

Effect of acclimation temperature on temperature responses of *Porphyra leucosticta* and *Enteromorpha linza* from the Gulf of Thessaloniki, Greece

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ABSTRACT: The effect of the acclimation temperature on the temperature tolerance of *Porphyra leucosticta*, and on the temperature requirements for growth and survival of *Enteromorpha linza* was determined under laboratory conditions. Thalli of *P. leucosticta* (blade or Conchocelis phases), acclimated to twenty-five degrees, survived up to 30°C, i.e. 2°C more than those acclimated to 15°C which survived up to 28°C. Lower temperature tolerance of both *Porphyra* phases that were acclimated to 15°C was -1°C after an 8-week exposure time at the experimental temperatures. The upper temperature tolerance of *E. linza* also increased by 2°C, i.e. from 31 to 33°C, when it was acclimated to 30°C instead of 15°C. The lower temperature tolerance increased from 1 to -1°C, when it was acclimated to 5°C instead of 15°C. *E. linza* thalli acclimated for 4 weeks to 5 or 10°C reached their maximum growth at 15°C, i.e. at a 5°C lower temperature than those acclimated to 15 or 30°C. These thalli achieved higher growth rates in percent of maximal growth at low temperatures than those acclimated to 15 or 30°C. Thalli acclimated for 1 week to 5°C reached their maximum growth rate at 20°C and achieved growth rates at low temperatures similar to those recorded for thalli acclimated to 15°C. Thalli of *E. linza* acclimated for 4 weeks to 5°C lost this acclimation after being post-cultivated for the same period at 15°C. That was not the case with thalli acclimated for 8 weeks to 5°C and post-acclimated for 4 weeks to 15°C. These thalli displayed similar growth patterns at 10–25°C, while a decline of growth rate was observed at 5 or 30°C. The significance of the acclimation potential of *E. linza* with regard to its seasonality in the Gulf of Thessaloniki, and its distribution in the N Atlantic, is also discussed.

INTRODUCTION

Seasonal changes of temperature and photoperiod in natural environments may have forced seaweeds to develop different strategies for survival. Among those strategies (Lüning, 1990), temperature responses to seasonal acclimation (sensu Berry & Björkman, 1980) may be related to perennial seaweeds or seaweeds with an isomorphic life cycle. For instance, *Laminaria* spp. shifted their upper survival limit from winter to summer by up to 5°C (Lüning, 1984). Far greater, seasonal changes have been demonstrated in the frost tolerance of macroalgae (Gessner, 1970; Lüning, 1990). The effect of temperature acclimation on photosynthetic responses of algae was recently reviewed by Davison

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(1991), while more extensive reviews of the same effect on higher plants are those by Berry & Björkman (1980) and Berry & Raison (1981).

Lampe (1935) showed a different acclimation potential of photosynthetic rates between eurythermal (e.g. *Fucus serratus*) or stenothermal (e.g. *Porphyra hiemalis*) species. A number of studies from marine invertebrates (reviews by Precht et al., 1973; Kinne, 1970) indicated that acclimation (or non-genetic adaptation in the terminology of Precht et al., 1973; Kinne, 1970) need not appear in all species, and is more often in eurythermal than in stenothermal ones. Several macroalgae change their temperature growth requirements (Egan et al., 1989; Orfanidis, 1990, 1993; Bischoff & Wiencke, 1993) and temperature tolerance (Schwenke, 1959; Feldmann & Lutova, 1963; Yarish et al., 1984) in response to acclimation temperature, but others do not (Yarish et al., 1987). Thus, the question raised by Yarish et al. (1987) about the ability of macroalgae to change their temperature responses in response to acclimation temperature still exists.

Temperature responses determined under laboratory conditions have been used in ecological biogeography over the last decades (Breeman, 1988; Lüning, 1990). In most cases, the tested seaweed was acclimated at a medium temperature, depending on its climatic affinity, either before being transferred directly to experimental conditions (Orfanidis, 1991; tom Dieck, 1993) or after a short acclimation procedure had taken place (Peters & Breeman, 1992; Bischoff & Wiencke 1993). In all cases, the significance of acclimation conditions was noted and in the case of ecotypic variation within a species it was extensively discussed (Breeman, 1988; Novaczek et al., 1989). However, less attention was paid to the possible importance of acclimation, for the explanation of limits of macroalgae (Orfanidis, 1993).

One objective of this study was to investigate the ability of *Porphyra leucosticta* or *Enteromorpha linza* from Thessaloniki, Greece to change their survival limits and/or the temperature requirements for growth. A second objective was to evaluate the significance of acclimation for seasonality and distribution of *E. linza* in the Gulf of Thessaloniki and in the N Atlantic Ocean.

MATERIALS AND METHODS

Unialgal cultures of *Porphyra leucosticta* and *Enteromorpha linza* were established from plants collected near Thessaloniki, Greece (Thermaikos Gulf; 40.38° N, 22.58° E) in February and April 1986. They were transported in an insulated cooling container to a laboratory of the Biologische Anstalt Helgoland in Hamburg. Unialgal cultures were propagated at $15 \pm 2^\circ\text{C}$ in 2- or 3-l glass-beakers filled with von Stosch's enriched seawater (VSES; modified after Guiry & Cunningham, 1984) and aerated with membrane-filtered air for at least two years before the experiments were started. A photon fluence rate of $20\text{--}40 \mu\text{mol m}^{-2} \text{s}^{-1}$ was provided at 16 h light per day by cool-white fluorescent tubes (Osram L 40 W/25 S). Cultivation methods and equipment used in this study were described in detail by Orfanidis (1991).

Temperature tolerance experiments were performed by incubating differently acclimated individuals at high (27–36°C) or low [(–1)–4°C] temperatures. Temperature-controlled water baths (Haake D8-V water bath-cryostat units; Haake, Karlsruhe, Germany) were used for temperatures $\geq 0^\circ\text{C}$ (all $\pm 0.1^\circ\text{C}$) and a constant-temperature room for -1°C ($\pm 0.5^\circ\text{C}$). Standard light conditions were cool-white fluorescent light, a photon

fluence rate of $30 \mu\text{mol m}^{-2} \text{s}^{-1}$ and 12 h light per day. After the treatments, individuals tested for lower temperature tolerance were post-cultivated at $15 \pm 2^\circ\text{C}$ and those tested for upper temperature tolerance at $20 \pm 1^\circ\text{C}$ ($20 \mu\text{mol photons m}^{-2} \text{s}^{-1}$, 16 h light per day). Four weeks later, the viability of the plants was investigated visually and microscopically to determine whether plants had either survived and exhibited normal coloration, or regenerated from injured thallus, or were dead. In cases where there was any doubt about the viability of the test material, the post-cultivation was prolonged for another 4 weeks.

Growth experiments for *E. linza* were performed in temperature-controlled water baths (Haake D8-V, Karlsruhe, Germany; $\pm 0.2^\circ\text{C}$) at 5, 10, 15, 20, 25 and 30°C . The photon fluence rate at the surface of the water baths was $60\text{--}80 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Osram L 65 W/25 S and Osram L 40 W/25 S). The day length was 16 h light per day. The growth of *E. linza* was determined as increase of fresh weight after a 1-week experimental period at each temperature in material which was acclimated at 5, 10, 15 and 30°C . Growth was calculated as follows:

$$\text{Relative growth rate (RGR)} = (\ln N_t - \ln N_0) / t \times 7 \text{ (week}^{-1}\text{)}$$

[N_0 = fresh weight; N_t = fresh weight after t days; t = experimental time (days)]

RESULTS

Effect of acclimation temperature on lower and upper temperature tolerance

The blade or Conchocelis phases of *Porphyra leucosticta* acclimated for at least two years to 15°C survived for 8 weeks at -1°C . The upper temperature tolerance of the blade phase of *P. leucosticta* as a function of exposure time is shown in Table 1.

Table 1. Upper temperature tolerance of the blade phase of *Porphyra leucosticta*. Plants were acclimated for at least 2 years to 15°C or for 12 weeks to 25°C (results in brackets). Results evaluated after 4 or 8 weeks postcultivation at 20°C , $20 \mu\text{mol photons m}^{-2} \text{s}^{-1}$, 16 h light per day; +: plants alive or regenerated from injured thallus; -: plants dead

Time (days)	Experimental temperatures ($^\circ\text{C}$)					
	27	28	29	30	31	32
1	+(+)	+(+)	+(+)	+(+)	-(+)	-(+)
2	+(+)	+(+)	+(+)	-(+)	-(+)	-(+)
3	+(+)	+(+)	+(+)	-(+)	-(+)	-(+)
4	+(+)	+(+)	+(+)	-(+)	-(+)	-(+)
5	+(+)	+(+)	+(+)	-(+)	-(+)	-(+)
6	+(+)	+(+)	+(+)	-(+)	-(+)	-(+)
7	+(+)	+(+)	+(+)	-(+)	-(+)	-(+)
10	+(+)	+(+)	-(+)	-(+)	-(+)	-(+)
14	+(+)	+(+)	-(+)	-(+)	-(+)	-(+)
21	+(+)	+(+)	-(+)	-(+)	-(+)	-(+)
28	+(+)	+(+)	-(+)	-(+)	-(+)	-(+)
35	+(+)	+(+)	-(+)	-(+)	-(+)	-(+)
42	+(+)	+(+)	-(+)	-(+)	-(+)	-(+)

Table 2. Upper temperature tolerance of the Conchocelis phase of *Porphyra leucosticta*. Plants were acclimated for at least 2 years to 15° C or for 8 weeks to 25° C (results in brackets). nt = not tested (see Table 1 for further details)

Time (days)	Experimental temperatures (°C)					
	27	28	29	30	31	32
14	+(+)	+(+)	-(+)	-(+)	-(+)	nt(-)
28	nt(+)	nt(+)	nt(+)	nt(+)	nt(+)	nt(-)
56	nt(+)	nt(+)	nt(+)	nt(+)	nt(-)	nt(-)

Table 3. Lower temperature tolerance of *Enteromorpha linza*. Plants were acclimated for at least 2 years to 15° C or for 8 weeks to 5° C (results in brackets). Results evaluated after 4- or 8-week post-cultivation at 15° C, 20 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$, 16 h light per day; +: plants alive; R: regeneration from injured thallus; -: plants dead

Time (days)	Experimental temperatures (°C)					
	-1	0	1	2	3	4
1	+(+)	+(+)	+(+)	+(+)	+(+)	+(nt)
3	+(+)	+(+)	+(+)	+(+)	+(+)	+(nt)
7	+(+)	+(+)	+(+)	+(+)	+(+)	+(nt)
14	R(+)	R(+)	+(+)	+(+)	+(+)	+(nt)
28	R(+)	R(+)	R(+)	+(+)	+(+)	+(nt)
42	-(R)	-(+)	R(+)	+(+)	+(+)	+(nt)
56	-(R)	-(+)	R(+)	+(+)	+(+)	+(nt)

Table 4. Upper temperature tolerance of *Enteromorpha linza*. Plants acclimated for at least 2 years to 15° C and for 8 weeks to 30° C (results in brackets). Results evaluated after 4- or 8-week post-cultivation at 20° C, 20 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$, 16 h light per day, (see Table 3 for explanation of symbols)

Time (days)	Experimental temperatures (°C)						
	30	31	32	33	34	35	36
1	+(+)	+(+)	+(+)	+(+)	R(+)	R(+)	-(+)
3	+(+)	+(+)	+(+)	+(+)	-(+)	-(+)	-(R)
7	+(+)	+(+)	+(+)	R(+)	-(+)	-(R)	-(+)
14	+(+)	+(+)	R(+)	-(+)	-(R)	-(+)	-(+)
28	+(+)	+(+)	R(+)	-(+)	-(R)	-(+)	-(+)
42	+(+)	+(+)	-(R)	-(R)	-(+)	-(+)	-(+)
56	+(+)	+(+)	-(R)	-(R)	-(+)	-(+)	-(+)

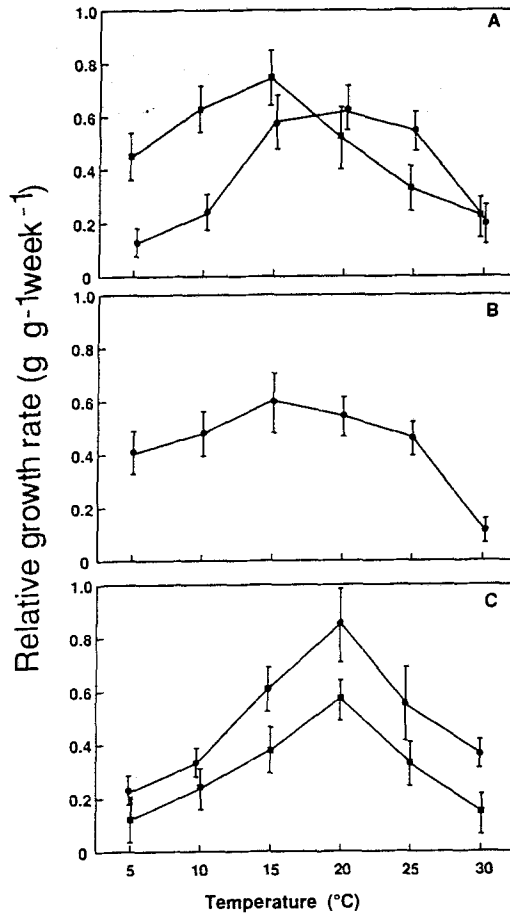


Fig. 1. Mean relative growth rates (RGR) of *Enteromorpha linza* ($n = 6-8$), measured at 5°C temperature intervals (vertical bars = 95% confidence intervals). Standard light conditions: 60–80 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$, 16 h light per day. A: Individuals acclimated for 1 week (●) or 4 weeks (■) to 5°C. B: Individuals acclimated for 4 weeks to 10°C (●). C: Individuals acclimated for at least 2 years to 15°C (●) or for 4 weeks to 30°C (■)

Individuals of the blade phase acclimated for at least two years to 15°C survived up to 28°C after 42 days exposure time, while individuals acclimated for 12 weeks to 25°C survived up to 30°C after the same exposure time. The upper temperature tolerance of the Conchocelis phase of *P. leucosticta* as a function of exposure time is shown in Table 2. Individuals of the Conchocelis phase acclimated for at least two years to 15°C survived up to 28°C after 14 days exposure time, while individuals acclimated for two months to 25°C survived up to 30°C after 56 days exposure time.

The lower temperature tolerance of *Enteromorpha linza* as a function of exposure time is shown in Table 3. The lower survival temperature of individuals acclimated for at

least two years to 15°C was 1°C after 56 days exposure time, while the lower survival temperature of individuals acclimated for 8 weeks to 5°C was -1°C after the same exposure time. The upper temperature tolerance of *E. linza* as a function of exposure time is shown in Table 4. Individuals acclimated for at least two years to 15°C survived up to 31°C after 56 days exposure time, while individuals acclimated for 8 weeks to 30°C survived up to 33°C after the same exposure time.

Effect of acclimation temperature on temperature growth requirements

Thalli of *Enteromorpha linza* acclimated for 4 weeks to 5 or 10°C reached their growth maximum at 15°C. Thalli acclimated for 1 week to 5°C for 4 weeks to 30°C, or for at least two years to 15°C, reached their growth maximum at 20°C (Fig. 1). Individuals acclimated for 4 weeks to lower temperatures (5 or 10°C) grew better to 5 (62–68 % of maximum growth rate) or 10°C (80–85 % of maximum growth rate) than did individuals acclimated to higher temperatures (15 or 30°C). Individuals acclimated to 15 or 30°C exhibited at 5 or 10°C 25–27 % or 39–44 % of their maximum growth rate, respectively. Thalli acclimated for 1 week to 5°C achieved similar percentage growth rates of the maximum value at 5 (20 %) or 10°C (38 %) as those acclimated to 15°C (Fig. 1). Growth rates of individuals acclimated for 4 weeks to 5 or 30°C or for at least two years to 15°C, declined linearly at temperatures of 20–30°C, whereas individuals acclimated for 1 week to 5°C or for 4 weeks to 10°C grew quite well at 25°C (88 and 77 % of maximum growth rate, respectively) (Fig. 1).

Individuals that were acclimated for 4 weeks to 5°C and then were transferred for 4 weeks to 15°C grew at a similar rate as those grown at 15°C. Individuals that were acclimated for 8 weeks to 5°C and then were transferred for 4 weeks to 15°C grew similarly at temperatures of 10–25°C (> 80 % of maximum growth rate), while growth rate declined at 5 and 30°C (34 and 55 % of maximum growth rate, respectively) (Fig. 2).

DISCUSSION

Although the temperature tolerance of a species is genetically determined (Gessner, 1970; Larcher, 1983; Lüning, 1984, 1990), it can gradually change with exposure time to a constant value (Levitt, 1980; Larcher & Bauer, 1981). Upper temperature tolerance of the blade phase of *Porphyra leucosticta* decreased by 2°C after 10–14 incubation days and stayed fixed afterwards (Table 1). The upper temperature tolerance of *Polynura hilliae* also became stable after an exposure time of 14 days (Yarish et al., 1987). The upper tolerance limit of *Enteromorpha linza* did not stabilize until after an exposure time of 6 weeks (Table 4), and in the filamentous gametophytes of *Laminaria* the upper tolerance limit still changed after 8 weeks of incubation (tom Dieck, 1993).

As far as low temperature tolerance is concerned, an exposure time of 6 weeks was sufficiently long for stabilizing the lower temperature tolerance of *E. linza* (Table 3). The lower survival limit for *Choristocarpus tenellus* became constant after an incubation time of 5 weeks (Orfanidis, 1991), while *Colpomenia peregrina* and *Gigartina teedii* reached their constant lower survival limit after an incubation time of 6 or 8 weeks (Orfanidis, 1993).

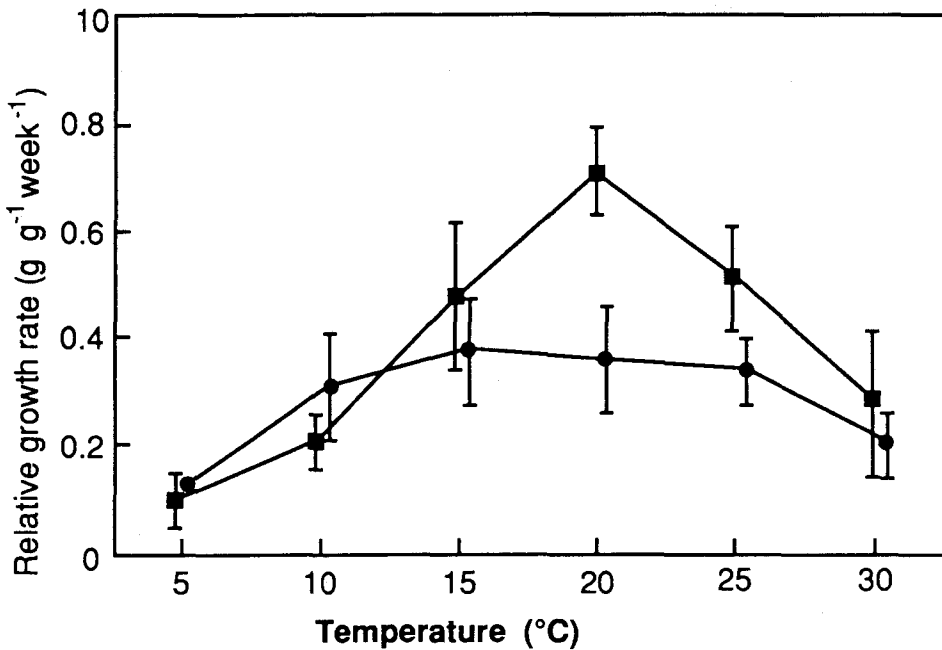


Fig. 2. Mean relative growth rates of *Enteromorpha linza* ($n = 6-8$). ■ Individuals acclimated for 4 weeks to 5°C and post-acclimated for 4 weeks to 15°C. ● Individuals acclimated for 8 weeks to 5°C and post-acclimated for 4 weeks to 15°C (see legend of Fig. 1 for further details)

Acclimation to different temperatures may influence the temperature tolerance of a species only in a genetically determined restricted interval (Precht et al., 1973; Kappen, 1981; Steponkus, 1981). *E. linza* thalli acclimated for 8 weeks to temperatures near to their lower or upper survival limits, exceeded the 'normal' tolerance limits by 2°C, compared to values determined for experimental algae acclimated to a medium temperature (15°C) (Tables 3, 4). *P. leucosticta* thalli acclimated to 25°C also survived 2°C more than did thalli acclimated to 15°C (Tables 1, 2). Yarish et al. (1987) acclimated nine species for one month in two temperatures differing by 10°C, but in all cases the survival limits obtained were identical. Yarish et al. (1984) also reported that the tropical species *Solieria tenera* survived for 42 days at 0°C, after being acclimated gradually for 2 weeks to 10 and 5°C.

Ecologically, the temperature tolerance acclimation of *E. linza* and *P. leucosticta* is probably of no importance in their native habitats. As the surface seawater temperature in the Gulf of Thessaloniki ranges between 7 to 27°C (Fig. 3), both species could easily survive without an acclimation potential.

Differences in temperature tolerance according to seasonal changes has often been demonstrated. *Laminaria* spp. and *Desmarestia aculeata* from Helgoland shifted their upper tolerance limit from winter to summer by 2–5°C (Lüning, 1984). The existence of a seasonal change in cold tolerance was reported for other algae (review by Gessner, 1970; Lüning, 1990). Feldmann & Lutova (1963) observed that the heat and cold tolerance of the

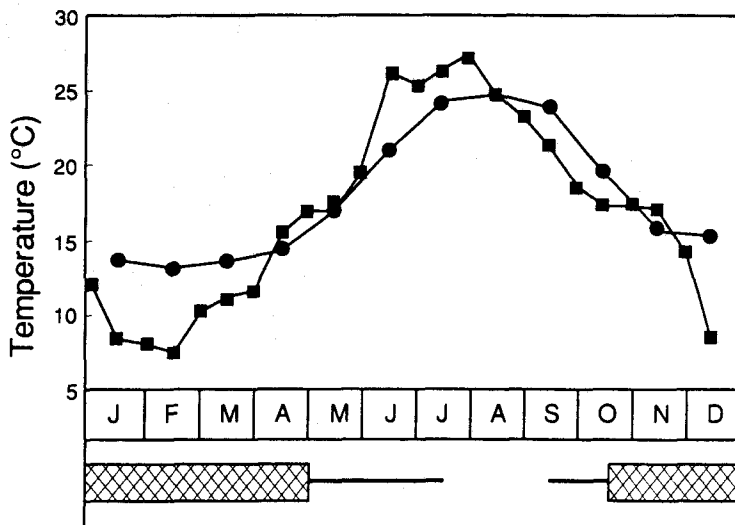


Fig. 3. Surface seawater temperatures in the Gulf of Thessaloniki. ● Monthly mean measurements for 20 years (1952–1972); ■ monthly measurements for 1971. Seasonal occurrence of the population of *Enteromorpha linza* in the Gulf of Thessaloniki: — presence; ▨ growth optimum (after Haritonidis, 1978)

brown algae *Fucus* spp. and *Ascophyllum nodosum* rises and falls in summer, while the opposite occurs in winter. Although these shifts in survival limits were regarded as an acclimation to seasonal changes in temperature, some recent evidence indicates that the lower survival temperature of an alga may increase with decreased day length (Cambridge et al., 1984, 1987, 1990, Yarish et al., 1984, 1986).

Sporophytes of *Laminaria longicuris* acclimated for 4 weeks to 5°C reached their growth maximum at 10–15°C, while those acclimated to 15°C grew maximally at 5°C (Egan et al., 1989). Five or 10°C-acclimated thalli of *E. linza* reached their growth maximum at 15°C, i.e. at a 5°C lower temperature than in the case of 15- or 30°C-acclimated thalli (Fig. 1). No shift of the growth optimum was observed in *Scytosiphon lomentaria* and *Gigartina teedii*, irrespective of acclimation temperature (Orfanidis, 1990). Germlings of *Scytosiphon lomentaria* acclimated to 15°C grew and developed into macrothalli at 5–27°C; while thalli acclimated to 5°C did the same at 5–25°C. Thalli of *Gigartina teedii* acclimated to 15°C grew better at low temperatures than did thalli acclimated to 5 or 30°C (Orfanidis, 1993).

E. linza grows almost all the year round in the Gulf of Thessaloniki, with maximum rates in winter and spring (Fig. 3). Based on the temperature requirements for growth of 15°C-acclimated thalli (maximum at 20°C) *E. linza* may be considered as a "warm-adapted plant". However, the growth vs. temperature curve shifted to lower temperatures, with acclimation to low temperatures. Plants acclimated to 5 or 10°C achieved higher growth rates in percentage of maximum growth at low temperatures than those acclimated to 15 or 30°C (Fig. 1). This potential for growth acclimation probably allows *Enteromorpha* to optimize its growth under limiting temperature conditions in winter and to act as a "cold-adapted plant" during this period.

The stabilization phase (Kinne, 1970) of growth acclimation of *E. linza* continued for more than 1 week. Individuals acclimated for 1 week to 5°C achieved similar growth rates at low temperatures as 15°C-acclimated individuals, when comparing the growth rates in percentage of maximum growth (Fig. 1). After 4 weeks of acclimation to 5°C, the growth rates of *E. linza* at 5°C increased three times more, and at 10°C twice more than the growth rates of 15°C-acclimated individuals, again when compared as percentage of maximum growth rate. An increase of growth rates within the first 2 weeks of acclimation at 0 or 5°C and a following stabilization of growth rates during the next 3 weeks was also reported for *Acrosiphonia sonderi* (Bischoff & Wiencke, 1993).

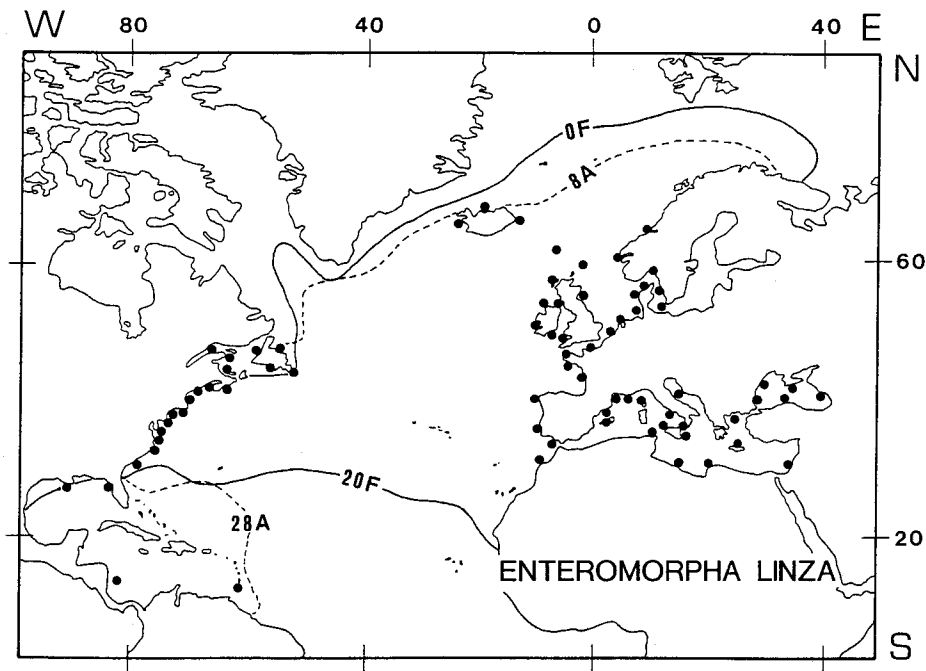


Fig. 4. Distribution of *Enteromorpha linza* in the North Atlantic Ocean. Map shows the geographic distribution and the ocean isotherms for February (F) and August (A) at the distribution boundaries. The oceanic isotherms were adopted from Gorskov World Ocean Atlas (1985). Sources: N Atlantic (South & Tittley, 1986), NE Atlantic (Børgesen & Jonsson, 1905), Iceland (Munda, 1977, 1983, 1985, 1987), Norway (Prinz, 1926; Sundene, 1953; Jorde, 1966), Sweden (Levring, 1935), Denmark (Christensen et al., 1985), Helgoland (Kornmann & Sahling, 1977), Netherlands (Stegenga & Mol, 1983), Belgium (Coppejans & Ben van der, 1980), British Isles (Blackler, 1956; Guiry, 1978; Norton & Powell, 1979; Wilkinson, 1982), N France (Feldmann, 1954; Gayral & Bert, 1965), W France (Lancelot, 1961; Bouxin & Dizerbo, 1971), NW Spain (Perez-Cirera, 1975), Portugal (Ardre, 1970), SW Spain (Seoane-Camba, 1965), Mediterranean (Furnari, 1984), Balears (Ribera & Gómez, 1985), S France (Belsher et al., 1976), Corsica (Boudouresque & Perret, 1977), Tunisia (Meñez & Mathieson, 1981), Libya (Nizamuddin et al., 1978), Israel (Lipkin & Safriel, 1971), Aegean Sea (Athanasiadis, 1987), Black Sea (Zinova, 1967). Morocco (Gayral, 1958), tropical W Africa (Lawson & Price, 1969), E Canada (Cardinal, 1967), N Carolina (Searles & Schneider, 1978), W Florida (Dawes, 1974), Lesser Antilles (Taylor, 1969), Colombia (Schnetter, 1978)

Biogeographically, the northern distribution limit of *E. linza* on the North Atlantic coast (Fig. 4) suggests a northern growth and/or reproduction boundary at the 8°C-August isotherm, which corresponds to a minimum mean summer temperature of 6°C permitting growth and/or reproduction. The experimental data (Fig. 1, Table 3) show that the northern boundary may not represent a growth boundary, but could be considered as a reproduction boundary at the 8°C-August isotherm, despite the absence of reproduction data. The growth acclimation potential of *E. linza* at low temperatures may provide better growth at its northern distribution boundary; it occurs from April to September at Helgoland (Kornmann & Sahling, 1977) and is a summer-fall annual in Iceland (Munda, 1977, 1983, 1985, 1987) and in Newfoundland (South & Hooper, 1980). The ability of *E. linza* to cope with temperatures of 0 or -1°C (Table 3) after being acclimated to 5°C explains its distribution along the eastern coasts of N America up to Newfoundland and in those regions of Europe, e.g. North Sea and Black Sea, in which extreme winter temperatures approach 0°C (Fig. 4). Due to the upper survival temperature limit at 31°C and the temperature requirements for growth of 15°C-acclimated plants, the southern distribution boundary of *E. linza* on the western coasts of the N Atlantic Ocean is a lethal boundary at the 28°C-August isotherm. The temperature tolerance acclimation potential may favour the existence of this species in regions with water temperatures rising to more than 30°C, e.g. at brackish-water habitats in warm temperate regions of N America (Lüning, 1990). The southern distribution limit of *E. linza* on the European/African coasts cannot be explained according to the experimental data (Fig. 1, Table 4). This species could be expected to penetrate further south along the western coasts of Africa.

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