state of the gametophytes at the end of the dark treatment was not recorded in more detail and, thus, is not indicated in Table

change in survival temperature between 1 and 2 wk but UST decreased by 1 to 2°C between Weeks 2 and

4. After 1 or 2 mo postcultivation there was, however, some regeneration in all species up to Month 16, indi-

Table 4. Dark tolerance of filamentous red-light grown Laminariales gametophytes. Development of gametophytes in post-cultivation conditions [PCC, (mo); 0 or 8°C, 16 h light d⁻¹] after 6 to 18 mo of dark treatment. TID: time in darkness (mo); v: gametophytes in PCC vegetative but alive; S: gametophytes formed sporophytes in PCC, · most of inoculum bleached; -: experiment was terminated after 1 mo in PCC, no further observation

Temp. (°C)	Species	TID: PCC:	6		7		8		9		10		12		15		16		18
			1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1
0	<i>Alaria esculenta</i>	v	-	v	-	v	-	v	-	v	-	v	-	v	-	v	v	v	v
	<i>Laminaria solidungula</i>	S	-	S	-	S	-	S	-	S	-	S	-	S	-	v	S	S	S
	<i>Saccorhiza dermatodea</i>	v	-	v	-	v	-	v	-	v	-	v	-	v	-	v	-	v	v
8	<i>L. digitata</i>	S	-	S	-	S	-	S	-	S	-	S	-	S	-	S	-	S	S
	<i>L. bongardiana</i>	v	S	v	-	v	S	S	-	S	-	S	-	·	S	·	S	·	·
	<i>L. hyperborea</i>	S	-	v	S	S	-	S	-	·	S	-	·	S	-	·	S ^a	·	·
	<i>L. ochroleuca</i>	S	-	v	S	v	-	v	-	v	S	·	S	S	-	·	S	v	v
	<i>L. pallida</i>	S	-	v	S	S	-	S	-	S	-	S	-	·	S	·	S	v	v
	<i>L. saccharina</i>	S	-	S	-	S	-	S	-	S	-	S	-	S	-	·	S	·	·
	<i>L. schinzii</i>	S	-	S	-	S	-	S	-	S	-	·	S	S	-	·	S	v	v
	<i>L. setchellii</i>	S	-	S	-	S	-	S	-	v	S	S	-	S	-	v	S	v	v
	<i>S. polyschides</i>	S	-	S	-	S	-	S	-	S	-	S	-	S	-	·	S	S	S

^aOnly 1 sporophyte formed

cated by the development of vegetative gametophyte thalli or sporophytes.

DISCUSSION

Methodological aspects

Several methodological aspects have to be taken into account when evaluating the results. Table 3 indicates the influence of the experimental duration for the determination of the upper temperature tolerance. Even after 2 wk the survival limit did not remain constant but was reduced by another 1 to 2°C after 8 wk and even then a constant value was not obtained. Other studies comparing 2 wk and 12 wk exposure times in subtropical and cold-temperate species obtained similar results (Cambridge et al. 1987, 1990, Novaczek & Breeman 1990, Novaczek et al. 1990) while the red alga *Polyneura hilliae* exhibited a constant upper survival temperature from the second week onwards that did not change over the following 6 wk (Yarish et al. 1987). This indicates that dependency of UST on its incubation period is not the same in different taxonomic groups. For biogeographical considerations a test period of 12 wk will probably better simulate a summer season in the field than of 2 wk. For practical reasons, however, 2 wk exposure times were chosen for this study.

An acclimatization of the inoculated material probably would have resulted in slightly higher UST values than obtained during the present investigation. The gametophytes of 3 Laminariales species which were acclimated for at least 4 wk to 20°C prior to the experiment exhibited UST which were 0.5 to 1.5°C higher than of the same species tested here (compare Tables 2 & 5; Peters & Breeman 1992, 1993). This could, however, also be an effect of the different day lengths used in both studies.

Besides treatment duration and acclimatization, the light period and light intensity may also alter the temperature tolerance. Photon fluence rates of 40 $\mu\text{mol m}^{-2} \text{s}^{-1}$ may reduce the UST by several degrees compared to 20 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (e.g. Yarish et al. 1986, Cambridge et al. 1987, 1990). Furthermore short day length may improve the long-term survival in low temperatures and alter it in both ways in high temperatures (e.g. Cambridge et al. 1984, 1987, Yarish et al. 1984, 1986). During this study intermediate day length (12:12 h light:dark cycle) and photon fluence rates (30 $\mu\text{mol m}^{-2} \text{s}^{-1}$) were chosen. Thus, there is the possibility that UST obtained during this investigation are slightly lower than under long-day (16:8 h light:dark) conditions and LST are slightly higher than under short-day (8:16 h light:dark) conditions.

Filamentous gametophytes which were used during the present investigation were of a spherical form and consisted of very many vegetative cells. Thus, the amount of inoculated material differed from test to test. At the upper 2 survival temperatures the outer cells of the inoculum were regularly damaged or dead whereas the inner part was still alive and regenerated during postcultivation. The initial size of the inoculum perhaps was critical for the survival limit and may partly account for the variation of the results. Bolton & Lüning (1982) compared the upper temperature tolerance of freshly released zoospores and filamentous gametophytes of *Laminaria saccharina*. The filamentous gametophytes were damaged at 23°C but regenerated from a few cells, while the zoospores died at 23°C supporting the idea that filamentous gametophytes yield higher survival values than zoospores. Similar differences became obvious in *Saccorhiza polyschides*. The lower survival temperature of female gametophytes directly derived from zoospores was 3°C after 2 wk (Norton 1977) while the filamentous gametophytes used in the present investigation survived 1°C over 8 wk (Table 2).

It is difficult to decide whether temperature ecotypes exist in kelp gametophytes as different isolates were tested only in a few cases and mostly not during the same study. All species that were tested with 2 isolates in this study (*Laminaria angustata*, *L. digitata*, *L. bongardiana*, *Ecklonia radiata*, *Macrocystis integrifolia*, *M. pyrifera*; Table 2) either exhibited no differences between isolates, or exhibited differences that were within the range of experimental error. The same upper survival limits were also found in different studies for different isolates of *L. saccharina* and *L. longicuris* (Bolton & Lüning 1982), *Chorda tomentosa* from eastern and western Atlantic (compare Tables 2 & 5; Novaczek et al. 1986), *M. angustifolia* from southern Australia and South Africa (compare Tables 2 & 5; Branch 1974), *Lessonia nigrescens* and *L. trabeculata* (compare Tables 2 & 5; Peters & Breeman 1993) as well as between northern and southern New Zealand isolates of *E. radiata* (Table 5; Novaczek 1984). However, *E. radiata* from New Zealand exhibited an upper temperature tolerance of only 24 to 25°C (Novaczek 1984) while Tasmanian and southern Australian isolates survived 27 to 28°C (Table 2). *E. radiata* sensu Womersley (1967) is a broad definition for a variable species (review of taxonomical problems: Bolton & Anderson 1993) and the differing survival limits may indicate that more than one taxon is involved.

Macrocystis pyrifera of the southwest Pacific region only inhabits cold temperate regions such as southern Tasmania or southern New Zealand. This implies a lower UST than for *M. pyrifera* isolates from southern California. During this investigation the New Zealand isolate survived 24°C and, thereby, exhibited a 1°C

Table 5. Compiled literature data on lower and upper survival temperature (LST/UST) of Laminariales gametophytes. *Growth limit. Locations: Chi3 = Tierra del Fuego, Chile; Chin = China; Esp = Espesrend, Norway; GB = Great Britain; LIS = Long Island Sound, USA; Med = Mediterranean Sea; Per = San Juan, Peru; SAfr = South Africa; other locations as in Table 1

Species	Location	LST/UST (°C)	Duration of experiment	Source
Chordaceae				
<i>Chorda filum</i>	Hax	/26-<28	?	Novaczek et al. (1986)
<i>C. tomentosa</i>	Hax	/24-<26	?	Novaczek et al. (1986)
Phyllariaceae				
<i>Phyllariopsis brevipes</i>	Med	>5/<25	?	Henry (1987)
<i>Saccorhiza polyschides</i>	GB	>3/25	2 wk	Norton (1977)
Laminariaceae				
<i>Laminaria abyssalis</i>	Bra	/24-26	2 wk	de Oliveira & de Oliveira (1987)
<i>L. digitata</i>	Hel	/22-23	2 wk	Bolton & Lüning (1982)
	Hax	/22-23	2 wk	Bolton & Lüning (1982)
	Hel	/20	1 wk	Lüning (1980)
<i>L. hyperborea</i>	Hel	/21	2 wk	Bolton & Lüning (1982)
	Hel	/20	1 wk	Lüning (1980)
<i>L. longicuris</i>	Hax	/23	2 wk	Bolton & Lüning (1982)
	Iglo	/23	2 wk	Bolton & Lüning (1982)
	LIS	/25	12 d	Egan et al. (1989)
<i>L. japonica</i>	Chin	/>24	?	Fang et al. (1963)
	?	0/25-27		Cheng (1969)
<i>L. pallida</i>	SAfr	/24.5-<26.5	30 d	Branch (1974)
<i>L. religiosa</i>	Jap	/25	10 d	Funano (1983)
<i>L. saccharina</i>	Hel	/23	2 wk	Bolton & Lüning (1982)
	IOM	/23	2 wk	Bolton & Lüning (1982)
	Bri	/23	2 wk	Bolton & Lüning (1982)
	Esp	/23	2 wk	Bolton & Lüning (1982)
	Hel	/21	1 wk	Lüning (1980)
	GB	/22	?	Kain (1969)
<i>L. solidungula</i>	Iglo	/18-20	2 wk	Bolton & Lüning (1982)
Alariaceae				
<i>Ecklonia biruncinata</i>	SAfr	/26	7 d	Bolton & Anderson (1987)
<i>E. maxima</i>	SAfr	/25-<28	7 d	Bolton & Anderson (1987)
	SAfr	/24.1-<26.5	30 d	Branch (1974)
<i>E. radiata</i>	NewZ	*8-9/24-25	?	Novaczek (1984)
<i>Eisenia arborea</i>	Bam	>3/	?	Maier (1984)
<i>Undaria pinnatifida</i>	Jap	-1/27.5-<30	?	Akiyama (1965)
	Jap	/30	?	Saito (1962) (in Saito 1975)
	Med	/29.5-29.7	2 wk	Peters & Breeman (1992)
Lessoniaceae				
<i>Macrocystis pyrifera</i>	Cal	>5/	?	Maier (1984)
	Chi1	-2/24.5	4/2 wk	Peters & Breeman (1993)
<i>M. angustifolia</i>	SAfr	/24.1-26.5	30 d	Branch (1974)
<i>Lessonia vadosa</i>	Chi3	-2/19.9-21.4	4/2 wk	Peters & Breeman (1993)
<i>L. nigrescens</i>	Chi1	-2/24.6	4/2 wk	Peters & Breeman (1993)
<i>L. trabeculata</i>	Per	-2/25.7-26.5	4/2 wk	Peters & Breeman (1993)

lower UST than the Californian isolate which is within the range of variability between experiments and thus, not significant. However, in a detailed study, Hay (1990) demonstrated that *M. pyrifera* does not persist at its geographical limit in New Zealand in areas where maximum summer temperatures exceed 18 to 19°C for several days, whereas in southern North America, *M. pyrifera* extends to areas where sea-surface maxima reach 27°C for several days. Here, a temperature ecotype for the sporophyte has been described (North 1972), which indicates that the game-

tophytes of a more southern isolate of *M. pyrifera* may also survive higher temperatures than 25 to 26°C as determined during this investigation. This either implies temperature ecotypes in *M. pyrifera* or non-conspicuity of Australian and Californian isolates.

Dark survival

The ability of 12 kelp species to survive 18 mo in darkness may have been influenced by the fact that

filamentous gametophytes were used. It was striking that often only the inner cells of a gametophyte inoculum were still pigmented after the prolonged dark treatment and regenerated during postcultivation. Embryo spores of *Laminaria saccharina*, *L. digitata* and *L. hyperborea* did not survive 15 mo in darkness (Lüning 1980).

The gametophytes of *Laminaria solidungula*, *Alaria esculenta* and *Saccorhiza dermatodea* which were kept at 0°C during the dark experiment were fully pigmented even after 18 mo of darkness and probably would have survived much longer dark periods, while the gametophytes that were kept at 8°C were for the most part bleached after 18 mo and only partly regenerated with few cells. This indicates that low temperatures may favour survival in darkness. As no species was tested at both temperatures in this study, the exact interrelation between temperature and survival in darkness remains to be tested. In *L. hyperborea*, zoospores which were tested at 10 and 17°C survived darkness slightly better in the cooler condition (Kain 1964).

It is not known whether filamentous gametophytes exist in nature, thereby forming a 'seed-bank' of microscopic forms. Such as a 'seed-bank' is, however, probable as the extensive dark tolerance of gametophytes (Table 4) and their ability to grow vegetatively under low light conditions will enable survival of those gametophytes that do not become fertile due to insufficient light or temperature conditions. With the ability of filamentous gametophytes to form sporophytes even after prolonged periods of darkness if light conditions become favourable again (Table 4) another requirement for a 'seed-bank' is fulfilled.

Temperature tolerance and biogeographical considerations

The upper survival temperature of Laminariales gametophytes ranges between 19–20 and 29–30°C (Tables 2 & 5) as determined during this investigation and including literature data. This 10°C range in UST of kelp gametophytes was determined in more than 50% of the species of the order including species of the most extreme cold and warm temperate waters inhabited by the Laminariales. Thus, one may expect that these data are representative for the whole order and that the survival range would not be substantially altered even if more species were tested.

The gametophytes of the 3 Arctic to cold-temperate northern hemisphere kelp species *Laminaria solidungula*, *Agarum cribrosum* and *Alaria esculenta* (Table 2) show the lowest upper survival limit (19 to 20°C) of all investigated species. The same low survival limit is

only known from *Lessonia vadosa* which inhabits the southernmost tip of South America (Peters & Breeman 1992). This is remarkable because the sporophytes of some northeastern Pacific kelp species (e.g. *Cymathere triplicata*, *Pleurophycus gardneri*) have been characterized as especially stenothermal with upper survival temperatures of 15 to 17°C (Lüning & Freshwater 1988), but their gametophytes survive 22°C. A temperature tolerance of 20°C is relatively high for *L. solidungula*, and this is further evidence for the probable conservative character of this parameter. The Arctic endemic species *L. solidungula* will be subject to water temperatures of only –1.5 up to 5°C throughout the year. Although it also occurs off Newfoundland, a region with higher sea-surface temperatures, it is restricted here to deep water (Lüning 1990) or to fjords with temperatures near freezing point (Hooper 1984). As it is assumed that the Laminariales evolved in the North Pacific and that some cold-temperate species entered the North Atlantic only after the first inundation of the Bering land bridge about 3.5 million yr ago (Lüning 1990, Lüning & tom Dieck 1990), adaptation to Arctic conditions in this group could not have started before the beginning of the last glaciation period about 2 million yr ago. This time period probably was not long enough to permit a further decrease in upper temperature tolerance in *L. solidungula* gametophytes. Even gametophytes of Antarctic Desmarestiales, which potentially had 10 million yr more time for cold adaptation because of the earlier formation of ice-covered Antarctica, still survive 13 to 16°C in similar test conditions although they only encounter temperatures of up to 5°C during the course of the year in nature (Wiencke & tom Dieck 1989).

In the South Atlantic there are no cold stenothermal kelps as in the northern hemisphere, except for *Lessonia vadosa* extending from Patagonia to Tierra del Fuego (Peters & Breeman 1992). The gametophytes of the Brazilian species of *Laminaria* and of the South African species of *Laminaria*, *Ecklonia* and *Macrocystis* had an upper survival limit of 25 to 26°C (Tables 2 & 5) and only partly survived –1.5°C. The genus *Laminaria* probably originated in the northern hemisphere, and the high temperature tolerance of Brazilian and South African *Laminaria* species (25 to 26°C) is consistent with the hypothesis that amphiequatorial distribution of temperate species with a heteromorphic life history results from long-distance dispersal of vegetative gametophytes (microthalli), as proposed by Peters & Breeman (1992) for amphiequatorial Desmarestiales gametophytes. According to paleoclimatic reconstructions, tropical summer sea-surface temperatures during the last glaciation period were about 24 to 26°C in the coldest regions, i.e. the eastern Atlantic and eastern Pacific (CLIMAP Project

Members 1981) thereby permitting passage of warm-tolerant microthalli. This hypothesis is supported by species of all other genera of the Laminariales with amphiequatorial distribution. The gametophytes of the southern hemisphere species all show UST of at least 25°C (e.g. *Ecklonia radiata*: 28°C, *Eisenia arborea*: 25 to 27°C, *Macrocystis pyrifera*: 24 to 25°C). As vegetative microthalli of the Laminariales are very persistent, may survive prolonged periods of darkness and thereby do not lose their ability to form sporophytes (Table 4), even a recent dispersal via the tropics by cooler deep-water currents may be taken into consideration.

There is a generally high survival limit of Japanese kelp species which reflects the extreme temperature conditions at the Japanese coasts. The Japanese coastline is characterized by compressed isotherms, by strong annual temperature fluctuations and a rapid change of temperature conditions from north to south (Funahashi 1973, Lüning 1990).

The Japanese species with the lowest UST of 24 to 25°C, *Laminaria angustata*, *L. longissima* and *L. coriacea*, are confined to the cooler Pacific side of Hokkaido and northern Honshu while the characteristic kelp species of the warm areas of Central and South Honshu and Kyushu tolerate temperatures of 28 to 30°C (*Undaria pinnatifida* and *Eisenia bicyclis*; Table 2). *E. bicyclis* and *Ecklonia cava* (not investigated) extend to the Pacific side of South Kyushu with an annual variation of temperatures between 17 and 27°C (Chihara 1975) and *U. pinnatifida* grows on the slightly cooler west coast of Kyushu (Saito 1972). Outside Japan, a temperature tolerance as high (27 to 28°C) was found only in *Ecklonia radiata* isolates from southern Australia and Tasmania. This species, which grows in warm temperate regions of Australia and New Zealand, extends to the southernmost coral reefs of western Australia (28 to 29°C) with mean monthly water temperatures of 20 to 25°C (Hatcher et al. 1987). Thus, in all species with very high UST, the distribution limit seems to be determined by upper lethal limits of the gametophyte and/or sporophyte. It is not expected that any gametophyte of the Laminariales will survive more than 30°C over a prolonged time.

An upper survival limit of 29°C seems to be sufficiently high for a transfer via the tropical belt as was outlined by Peters & Breeman (1992) for *Undaria pinnatifida*, a species recently introduced to New Zealand and Tasmania. It may thus be only a question of time until other warm-temperate kelp species, such as *Eisenia bicyclis*, may be accidentally introduced with ballast water for instance to warm temperate coastlines outside Japan.

It is striking that all investigated Japanese isolates of the Laminariales have consistently higher survival limits

than related taxa of the northern hemisphere. The same phenomenon was observed in amphioceanic taxa of *Desmarestia*, *D. ligulata* and *D. viridis*, with Japanese isolates showing higher upper survival limits than other northern hemisphere strains of the same species (Peters & Breeman 1992). The explanation may be found in glacial conditions. In Japan, large annual temperature ranges were also present to some extent during glaciations, in contrast to the eastern Pacific and eastern and western North Atlantic (van den Hoek & Breeman 1990). Thus, in Japan selection pressure has probably consistently operated in improving tolerance to high temperatures in contrast to all other regions.

The upper survival temperature of all tested Laminariales gametophytes shows striking discrepancies between temperature tolerance of the gametophytes and the distribution limit of the species. Some species with a high temperature tolerance are not distributed as close to the Equator as other species with a lower or similar temperature tolerance, and vice versa. Northeastern Pacific species clearly show this phenomenon. The 2 cold-temperate species *Agarum cribrosum* and *Cymathere triplicata* with an upper survival limit of 21 to 22°C do not extend further south than San Juan Island and Whidbey Island respectively, while *Laminaria bongardiana* with an upper survival limit of 21°C is distributed as far south as Oregon and has isolated populations in California (Druehl 1970). Similarly the southern distribution limit of several northern species, such as *Macrocystis integrifolia*, *L. setchellii*, *Alaria marginata*, *Nereocystis luetkeana*, *L. sinclairii* and *Costaria costata*, is situated near Point Conception, but this cannot be explained by their gametophyte upper temperature tolerance which ranges from 21–22 to 26–27°C. Other species with a similar temperature tolerance of 23 to 25°C, such as *L. farlowii* and *Pterygophora californica*, extend 5° further south to the Baja California peninsula (Druehl 1970).

The available data for Laminariales indicate that the upper temperature tolerance of sporophytes is 1 to 7°C lower than that of gametophytes (compare Tables 2 & 5 with: Sundene 1962, Munda & Lüning 1977, Lüning 1984, Novaczek et al. 1986, Lüning & Freshwater 1988, tom Dieck 1992, tom Dieck & de Oliveira 1993). As lethal limits of the non-hardest stage (often macrothalli) in a life cycle were found to be irrelevant in explaining distribution limits in many seaweeds (Breeman 1988), distribution in Laminariales often is probably determined by temperature requirements for gametogenesis (being relevant for the formation of sporophytes) or reproduction rather than by temperature tolerance of gametophytes or sporophytes. Exceptions may be found either in annual species that survive the unfavourable season with the help of the hardest stage, the microthallus (e.g. *Chorda filum* and

C. tomentosa; Breeman 1988) or in those species whose distribution may be influenced by the El Niño as outlined by Peters & Breeman (1993) for South American *Lessonia trabeculata* and *L. nigrescens*, or in species inhabiting very warm waters, such as *Undaria pinnatifida*, *Eisenia bicyclis* and *Ecklonia radiata* (see above).

CONCLUSION

The range in upper temperature tolerance of only 10°C for 1 specific stage of the life cycle of the Laminariales seems to be low for an entire order. The closely related order Desmarestiales spans at least 15°C in UST for the gametophytes. Gametophytes of Antarctic *Desmarestia anceps*, *D. menziesii*, *Phaeurus antarcticus* and *Himanthothallus grandifolius* survived 13, 16 to 17, 15 to 16 and 15 to 16°C respectively (Wiencke & tom Dieck 1989, 1990) and gametophytes of cold-temperate South African *D. firma* survived 22 to <26°C (Anderson & Bolton 1989). Eleven South American and northern hemisphere *Desmarestia* species were tested with upper survival limits of gametophytes between 21.8 and 28.5°C (Peters & Breeman 1992, 1993). Considering the distribution of the genus *Desmarestia* (Anderson & Bolton 1989, Lüning 1990), it is not expected that this range will increase by much even if more species were tested. Comparison with other algal orders is difficult due to insufficient data. In the red algal order Gigartinales, the genus *Gigartina* alone comprises species with upper survival limits ranging between 15 and 33°C, a 18°C difference in total (Guiry et al. 1987, Wiencke & tom Dieck 1990). In this case it is, however, not certain that the same phase in the life cycle was tested for all species (i.e. gametophyte or tetrasporophyte). The primitive brown algal order Ectocarpales could have a still broader range as members of this order are distributed in all oceans. Existing data for different isolates of the species *Ectocarpus siliculosus* (Bolton 1983) and for Antarctic/cold temperate *Geminocarpus geminatus* (Wiencke & tom Dieck 1990) already span a range in UST of 19°C.

Recent research into the morphology (Mathieson et al. 1981), historical biogeography (Lüning & tom Dieck 1990), hybridization (Sanbonsuga & Neushul 1978, Lewis 1991) and molecular biology (Bhattacharya & Druehl 1988, Fain et al. 1988, Stam et al. 1988, Bhattacharya et al. 1991, Saunders & Druehl 1991, 1992) of the Laminariales provides increasing evidence for a recent radiation of kelps. This was outlined explicitly by Saunders & Druehl (1992) who assume a radiation time of 16 to 20 million yr ago or at most 30 million yr ago. The small range in temperature tolerance of Laminariales gametophytes may be a further indication for the young phylogenetic age of the order.

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