

Laminaria longicruris, *L. saccharina*, *L. digitata*, and *L. nigripes*, the kelps

Background

Laminaria is a genus of brown algae common on temperate and arctic exposed rocky shores in the low intertidal and subtidal zones. In eastern North America the species ranges and depth zones are: *Laminaria longicruris* from Ellesmere Island to Long Island Sound (Taylor 1957), common north of Cape Cod, inhabits the sublittoral region to a depth of 20 m (Sears 2002); *L. saccharina* from Cornwallis Island (Taylor 1957) to Long Island Sound, the dominant kelp in our waters, found in tide pools and from the sublittoral fringe to 5-20 m (Sears 2002); *L. digitata* from Hudson Bay to Connecticut, common north of Cape Cod (Taylor 1957), occupying tide pools and the low littoral zone to 10 m or more (Sears 2002); and *L. nigripes* from the northern tip of Labrador and adjacent northern Quebec (Taylor 1957), the St. Lawrence River estuary, and perhaps a southern extension in offshore, deep water habitats (30-40 m) in the Gulf of Maine (Sears 2002). *Laminaria longicruris* inhabits more sheltered coasts and estuaries; *L. digitata* and *L. nigripes* prefer highly exposed coasts. In all *Laminaria* species each plant attaches to the substrate with a holdfast. In these species the sexes are separate. Each species displays true alternation of generations in which a diploid sporophyte phase alternates with a microscopic haploid gametophyte. In *L. longicruris* maximum reproduction occurs in the fall in the southernmost part of its range, with a secondary peak in the winter months (Van Patten and Yarish 1993). At its southern North American limit zoospore release of *L. saccharina* is at a maximum in May and quickly subsides; reproductive success of female gametophytes also was at a maximum in spring (Lee 1984). In Europe *L. saccharina* sporophytes produce zoospores from autumn to winter, but during all seasons in the Arctic (<http://www.marlin.ac.uk/BIOTIC/> and references therein). *Laminaria digitata* reproduces year-round in Europe with maxima in July-August and November-December (<http://www.marlin.ac.uk/BIOTIC/>). Information on reproduction of *Laminaria nigripes* could not be found. These species exhibit low dispersal (<http://www.marlin.ac.uk/BIOTIC/> and references therein). For example, flagellated zoospores of *Laminaria digitata* may be transported at least 200 m from the parent, and substantial recruitment to areas barren of kelp plants is possible up to 600m away from reproductive plants. But since male and female gametes must settle at a high density (within 1mm of each other) for successful fertilization, it seems unlikely that reproductive stages are a viable mechanism for long distance dispersal. Van den Hoek (1987) concluded that “there is not any evidence available for either supporting or discounting the role of planktonic stages of seaweeds in long-range dispersal”. Long range dispersal of drifting adult *Laminaria* is feasible but only if attached to floating objects or other floating algae such as *Fucus* or *Ascophyllum* (van den Hoek 1987).

Laminaria longicruris was harvested in southwestern Nova Scotia between 1940 and 1949, with sporadic harvesting since (Chapman 1987). *Laminaria digitata* is one of the seaweeds harvested in waters from Newfoundland to Maine for use in agricultural products, livestock feeds, and as a stabilizer and conditioner in paints, cosmetics, and foods.

Temperature limits, critical thresholds, vulnerability, and barriers to adaptation

Laminaria nigripes was not investigated further due to its disjunct distribution and lack of information for the species. For each of the other three species the SSTs in the current distribution range from a February minimum of -2.1°C to an August maximum of 22.8°C.

These brown algae are cold water species as evidenced by their northern distributions and the SSTs they experience. *Laminaria* species have been described as genetically conservative with respect to temperature tolerance, with temperature optima at or above 10°C (Bolton and Lüning 1982, Lüning 1980). Yet these high latitude kelps are adapted to maintain productivity in their extreme environment (Dunton and Dayton 1995). In winter these species experience the coldest water temperatures on earth, yet exhibit adult sporophyte growth, though at a suboptimal level, at least up to 20°C (Bolton and Lüning 1982). Sporophyte temperature optima generally are in the 10-15°C range, though in *L. longicruris* growth decreases prior to temperatures reaching 15°C; at 2-3°C *L. longicruris* continues to grow well but slows considerably at 0°C, while in *L. digitata* good growth continues at 0°C; above the optimal range growth also slows, with upper lethal temperatures among species of 23-24°C (Bolton and Lüning 1982, Egan *et al.* 1989, Egan and Yarish 1990). Gametophyte optima are 10-20°C for *L. longicruris* (Egan *et al.* 1989), and 10-19°C for *L. saccharina*, and 15-18°C for *L. digitata* (Lüning 1980). Upper lethal temperatures for these *Laminaria* gametophytes are 22°C to above 25°C (Bolton and Lüning 1982, Egan *et al.* 1989). Optimal temperatures for fertilization in *L. longicruris* are 10-20°C, but fertilization is prevented at 25°C (Egan *et al.* 1989). Rapidly rising spring temperatures in the southern part of this species' range may be the reason reproduction is delayed to the autumn. Genetic differentiation in temperature tolerance and seasonal acclimation to high summer temperatures in *Laminaria* at different life stages have been reported and were summarized by Egan and Yarish (1990). In addition, populations adapted to unfavourable environments may be more productive under suboptimal conditions (Boyer 1982, in Gerald *et al.* 1987). However, the critical temperatures reported above encompass this thermal flexibility.

Laminaria species, like the rockweeds, ranked the most sensitive of all species in this study. Primarily this was because of their lack of mobility at all life stages, limiting dispersal as a means of adapting to changing temperatures. Eurythermal capacity contributed to low sensitivity only in *L. digitata*, and was due to its more restricted distribution. Within each species it appears that one stage is no more thermally critical than another as optimal temperature ranges and lethal limits are similar across life stages.

Impacts

A 4°C rise in global temperature will impact the future distribution of kelp species in the western North Atlantic to somewhat differing degrees. All models and scenarios suggest that waters will be thermally unsuitable for *L. longicruris* and *L. saccharina* in the southernmost part of their range northward to Cape Cod or the southern Gulf of Maine. For both species half of the model/scenario combinations indicate habitat loss in the

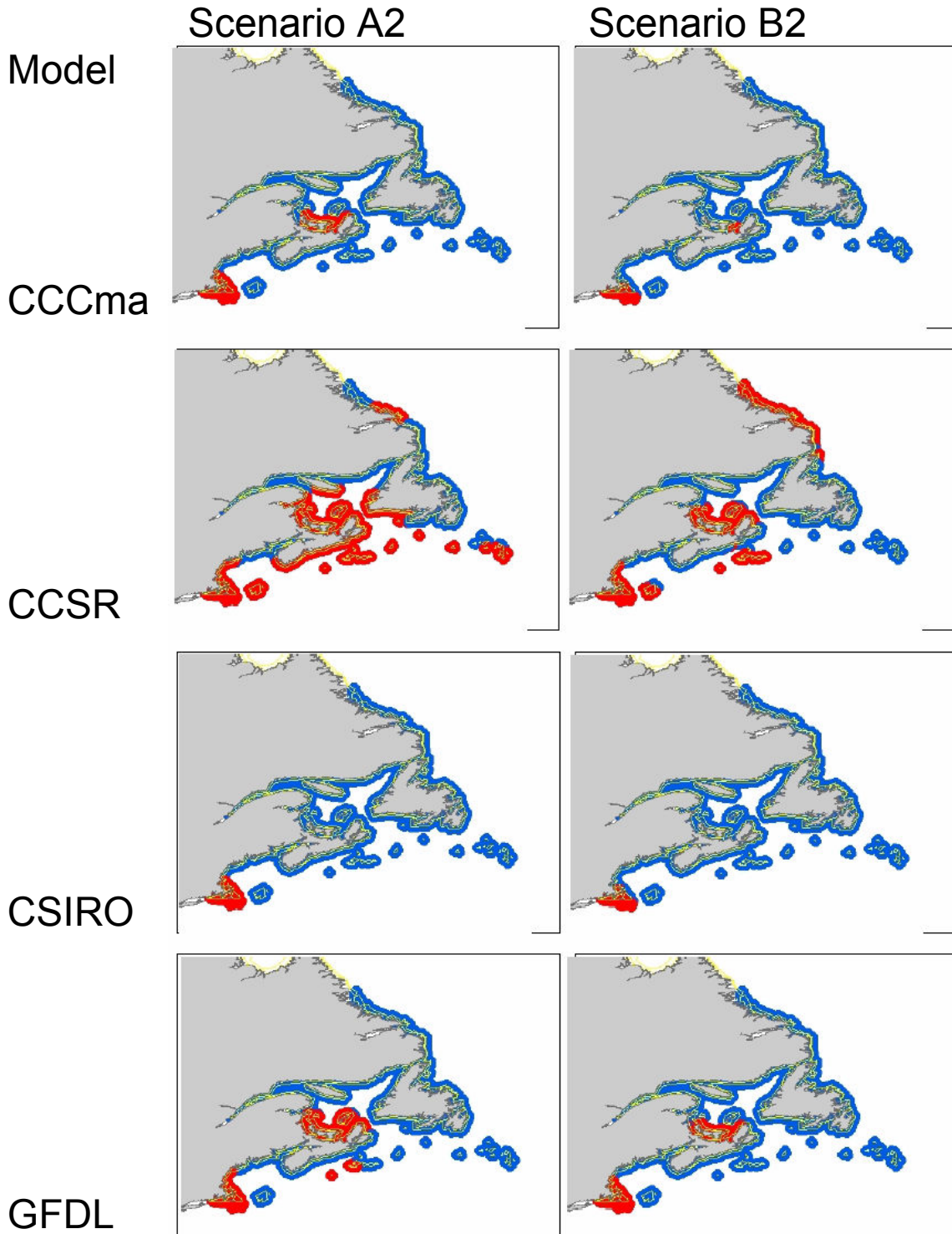
southern Gulf of St. Lawrence. Model CCSR also shows habitat loss in the waters of the northern Scotian Shelf and southern Labrador. Greater Impact is predicted for the distribution of *L. digitata*. All models indicate a loss of thermal habitat from the southern Gulf of Maine southward. Six model/scenario combinations show habitat loss to varying degrees in the southern Gulf of St. Lawrence, with CCSR Scenario A2 predicting additional loss in waters of the northern Gulf, off southern Newfoundland, and all around Nova Scotia. Both scenarios in this model predict loss in southern Labrador waters. All other waters will remain suitable for these *Laminaria* species. No habitat gain was noted as all species range well north of our study region. There likely will be a negative economic impact on the harvest of *L. digitata* in waters of Atlantic Canada which become thermally unsuitable. Economic impact is not a factor for *L. longicuris* or *L. saccharina* as they are not harvested commercially.

Laminaria lack mobility at all life stages, limiting dispersal as a means of adapting to changing temperatures. The existence of these species will not be threatened as their distributions extend into northern waters where conditions will remain thermally suitable. But where temperatures become unsuitable plants will be unable to survive, despite the adaptation of more southern individuals to higher temperatures, as in *L. saccharina* (Gerard *et al.* 1987). This is because the southern limits of these species correspond to their southern lethal boundary (van den Hoek 1982, in Egan *et al.* 1989). With global warming kelp growth will increase in regions where optimal temperatures are experienced for longer portions of the year. But in more southern regions temperatures will rise above the growth optima for longer periods, extending the duration of reduced growth. Production of sorus (reproductive) tissue in *L. longicuris* in southern regions is minimal during the hottest months (Egan and Yarish 1990). Likely climate warming will extend the summer season of low sorus production in these waters. Egan and Yarish (1990) hypothesized that seasonal changes in kelp blade morphology (smooth versus indented/corrugated outer edges) are survival adaptations for temperature extremes in southern waters. Smooth edges provide less surface area exposed to adverse temperatures. Thus global warming may lead to geographic changes in kelp blade morphology as higher temperatures are experienced further north. As surmised for *Ascophyllum nodosum* (Bertness *et al.* 1999), loss of the algal canopy, particularly in the upper intertidal zone of rocky shores, will increase substantially substrate temperatures and evaporative water loss, and negatively impact recruitment, growth, and survival of understory organisms. This thermal stress may lead to variable changes in ecological dynamics of predators, prey, and the algal canopy, such as a lowering of the vertical intertidal limit of barnacles resulting from canopy loss (Leonard 2000).

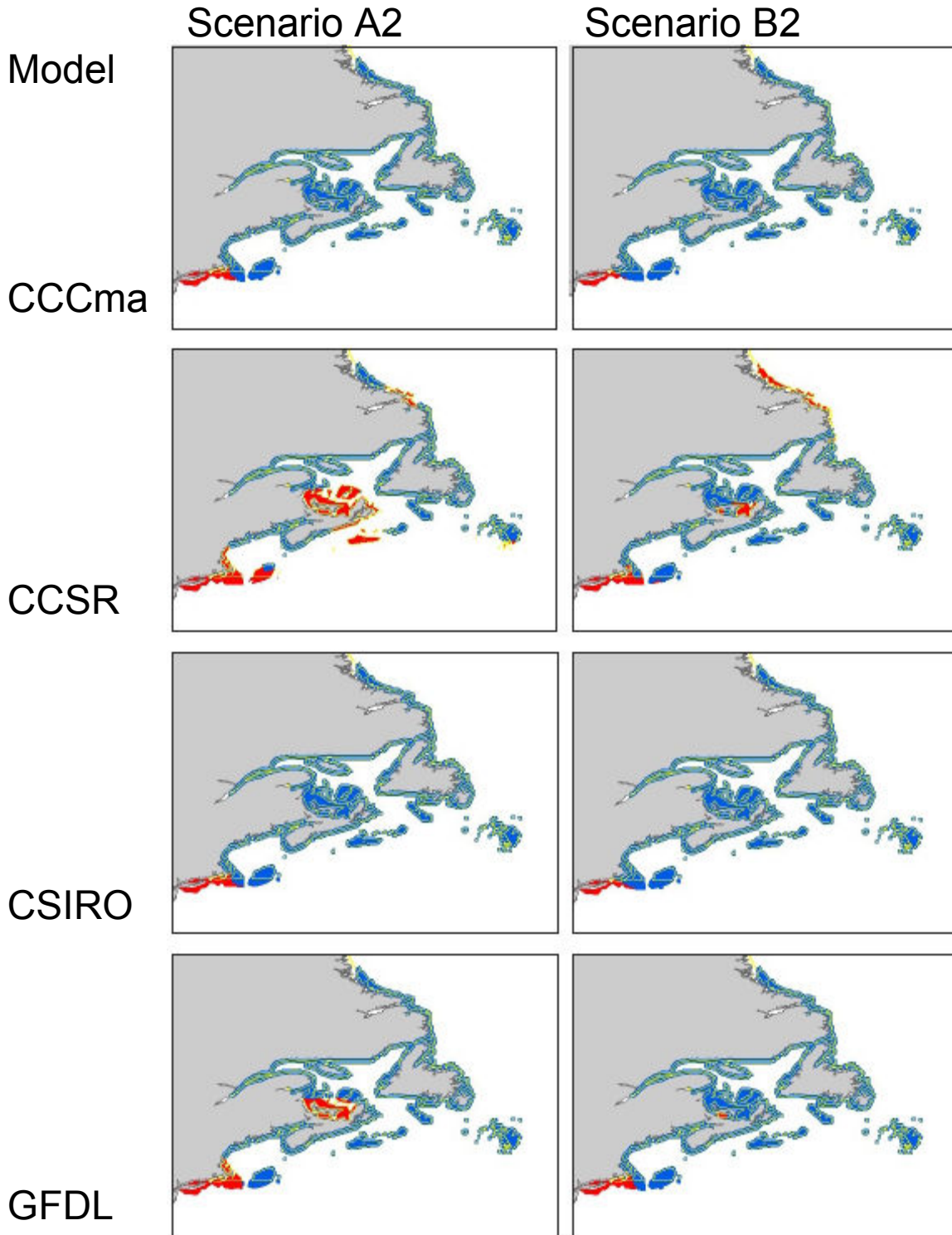
References

- Bertness, M.D., G.H. Leonard, J.M. Levine, P.R. Schmidt, and A.O. Ingraham. 1999. Testing the relative contribution of positive and negative interactions in rocky intertidal communities. *Ecology* 80(8): 2711-2726.
- Bolton, J.J., and K. Lüning. 1982. Optimal growth and maximal survival temperatures of Atlantic *Laminaria* species (Phaeophyta) in culture. *Marine Biology* 66: 89-94.

- Chapman, A.R.O. 1987. The wild harvest and culture of *Laminaria longicruris* in Eastern Canada. In: Doty, M.S., J.F. Caddy, and B. Santelices (Eds.). Case Studies of Seven Commercial Seaweed Resources. *FAO Fisheries Technical Paper* 281.
- Dunton, K.H., and P.K. Dayton. 1995. The biology of high latitude kelp. In: Ecology of fjords and coastal waters: Proceedings of the mare Nor Symposium on the ecology of fjords and coastal waters, Tromsø, Norway, 5-9 December 1994, pp. 499-508.
- Egan, B., A. Vlasto, and C. Yarish. 1989. Seasonal acclimation to temperature and light in *Laminaria longicruris* de la Pyl. (Phaeophyta). *Journal of Experimental Biology and Ecology* 129: 1-16.
- Egan, B., and C. Yarish. 1990. Productivity and life history of *Laminaria longicruris* at its southern limit in the western Atlantic Ocean. *Marine Ecology Progress Series* 67: 263-273.
- Gerard, V.A., K. DuBois, and R. Greene. 1987. Growth responses of two *Laminaria saccharina* populations to environmental variation. *Hydrobiologia* 151/152: 229-232.
- Lee, J.A. 1984. Seasonal reproduction patterns of *Laminaria saccharina* (L.) Lamour (Phaeophyta) at its southern limit of distribution in the western Atlantic Ocean. *Journal of Phycology* 20. Viewed online in Aquatic Sciences and Fisheries Abstracts, CSA Illumina, <http://www.csa.com/>.
- Leonard, G.H. 2000. Latitudinal variation in species interactions: a test in the New England rocky intertidal zone. *Ecology* 81(4): 1015-1030.
- Lüning, K. 1980. Critical levels of light and temperature regulating the gametogenesis of three *Laminaria* species (Phaeophyceae). *Journal of Phycology* 16: 1-15.
- Sears, J.R. (Ed.). 2002. *NEAS keys to benthic marine algae of the northeastern coast of North America from Long Island Sound to the Strait of Belle Isle*. 2nd edition. Express Printing, Fall River, MA. NEAS Contribution Number 2.
- Taylor, W.R. 1957. *Marine algae of the northeastern coast of North America*. University of Michigan Press, Ann Arbor, MI. 509 p.
- van den Hoek, C. 1987. The possible significance of long-range dispersal for the biogeography of seaweeds. *Helgoländer Meeresunters* 41: 261-272.
- Van Patten, M.S., and C. Yarish. 1993. Allocation of blade surface to reproduction in *Laminaria longicruris* of Long Island Sound (USA). *Hydrobiologia* 260-261(1): 173-181.



Changes predicted in the thermal range of *Laminaria digitata* on the Northwest Atlantic as a result of sea surface temperature changes expected to accompany a 4°C global average increase in surface air temperature projected by four AOGCMs through the A2 and B2 scenarios. Red indicates loss of thermal range, green increase, and blue no change. Cross-hatching indicates the species' modern distribution.



Changes predicted in the thermal range of *Laminaria longicruris* on the Northwest Atlantic as a result of sea surface temperature changes expected to accompany a 4°C global average increase in surface air temperature projected by four AOGCMs through the A2 and B2 scenarios. Red indicates loss of thermal range, green increase, and blue no change. Cross-hatching indicates the species' modern distribution.