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ORIGINAL PAPER

Temperature mediates the outcome of species interactions in early life-history stages of two sympatric kelp species

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Abstract

Ocean warming can mediate species interactions and provoke changes in community structure worldwide. Species interactions vary along environmental gradients and life-history stages and increasing temperatures may change competitive dominance between species. Kelps, being marine foundation species, have a complex heteromorphic life cycle, with the early developmental stages being a bottleneck for successful establishment of the adult population. Here, we investigated how temperature influences interactions in early life-history stages of two kelp species with different thermal affinities (*Alaria esculenta* and *Laminaria digitata* from Spitsbergen) by cultivating them in mono- and co-culture and different temperatures. Irrespectively of cultivation treatment, spore germination, gametogenesis, and sporophyte development of both species were mostly positively stimulated by a temperature increase from mean ambient summer temperatures (4–5 °C) to a global warming scenario for the Arctic future (9–10 °C) but not at 15 °C which is the southern temperature limit of *A. esculenta*. At 15 °C gametogenesis and sporophyte formation of *A. esculenta* were greatly inhibited in monoculture but not so in *L. digitata*. On the other hand at 5 °C and 10 °C, gametogenesis and sporophyte growth were generally faster in *A. esculenta* than in *L. digitata*, leading to a competitive advantage of *A. esculenta* over *L. digitata* in the co-cultivation treatments. The interactive effects of co-cultivation and temperature were evident, where development of *A. esculenta* was accelerated in the presence of *L. digitata* at 9 °C but not at 4 °C. Although the mechanisms triggering interspecific interactions were not determined in this study, future global warming was found to give competitive advantage of *A. esculenta* over *L. digitata*, which could affect community structure and dominance in coastal environments.

Introduction

In the marine realm kelp, forest ecosystems are essential elements of eulittoral and sublittoral zones in temperate-to-polar seas (Bold and Wynne 1985). In terms of biomass, the dominant kelps (Laminariales, Phaeophyceae) are not only important primary producers but also fundamental in the formation of habitats. They provide structural heterogeneity and increase the number of ecological niches (Dayton 1985; Bartsch et al. 2008).

The three most important processes that control the development of kelp forests are recruitment, growth, and competition (Steneck et al. 2002). Both recruitment and growth rely on the interaction of a diversity of abiotic factors, most importantly nutrient availability, light, and temperature (Steneck et al. 2002), and may influence the outcome of species interactions (Hurd et al. 2014; Brooks and Crowe 2018). While plant–herbivore interactions are manifold and well documented (e.g., Morelissen and Harley 2007, reviewed in Hurd et al. 2014), kelp–kelp interactions have only rarely been studied (e.g., Reed 1990; Dayton 1985; Traiger and Konar 2017). Interspecific interactions are considered as a major selective force in structuring marine benthic communities (Connell 1983; Branch 1984). They are classified in either negative (competition) or positive

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interactions (facilitation) (Hurd et al. 2014). Interspecific interactions between seaweeds have been shown to be mostly negative, and can be divided into exploitative competition (e.g., more effective utilization of resources or reservation/retention) and interference competition (overgrowth or allelopathy) (Nabivailo and Titlyanov 2006; Hurd et al. 2014). However, some positive interactions have been reported as well (reviewed in Santelices 1990; Barner et al. 2016, Hurd et al. 2014).

Observing species interactions in kelps in nature is especially complicated as they have a complex heteromorphic, diplohaplontic life cycle including very small life-history stages (Reed 1990). Perennial diploid sporophytes of up to several meters length release haploid unicellular motile spores, which settle and form female and male microscopic haploid gametophytes (Bold and Wynne 1985). During gametogenesis, eggs and sperm are released from the gametophytes. They fuse and grow into a macroscopic sporophyte again, closing the cycle. Once the spores have settled on hard substrate, several kelp species co-exist in space and time and interspecific interactions become more likely than in the planktonic phase. Interspecific interactions during the microscopic phase of kelp development have the potential to be a deciding factor in regulating adult macroalgal assemblages (Amsler et al. 1992; Traiger and Konar 2017).

Reed (1990) showed that interspecific competition already occurred between microscopic kelp stages and caused species-specific differences in early mortality. In the NE Pacific, spore settlement of the kelp *Pterygophora californica* generally inhibited the recruitment of *Macrocystis pyrifera*, possibly due to a faster gametogenesis of the first species or chemical interaction between both species, while on the other hand, settlement of *Macrocystis* spores did not influence *Pterygophora* recruitment (Reed 1990). In another competition study on macroalgae, the green ephemeral alga *Ulva* reduced growth of a fucoid species in New Zealand in laboratory experiments (Alestra and Schiel 2014). The outcome of the interactions between the two species was strongly altered by abiotic and biotic factors, such as salinity, nutrient concentration, and grazing pressure.

The recent report of the Intergovernmental Panel on Climate Change identified the Arctic as one of the most rapid warming sub-regions of the world (IPCC 2012). Arctic seawater surface temperatures are predicted to rise between 2 and 5 °C or even more until the end of this century, depending on the used model (IPCC 2012). Since temperature is one of the most fundamental determinants for the development of kelps during all life-history stages, including germination, gametogenesis, and recruitment (Lüning 1990), changing temperatures may not only affect the development of single species but also alter species interactions (Nabivailo and Titlyanov 2006; Lathlean et al. 2017; Griffith et al. 2018; Brooks and Crowe 2018). Furthermore, within one species, each life-history stage has its own optimum temperature for development and survival (e.g., Lüning 1980; tom Dieck 1992; Martins et al. 2017).

The two kelp species *A. esculenta* (Linnaeus) Greville and *L. digitata* (Hudson) J.V. Lamouroux are sympatric throughout most of their distribution area (Lüning 1990). In the North-East Atlantic, records of both species range from Arctic Svalbard (Fredriksen and Kile 2012) to southern range-edge populations in Brittany, France (Loiseaux-de Goër and Noailles 2008). *Laminaria digitata* has a wider temperature tolerance range than *A. esculenta* and the latter is considered to be the more northern species as it does not occur in the North Sea or English Channel (Munda and Lüning 1977). While *L. digitata* sporophytes usually survive 19–20 °C (Bartsch et al. 2013), *A. esculenta* sporophytes perish already at 16–17 °C in the field (Sundene 1962; Munda and Lüning 1977). Similarly, gametophytes of *L. digitata* are more tolerant surviving 23–24 °C while those of *A. esculenta* only survive 19–21 °C (tom Dieck 1993). In Kongsfjorden, Spitsbergen, at our sampling site, both species co-exist at depths between 0 and 10 m but exhibit variable dominance patterns, which have changed in recent years (Hop et al. 2002, 2012, 2016; Bartsch et al. 2016). While in 1997/98, video-transects along Kongsfjorden revealed a similar amount of both kelp species at 3–5 m depths, *A. esculenta* seemed to be more prominent at deeper sites (Hop et al. 2016). Recently, *L. digitata* became more dominant at low depths (2.5 m), while *A. esculenta* increased its depth distribution (Bartsch et al. 2016). This change can be partly explained by abiotic changes, such as temperature increase, sea ice loss, and changed irradiance conditions, but altered biotic interactions may have contributed to these changes as well. Both species are summer-fertile (Olischläger and Wiencke 2013), and as their sporophytes co-exist in the field, their microscopic life-history phases potentially interact as shown for other species (Reed 1990; Santelices 1990; Traiger and Konar 2017). As *A. esculenta* sporophytes are more sensitive to higher temperatures than *L. digitata* (tom Dieck 1992, 1993; Munda and Lüning 1977), changes in the temperature conditions during the microscopic life-history stage may possibly affect the competitiveness of both species and thereby have the potential to cause a structural reorganization of the entire seaweed community (Nabivailo and Titlyanov 2006). If a species with a different ecosystem engineering function becomes more dominant, the local biodiversity may change. This has been demonstrated in the western English Channel. A kelp forest dominated by *Laminaria hyperborea*, a species bearing a rich stipe epibiont community, was invaded and partially replaced by *Laminaria ochroleuca,* a species with a smooth clean stipe without epibionts, resulting in functional changes of the kelp forest (Smale et al. 2015).

Early life-history stages are particularly known to suffer from high mortality and represent a critical bottleneck

in the development and persistence of adult stands (Vadas et al. 1992; Alestra and Schiel 2014). The variation in spore settlement, abiotic condition (Wiencke et al. 2006; Zacher et al. 2016), and early interspecific interactions, may all significantly affect patterns of kelp recruitment. Effects between these factors may be interactive with varying relative importance between species, location, and time (Reed 1990; Santelices 1990). To investigate how temperature affects species interactions between kelp species from Kongsfjorden, uncontrollable factors needed to be excluded. In addition, a direct observation of these small stages in the field is difficult. Thus, a mechanistic approach under controlled conditions in the laboratory was chosen (Edwards and Connell 2012; Hurd et al. 2014). We investigated the species interactions of all microscopic stages (spores, gametophytes, and juvenile sporophytes) of *A. esculenta* and *L. digitata* at present and potential future Arctic summer seawater temperatures (4–5 °C and 9–10 °C) and at temperatures near to the current southern distribution limit of the species (15 °C). As the competitive ability of organisms is affected by abiotic conditions, we hypothesized that an increase in temperature changes species interactions in the two kelp species, possibly varying along the different life-history stages. By comparing responses of co-cultivated and mono-cultivated life-history stages in a factorial design along a temperature gradient, we add data to the low body of evidence supporting that species interactions between both kelp species take place at all investigated developmental levels. Thereby, we broaden the mechanistic understanding on interspecific interactions in relation to temperature in important kelp species.

Materials and methods

Experimental design

Three laboratory experiments on early life-history processes of *A. esculenta* and *L. digitata* from Spitsbergen populations were performed. An overview of all experiments is given in Fig. 1. Potential interspecific interactions of early life-history stages between species was investigated in two-factorial experiments (factors cultivation and temperature) starting from different points in their life history, i.e., from field-derived spores (experiment 1), from juvenile sporophytes obtained from cultures (experiment 2 and 3b) and from dormant (vegetative) gametophytes from cultures (experiment 3a). All experimental set-ups were controlled via their initial density and subjected to two temperatures, either simulated current and projected summer temperatures at Spitsbergen (4° and 9–10 °C; experiments 1 and 2) or simulated mean summer temperatures at the northern and southern distribution boundary of both species (5° and 15 °C; experiment 3).

Theoretical background and derivation of hypotheses

The intention of the experiments was to reveal possible interspecific interactions between *A. esculenta* and *L. digitata* during their different life-history stages along an ecologically derived temperature gradient. To do so, we either cultivated the species in monoculture or in co-culture, mixing different life-history stages of both species in a controlled

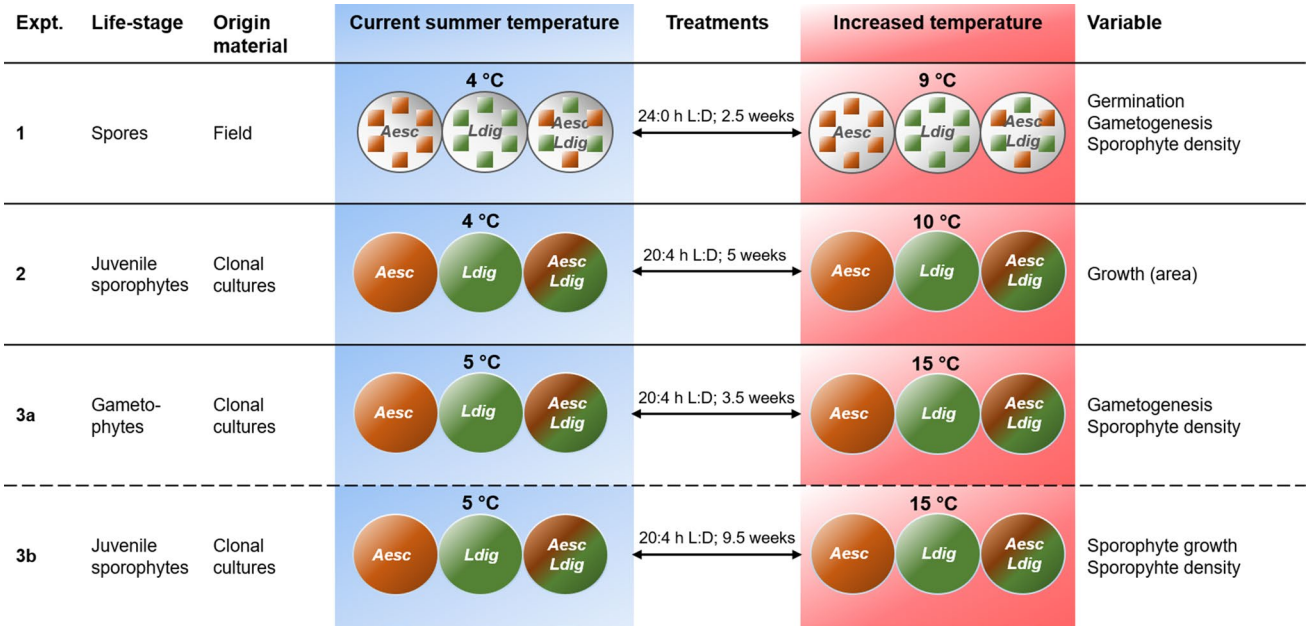

Fig. 1 Overview over the experimental design of the three experiments. L:D = light:dark hours, $n = 5$; irradiance all experiments 12–13 µmol m^{-2}

manner. Our experimental design will allow us to measure response variables, e.g., growth ability under monoculture in comparison to their competitive ability to grow in co-culture, but will not allow us to determine the mechanism of competition, e.g., consumption of nutrients or exudation of allelochemicals, to suppress a competitor. Due to the fact that both kelp species have a different temperature performance (Munda and Lüning 1977; tom Dieck 1993), we assumed that co-cultivation of both species may lead to interspecific interactions mediated by temperature.

During gametogenesis, interference competition through allelochemical compounds, e.g., pheromones (Lüning and Müller 1978; Müller 1981), has been discussed earlier (Reed 1990; Bollen 2017; Martins et al. 2019), but final evidence has not been provided. We hypothesized that the species with a faster egg release will negatively influence the recruitment of the species with a slower gametogenesis in co-cultivation treatments. Male gametophytes of both species will potentially release their sperm upon the universal pheromone signaling after egg release of the faster species. This would become visible in a reduced recruitment of juvenile sporophytes of the respective slower species in the co-cultivation treatment compared to the mono-cultivation treatment (experiment 1 and 3a). As gametogenesis in kelps is temperature dependent (tom Dieck 1992; Martins et al. 2017, 2019), this pattern should vary along the temperature gradient.

During sporophyte recruitment and sporophyte growth (experiment 2 and 3b), we hypothesized that exploitative competition is more likely to occur as juvenile sporophytes grow very fast, possibly favoring the species with the better or higher nutrient uptake capacity (Brooks and Crowe 2018) in co-cultivation treatments and suppressing growth or outcompeting the slower species. As temperature is considerably influencing sporophyte recruitment and growth rate in a species-specific manner (e.g., Zacher et al. 2016; Martins et al. 2019), and uptake kinetics of nutrients have also been shown to be species-specific and life-history dependent (Lubsch and Timmermanns 2019; Roleda and Hurd 2019), the interaction could change along the temperature gradient and developmental stage of the kelp. It is known that interspecific interactions may change under changing temperature conditions from, e.g., a neutral interaction between sympatric species under current temperatures to an interaction that becomes negative for one of the two species and/or positive for the other under increasing temperatures.

Experiment 1: effects of co-cultivation on germination, gametogenesis, and sporophyte density at current and projected Arctic summer temperatures

Material Fourteen fertile individuals of *A. esculenta* and eight fertile individuals of *L. digitata* were collected by SCUBA divers in August 2014 at Hansneset, Kongsfjorden (78′ 99° N, 11′ 57° E, Spitsbergen) in 2–7 m water depth. The kelps were brought directly to the laboratory and kept in running seawater (ambient temperatures approx. 5 °C) until further processing. Spores were released according to Clayton and Wiencke (1986). The spores of all individuals per species were checked for viability under the microscope and pooled if they looked healthy. Spore densities were determined with an improved Neubauer counting chamber (Brand, Wertheim, Germany) and normalized to approx. 12.500 spores cm^{-2} for both species by dilution with sterile filtered seawater (2.7 µmol GF/D filter; Whatman, GE Healthcare Life Sciences, Little Chalfont, Great Britain) and enriched with full Provasoli nutrient solution (PES; after Provasoli 1968 but with HEPES instead of TRIS buffer and double amount of phosphate).

Experimental set-up Spore solutions of each species were seeded separately into plastic dishes (Ø 9 cm) containing 100 mL filtered PES and six cover slips (No 3, Menzel, Germany). The cover slips containing *A. esculenta* were marked with a diamond pen for identification in the co-cultivation treatment. After 24 h, the spores had settled and the cover slips were transferred to experimental plastic dishes (Ø 9 cm, with 100 mL PES). In a two-factorial design, the dishes ($n = 5$) were exposed to two temperatures (4 °C and 9 °C) and to the following cultivation treatments over 16 days: (1) mono-specific *A. esculenta* (six coverslips per plastic dish), (2) mono-specific *L. digitata* (six coverslips per plastic dish), and (3) co-cultivated *A. esculenta*/*L. digitata* (three cover slips of each species alternately combined in one plastic dish with approx. 0.5 cm distance between each cover slip, see Fig. 1). Although gametophytes and small sporophytes were not identifiable to species level during the experiment, species in the co-cultivation treatment could be identified by the mark on the *A. esculenta* slips. Irradiance was set to 13 µmol photons m^{-2} s^{-1} (OSRAM L36 W/965, Biolux, München, Germany) with 24 h continuous light and measured regularly with an LI-COR LI-250A light meter (LI-COR Inc., Lincoln, USA). The culture medium was exchanged once on day 15.

Quantification of germination and gametogenesis Germination rates were counted on day 3. A spore was classified as germinated if a germ tube was visible. Gametogenesis and sporophyte density were quantified microscopically with a 20 × seawater immersion objective on days 10 and 16 by recording the furthest developmental stage per female gametophyte in 4 classes: (1) vegetative female gametophyte, (2) female gametophyte with oogonium, (3) female gametophytes with released eggs, and (4) juvenile sporophytes. Sporophytes were classified as such after the first cell division of zygotes became visible. In each replicate, 300 spores/female gametophytes in the mono-specific and 200 spores/gametophytes per species in the co-cultivation treatments were classified with a net micrometer (No. 464027, Zeiss,

Göttingen, Germany). The use of the net micrometer allowed to additionally calculate the density per area. We did not count male gametophyte development as it was not possible to convincingly quantify unreleased versus released antheridia. The latter comparison would be essential to determine whether male gamete release from one species is induced in the presence of the co-occurring other female gametophytes. In another study, we observed qualitatively that male gametophytes were densely covered with unreleased antheridia if cultivated alone. In the presence of *L. digitata* females, on the other hand, male *A. esculenta* showed released antheridia under otherwise identical cultivation conditions (Daniel Moreno 2015).

Experiment 2: effects of co-cultivation on growth of juvenile sporophytes at current and projected Arctic summer temperatures

Material Vegetative clonal gametophyte stock cultures originally derived from Kongsfjorden, Spitsbergen, were used. Each pair of gametophytes was derived from one single sporophyte. Four clonal gametophyte strains of *A. esculenta* were pooled in similar quantities (AWI culture numbers 3405♀/3406♂, 3413♀/3414♂, 3415♀/3416♂ and 3417♀/3418♂, isolated in 2012), while only one gametophyte strain of *L. digitata* was available (AWI culture number 3200♀/3199♂, isolated in 2002). The gametophytes were carefully ground with pestle and mortar, fertilized and pre-grown for 7 weeks at 12 °C, in a 16:8 h light:dark (LD) cycle and an irradiance of 7 µmol photons m^{-2} s^{-1} according to the methods of tom Dieck (1992) to grow juvenile sporophytes. After fertilization, juvenile sporophytes were cultivated until they reached a suitable size for the experiment. During this pre-cultivation phase, hundreds of sporophytes (ranging in sizes from mm to cm) were kept in suspension in aerated 5 L glass beakers filled with sterile seawater and nutrient addition. The medium was exchanged weekly. One week prior to the start of the experiment, 620 juvenile sporophytes of each species with 1–3 cm length were separated and further grown at 9 °C in aerated 2 L glass beakers containing sterile filtered PES (2.7 µmol GF/D filter; Whatman, GE Healthcare Life Sciences, Little Chalfont, Great Britain).

Experimental set-up In a two-factorial design, pre-cultivated sporophytes of the same size class (see below) were exposed to two temperatures (4 °C and 10 °C) and to the following cultivation treatments in aerated 2 L beakers filled with 1800 mL PES ($n = 5$) for 5 weeks: (1) mono-specific *A. esculenta* (30 sporophytes per beaker), (2) mono-specific *L. digitata* (30 sporophytes per beaker), and (3) co-cultivated *A. esculenta*/*L. digitata* (15 sporophytes of each species per beaker). The young sporophytes of both species in the combined culture could be clearly distinguished by their different morphology (see Fig. 2). Irradiance was set to 12 µmol photons m^{-2} s^{-1} (OSRAM L36 W/965, Biolux, Muenchen, Germany) in a 20:4 h LD cycle and measured regularly with an LI-COR LI-250A light meter (LI-COR Inc., Lincoln, USA). Culture medium was exchanged weekly and the sporophytes were transferred to bigger glass bottles containing 5 L PES after 2 weeks.

Growth determination growth was determined every 7 days as per the increase of blade area of all sporophytes per replicate by taking digital photographs on a light table together with a reference square over 5 weeks. Blade areas were analyzed with the imaging software WinFolia Pro 2006a (Rainbow Technologies, USA). At the beginning of the experiment, 15 randomly sampled sporophytes of each species were measured and taken as the starting point. All data in the mono-specific treatments were normalized to 15 sporophytes to be comparable to the respective co-cultivation treatments.

Experiment 3: effect of co-cultivation on gametogenesis and sporophyte growth at temperatures simulating summer temperatures near the northern and southern distribution range

Two integrated two-factorial experiments were set up, following the response in two consecutive life-history phases. In experiment 3a, gametogenesis and early sporophyte development were observed until day 24. In experiment 3b, sporophyte length and density was quantified until day 67 (see Fig. 1).

Material The same vegetative clonal gametophyte stock cultures of *A. esculenta* and *L. digitata* were used as described in experiment 2. Multicellular vegetative male and female gametophytes of each species were ground carefully into few-celled gametophyte fragments with pestle and mortar. The suspensions were sieved through a sterile 100 µm sieve and the filtered material was subsequently sieved through a sterile 63 µm sieve. The remaining gametophyte fraction consisted of multicellular gametophytes with a mean length of 196 µm (variation 49–441 µm) which was diluted with 150 mL sterile seawater and served as stock solution for the experiment. The gametophyte density of each stock solution was determined with a net micrometer (No.464027, Carl Zeiss Microscopy GMBH, Germany) and was adjusted to 300–400 gametophyte fragments cm^{-2} with sterile filtered PES.

Experimental set-up The gametophyte stock solutions were seeded into small petri dishes (∅ = 5.3 cm) containing 12 mL PES (Experiment 3a) and into sterile crystal dishes (∅ = 9 cm) equipped with 5 frosted glass slides (2.5 × 1.9 cm) containing 50 mL PES (Experiment 3b). In a two-factorial design, the small petri dishes and the crystal dishes ($n = 5$, each) were exposed to two temperatures

Fig. 2 Morphological differentiation between juvenile *A. esculenta* (above) and *L. digitata* (below). Scale bars: 1 cm

(5 °C and 15 °C) and to the following cultivation treatments for 24 and 67 days, respectively: (1) mono-specific *A. esculenta* (300–400 gametophyte fragments cm^{-2}, ½ male and ½ female of *A. esculenta*), (2) mono-specific *L. digitata* (300–400 gametophyte fragments cm^{-2}, ½ male and ½ female of *L. digitata*), (3) co-cultivated and pooled *A. esculenta* and *L. digitata* (300–400 gametophyte fragments cm^{-2}, ¼ male and ¼ female of *A. esculenta*, ¼ male and ¼ female of *L. digitata*). Identification of species in the pooled co-cultivation treatment was not possible during the microscopic phase (Experiment 3a), because gametophytes and sporophytes were too small at this stage of the experiment. Therefore, in experiment 3b, kelps were cultivated until day 67, when it became possible to distinguish the two species in the co-cultivation treatment by their characteristic morphology (see Fig. 2). Irradiance was set to 12 ± 1 µmol photons m^{-2} s^{-1} (OSRAM L36W/965, Biolux, München, Germany) over a 20:4 h LD cycle and measured regularly with an LI-COR LI-250A light meter (LI-COR Inc., Lincoln, USA). Culture medium in the small petri dishes was exchanged partly on day 18 (Experiment 3a). The frosted glass slides from the crystal dishes were transferred to 3 L beakers on day 19 to provide sufficient space and medium for the growing sporophytes and culture medium was subsequently changed weekly (Experiment 3b).

Experiment 3a Gametogenesis was observed microscopically (Axiophot Ilford, FR4 135 DX 36, Germany) in the small petri dishes on days 4, 8, 12, 16, 20, and 24 by counting 300 female gametophytes per replicate and recording the furthest developmental stage as described for Experiment 1.

Experiment 3b On day 67, when it became possible to distinguish the two species by their characteristic morphology (see Fig. 2), all material was scraped off the slides and the length of the 10 largest sporophytes per replicate was measured. The density of all sporophytes ≥ 0.5 cm was counted per replicate to calculate total sporophyte densities. Smaller sporophytes were not readily discernable to species level and thus not considered.

Statistical analyses

All statistics were performed with Statistica 6 or 7 (StatSoft Inc., Tulsa, OK, USA) or Graph Pad Prism 6.03. Homogeneity of variances were tested with the Levene's test, Cochran test, or the Brown–Forsythe test. Percentage sporophyte data were arcsin transformed (Experiment 3a). When repeated-measures (RM) ANOVAs were performed, sphericity was tested (Mauchley's test) and if significant, P values were adjusted according to Greenhouse–Geisser. Differences between groups were evaluated with the Tukey post hoc test. The significance level was $P < 0.05$.

Experiment 1 Similarity of initial spore densities (day 3) was tested with a uni-factorial ANOVA. Two two-factorial ANOVAs were performed to test for cultivation and temperature effects on the germination rates of *A. esculenta* and *L. digitata,* respectively (on day 3), and for absolute sporophyte numbers on day 16 for each species separately. Two RM ANOVAs were performed to test for cultivation and temperature effects on sporophyte densities over time for each species separately (Online Resources 1 and 2).

Experiment 2 Similarity of initial blade areas (day 0) was tested with a *t* test for independent samples between both species. Two RM ANOVAs were performed to test for cultivation and temperature effects on blade area over time for each species separately.

Experiment 3*a* Similarity of initial gametophyte density (day 0) was tested with a two-way ANOVA (species and temperature treatment). The pace and magnitude of sporophyte development in mono-specific cultures of *L. digitata* and *A. esculenta* was tested in an RM ANOVA (factors 'species' and 'time') between days 8–24 for the 5 °C treatment. The speed and magnitude of sporophyte development in mono-specific cultures of *L. digitata* in relation to temperature was tested in an RM ANOVA (factors 'temperature' and 'time') between days 8–24 for the 5 and 15 °C treatment. *Alaria esculenta* was excluded from the analysis as it did not form sporophytes at 15 °C. As species identification was not possible during the microscopic phase, potential effects of co-cultivation on sporophyte development could only be related to an expected reference value, namely the mean of the two mono-specific treatments (length and density of sporophytes). Values differing significantly from the mean of the expected values in a one-sided *t* test indicate a possible interaction between both species in the co-cultivation treatment. As no *A. esculenta* sporophytes developed at 15 °C, this test was only performed for day 20 at 5 °C when sporophyte development was first saturated in *A. esculenta*.

Experiment 3*b* 5 °C: On day 67, sporophyte identification was possible to species level. All sporophytes > 0.5 cm were counted and assigned to either *L. digitata* or *A. esculenta* (see Fig. 2), and their density and the length of the 10 largest sporophytes were tested in a one-way ANOVA. This was carried out for the 5 °C treatment only as the 15 °C culture was contaminated and could not be evaluated. *Laminaria digitata* from the co-cultivation treatment was excluded as there were only zero values.

Results

Experiment 1: effects of co-cultivation on germination, gametogenesis, and sporophyte density at current and projected Arctic summer temperatures

No significant difference between spore density of the two species in both temperature treatments was detected (day 3; mean = 13,000 spores $cm^{-2} \pm 3000$ SD, one-way ANOVA, $P = 0.78$). In general, germination rates of both species were significantly higher at 9 °C compared to 4 °C (Fig. 3a and b, Tables 1 and 2). When *A. esculenta* was co-cultivated with *L. digitata,* the germination rate was significantly higher compared to the mono-specific *A. esculenta* treatment, but only at higher temperatures (temperature*cultivation interaction, Fig. 3a, Table 1). No interactive effect was present in *L. digitata* (co-cultivated vs. mono-specific treatment) (Fig. 3b, Table 2).

Table 1 Experiment 1: results from analyses of variance (two-way ANOVA) for single and combined effects of 'cultivation' (mono-specific vs. co-cultivated spores) and 'temperature' (Temp; 4 and 9 °C) on germination rates of *A. esculenta* ($n = 5$)

	SQ	FG	MQ	F	*P*
Temp	0.046	1	0.046	33.500	< 0.0001
Cultivation	0.004	1	0.004	2.951	0.105
Temp*cultivation	0.006	1	0.006	4.500	0.049

Significance level $P < 0.05$

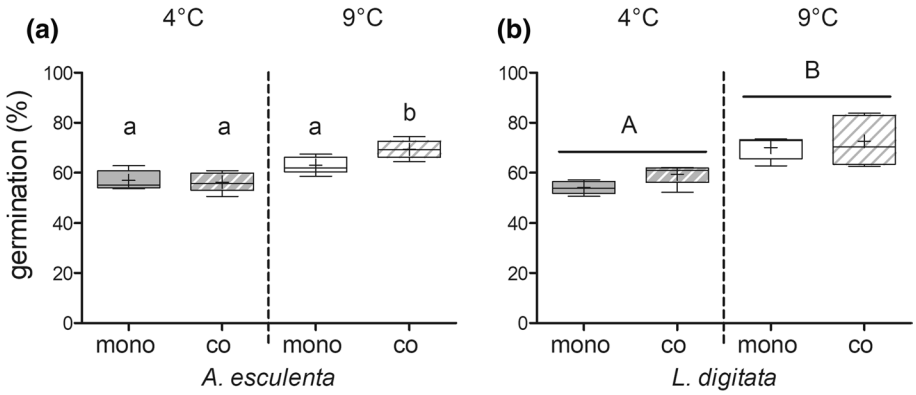

Fig. 3 Germination rates of *A. esculenta* (**a**) and *L. digitata* (**b**) in mono-specific ("mono", filled boxes) and co-cultivation ("co", broken boxes) treatments at 4° and 9 °C counted on day 3. All graphs show box-plots with Tukey whiskers: median, mean, 25 and 75% percentile and 1.5 interquartile range, $n = 5$. Different letters indicate significant differences (Tukey post hoc test)

Table 2 Experiment 1: results from analyses of variance (two-way ANOVA) for single and combined effects of 'cultivation' (mono-specific vs. co-cultivated spores) and 'temperature' (Temp; 4 and 9 °C) on germination rates of *L. digitata* ($n=5$)

	SQ	FG	MQ	F	*P*
Temp	0.107	1	0.107	29.906	< 0.0001
Cultivation	0.008	1	0.008	2.135	0.163
Temp*cultivation	0.001	1	0.001	0.288	0.599

Significance level $P<0.05$

Table 3 Experiment 1: results from analyses of variance (two-way ANOVA) for single and combined effects of 'cultivation' (mono-specific vs. co-cultivated spores) and 'temperature' (Temp; 4 and 9 °C) on sporophyte density of *A. esculenta* (day 16) ($n=5$)

	SQ	FG	MQ	F	*P*
Temp	10,269,194	1	10,269,194	34.3	< 0.0001
Cultivation	976,025	1	976,025	3.26	0.031
Temp*cultivation	1,157,871	1	1,157,871	3.867	0.048

Significance level $P<0.05$

The density of sporophytes on day 16 was higher in *A. esculenta* than in *L. digitata,* irrespective of temperature (Fig. 4). In general, sporophyte development was faster in *A. esculenta* compared to *L. digitata* (Online Resource 3). On day 10 at 4 °C, ~ 45% of all female gametophytes in the *A. esculenta* mono-specific treatments had developed young sporophytes, whereas only ~ 25% in the *L. digitata* mono-specific treatments (Online Resource 3). Sporophyte development was significantly accelerated in both species at elevated temperatures (Online Resources 1 and 2). On day 16, *A. esculenta* had formed 66% sporophytes at 4 °C compared to 88% at 9 °C, while in *L. digitata,* the ratio was 28% at 4 °C vs. 61% at 9 °C (Online Resource 3).

When *A. esculenta* was co-cultivated with *L. digitata,* the sporophyte density was significantly higher compared to the mono-specific *A. esculenta* treatment, but only at higher temperatures (9 °C) (temperature*cultivation interaction; Fig. 4a, Table 3). This is similar to the results of the germination (Table 1, Fig. 3a). On the other hand, when *L. digitata* was co-cultivated with *A. esculenta,* the sporophyte density was significantly lower compared to the mono-specific *L. digitata* treatment, but again only at higher temperatures (temperature*cultivation interaction; Fig. 4b, Table 4).

Table 4 Experiment 1: results from analyses of variance (two-way ANOVA) for single and combined effects of 'cultivation' (mono-specific vs. co-cultivated spores) and 'temperature' (Temp; 4 and 9 °C) on sporophyte density of *L. digitata* (day 16) ($n=5$)

	SQ	FG	MQ	F	*P*
Temp	1,936,806	1	1,936,806	132,771	< 0.0001
Cultivation	442,593	1	442,593	30,340	< 0.0001
Temp*cultivation	171,562	1	171,562	11,761	< 0.0001

Significance level $P<0.05$

Experiment 2: effects of co-cultivation on growth of juvenile sporophytes at current and projected Arctic summer temperatures

Initial blade area of both species was not significantly different (sum of area: *A. esculenta*: 7.3 cm^2, *L. digitata*: 8.6 cm^2; *t* test, $t_{38}=1.94$, $P=0.059$). In general, sporophytes of *A. esculenta* grew faster than sporophytes of *L. digitata* (Fig. 5). After 5 weeks, the overall blade area of *A. esculenta* sporophytes had increased to approx. 550 cm^2, but only to 225 cm^2 in *L. digitata*.

Sporophyte growth of *A. esculenta* at 10 °C was significantly lower than at 4 °C (Fig. 5a, Table 5) and sporophytes

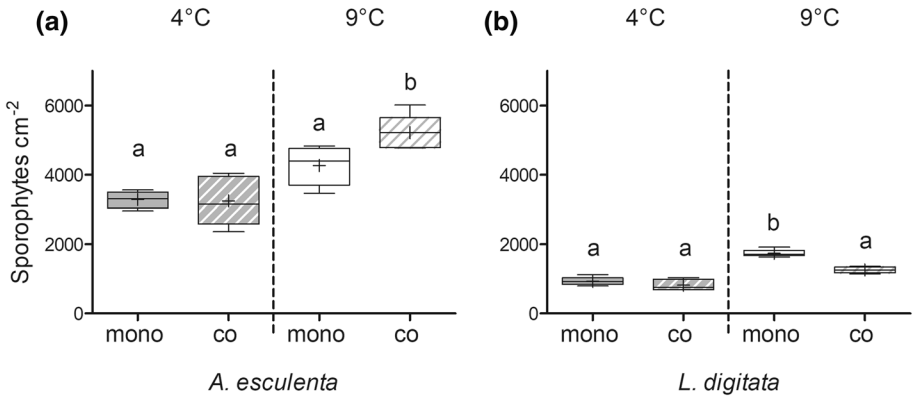

Fig. 4 Density of *A. esculenta* (**a**) and *L. digitata* (**b**) sporophytes in mono-specific (mono, filled boxes) and co-cultivation (co, broken boxes) treatments at 4° and 9 °C on day 16. All graphs show boxplots with Tukey whiskers: median, mean, 25 and 75% percentile and 1.5 interquartile range, $n=5$. Species in the co-cultivation treatments could be identified due to spatial separation in the experimental dishes. Different letters indicate significant differences (Tukey post hoc test)

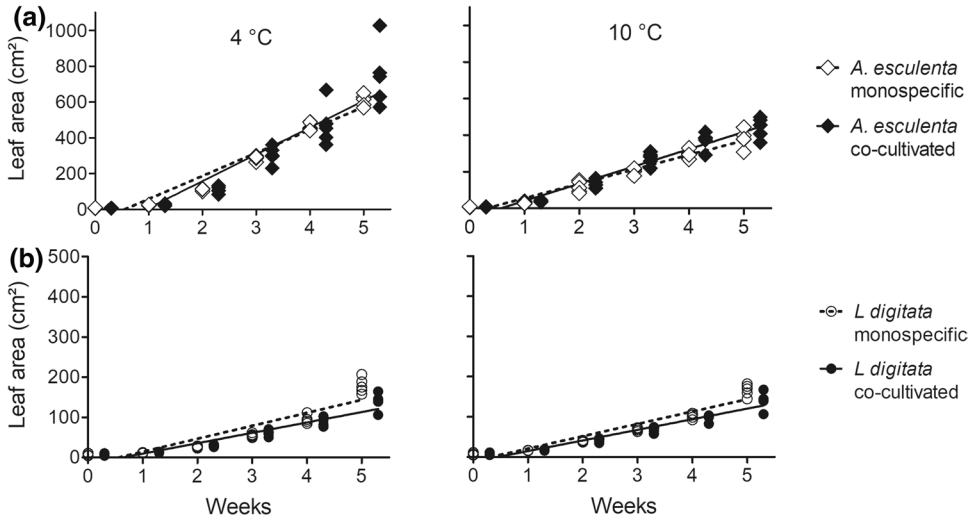

Fig. 5 Increase of blade area of *A. esculenta* (**a**) and *L. digitata* (**b**) sporophytes in mono-specific (white symbols) and co-cultivation (black symbols) treatments at 4 and 10 °C over 5 weeks (single values plus linear regression lines; $n=5$; all values normalized to 15 sporophytes). Note different scaling for *A. esculenta* and *L. digitata*

became significantly larger when in co-cultivation with *L. digitata* compared to the mono-specific treatment. While the blade area increased with the same speed during the first 2 weeks at 4 and 10 °C, from week 3 onwards, growth at 4 °C was enhanced (cultivation*time effect; Table 5).

In contrast, in *L. digitata,* growth was independent from temperature but co-cultivation with *A. esculenta* significantly suppressed growth of *L. digitata* in week 5 (Table 6; Fig. 5b).

Experiment 3a + b: effect of co-cultivation on gametogenesis and sporophyte growth at temperatures simulating summer temperatures near the northern and southern distribution range

Microscopic phase (*experiment* 3*a*) Initial gametophyte density was not significantly different between species in all temperature treatments and ranged between 351 and 400 fragments cm^{-2} (two-way ANOVA, $F_{(2,\ 2117)}=2.399$, $P=0.133$).

Development at 5 °*C* Until day 8, mostly vegetative gametophytes, gametophytes with oogonia or with released egg cells were present and only a small fraction of embryonic sporophytes had been formed, but from day 12 onwards, sporophytes developed in mono-specific and co-cultivation treatments of both species (Fig. 6a). Significantly more sporophytes were present in mono-specific *A. esculenta* cultures than in mono-specific *L. digitata* cultures, as was observed in experiment 1 (Fig. 6a, Table 7). From day 20 onwards, sporophyte formation in *A. esculenta* was 100% saturated, whereas in *L. digitata,* only a slow increase in the relative density of sporophytes was observed (significant time*species interaction, Fig. 6a, Table 7) and did not reach a saturation point even after 24 days. As species identity could not be distinguished in the co-cultivation treatment during this microscopic phase, the mean relative density of sporophytes in the co-cultivation treatment on day 20 was tested against the expected value (mean of relative sporophyte density in mono-specific treatments of *A. esculenta* and *L. digitata*). There was no effect of co-cultivation on sporophyte development during this ontogenetic stage (one-sided *t* test, $t_4=-2.33$, $P=0.081$).

Development at 15 °C *Alaria esculenta* did not develop any sporophytes at this temperature. The most developed

Table 5 Experiment 2: results from analyses of variance (repeated-measures ANOVA) for single and combined effects of 'cultivation' (mono-specific vs. co-cultivated sporophytes), 'temperature' (Temp; 4 and 10 °C), and time (5 weeks) on total blade area of *A.esculenta* sporophytes normalized to 15 individuals ($n=5$)

	SQ	FG	MQ	F	*P*
Temp	157,003	1	157,003	29.765	< 0.0001*
Cultivation	30,552	1	30,552	5.792	0.029*
Temp*cultivation	740	1	740	0.140	0.713
Time	4,637,354	5	927,471	470.502	< 0.0001
Time*temp	307,864	5	61,573	31.236	< 0.0001
Time*cultivation	34,877	5	6975	3.539	0.056
Time*temp*cultivation	15,441	5	3088	1.567	0.229

Significance level $P<0.05$. *Homogeneity of variances was not given at week 2 only

Table 6 Experiment 2: results from analyses of variance (repeated-measures ANOVA) for single and combined effects of 'cultivation' (mono-specific vs. co-cultivated sporophytes), 'temperature' (Temp; 4 and 10 °C), and time (5 weeks) on total blade area of *L. digitata* sporophytes normalized to 15 individuals ($n=5$)

	SQ	FG	MQ	F	*P*
Temp	722.0	1	722.0	3.330	0.087
Cultivation	905.6	1	905.6	4.178	0.058
Temp*cultivation	23.9	1	23.9	0.110	0.744
Time	317,015.3	5	63,403.1	1071.893	< 0.0001
Time*temp	1231.0	5	246.2	4.162	0.043
Time*cultivation	4839.3	5	967.9	16.363	< 0.001
Time*temp*cultivation	292.8	5	58.6	0.990	0.356

Significance level $P<0.05$

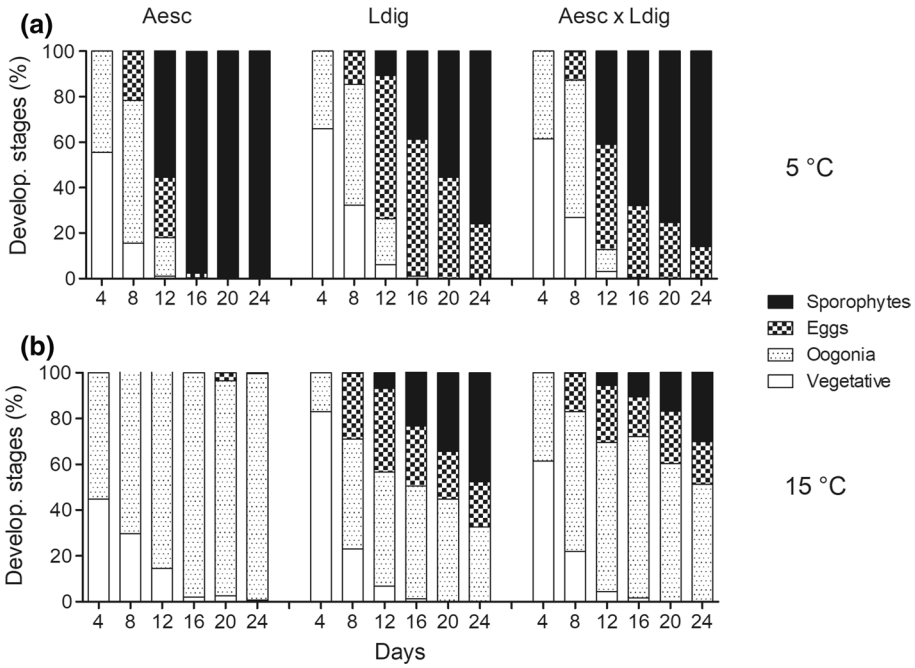

Fig. 6 Effects of temperature 5 °C (**a**) and 15 °C (**b**) and cultivation treatment on the development of ontogenetic stages of *A. esculenta* and *L. digitata* over time (days 4, 8, 12, 16, 20, and 24) (mean values; $n=5$). Aesc Mono = *A. esculenta* mono-specific culture, Ldig Mono = *L. digitata* mono-specific culture, Aesc × Ldig = co-culture of *A. esculenta* and *L. digitata*. Species in the co-cultivation treatments could not be identified to species due to fully mixed cultures

Table 7 Experiment 3a: results from analyses of variance (repeated-measures ANOVA) for single and combined effects of 'species' and 'time' (day 8–24) on relative sporophyte density of *A. esculenta* and *L. digitata* in mono-specific cultures at 5 °C ($n=5$)

	SQ	FG	MQ	F	*P*
Species	4.877	1	4.86774	2138.14	< 0.0001*
Time	10.513	4	2.62836	1498.35	< 0.0001
Time*species	1.645	4	0.41126	234.44	< 0.0001

Significance level $P<0.05$. *At four out of five time points still heterogeneous after transformation

stage observed were some eggs, but mainly oogonia were present (Fig. 6b). Therefore, *A. esculenta* was excluded from further statistical analyses. *Laminaria digitata* only formed vegetative gametophytes, gametophytes with oogonia or with released egg cells in mono-specific and co-cultivation treatments until day 8 as for 5 °C (Fig. 6b). After that, sporophyte density was significantly lower and sporophyte formation was significantly slower compared to 5 °C (e.g. 76% vs. 48% sporophytes at 5 and 15 °C on day 24, respectively; Fig. 6a and b, Table 8). Similarly, as for the 5 °C treatment, sporophyte development in the co-cultivation treatment at 15 °C did not deviate from the expected values on day 20 (one-sided *t* test, $t_4=1.12$, $P=0.327$).

Macroscopic phase (*experiment 3b*) There were sufficient morphological differences between sporophytes for species identification on day 67 (all sporophytes > 0.5 cm, see Fig. 2). As the 15 °C treatments were contaminated by filamentous brown algae, only the results from the 5 °C treatment were analyzed (Fig. 7). In mono-specific cultures, the density of *A. esculenta* sporophytes (32 sporophytes cm^{-2})

Table 8 Experiment 3b: results from analyses of variance (repeated-measures ANOVA) of single and combined effects of 'temperature' (5 and 15 °C) and 'time' (day 8–24) on relative sporophyte density of *L. digitata* in mono-specific cultures ($n=5$)

	SQ	FG	MQ	F	*P*
Temp	0.329	1	0.329679	118.321	<0.0001*
Time	3.054	4	0.763423	442.577	<0.0001
Time*temp	0.219	4	0.054984	31.876	<0.0001

Significance level $P<0.05$. *Day 16 still heterogeneous after transformation

was significantly higher compared to *L. digitata* (13 sporophytes cm^{-2}) (Fig. 7a, Table 8). Remarkably, there was no difference between the sporophyte density of *A. esculenta* in the mono-specific and in the co-cultivation treatment, although the initial gametophyte density of *A. esculenta* in the co-cultivation treatment had only been half of the mono-specific density. There was a complete lack of *L. digitata* sporophytes > 0.5 cm in the co-cultivation treatment indicating a strong suppression of *L. digitata* development in the presence of *A. esculenta* (Fig. 7a). Mean sporophyte length of mono-specific *A. esculenta* (4.9 cm) was significantly larger than length of mono-specific *L. digitata* sporophytes (1.6 cm) but similar to those co-cultivated with *L. digitata* (4.8 cm; Fig. 7b, Table 8).

Discussion

The current experiments between early life-history stages of the North Atlantic sympatric kelps *A. esculenta* and *L. digitata* provide a mechanistic understanding of kelp interactions along a temperature gradient for different life-history processes. Our results reveal interspecific interactions during developmental processes in different early life-history stages (spore germination, gametogenesis, and sporophyte development and growth)—all of which are likely to set the trajectory for the development of the adult kelp population. Interactions between both species were mediated by temperature. In general, *A. esculenta* gametophyte and sporophyte development and growth benefited from co-cultivation with *L. digitata,* especially under the future simulated Arctic temperature scenario (9–10 °C). *Laminaria digitata*, on the other hand, showed reduced sporophyte development and growth when co-cultured with *A. esculenta* compared to the monoculture while there were no effects (neither negative nor positive) of co-cultivation during germination or gametogenesis of *L. digitata* (Fig. 8). This confirms former studies stating that species interactions are not static and need special attention when multiple life-history stages are involved (Barner et al. 2016) and become even more complex along environmental gradients (Bertness and Callaway 1994).

The settlement density of kelp spores in nature is basically unknown. We thus relied on the only available experimental field study and used similar spore densities in our experiment 1 (125 spore mm^{-2} vs. medium-density treatment of Reed 1990: 100–200 spores mm^{-2}). In experiment 3, we used lower gametophyte densities (3–4 gametophytes mm^{-2}) as the dormant gametophytes consisted of approx. 8–11 female and 15 male cells/gametophyte (Daniel Moreno 2015). As observed in field studies (Reed and Foster 1984; Reed 1990), early mortality rates were high in our laboratory study starting from freshly released spores. Estimated survival rates of kelp spores in the field are extremely low. A potential spore production of 20.02×10^9 m^{-2} per year was estimated for *L. digitata* from which 0.98×10^6 m^{-2} per year grew to microscopic sporophytes (6–10 weeks old), resulting in survival rates of < 0.1% (Chapman 1984). Deysher and Dean (1986) observed similarly low survival rates for

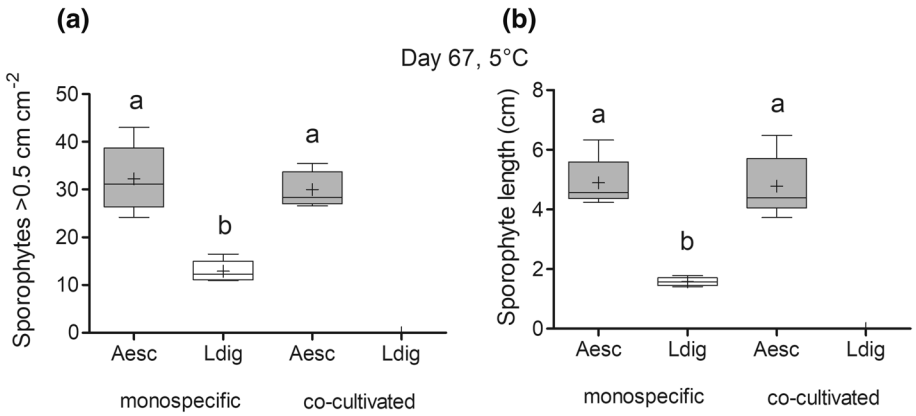

Fig. 7 Sporophyte density cm^{-2} (**a**) and sporophyte length of the 10 largest sporophytes (**b**) of mono-specific *A. esculenta* (Aesc), mono-specific *L. digitata* (Ldig) and co-cultivated treatments (Aesc × Ldig) at 5 °C on day 67. All graphs show box-plots with Tukey whiskers: median, mean, 25 and 75% percentile and 1.5 interquartile range, $n=5$. Different letters indicate significant differences (Tukey post hoc test). The zero values for Ldig co-cultivation treatment were removed from the analysis

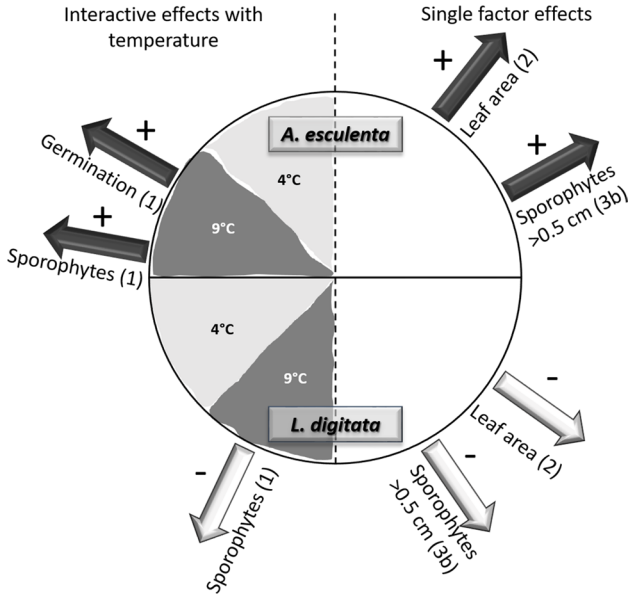

Fig. 8 Schematic view of significant effects of co-cultivation between *A. esculenta* and *L. digitata*. Interactive effects with temperature left, single effects right. Positive effects: dark gray arrow marked with a „+", negative effects: light gray arrow marked with a „−". Experiment number in parenthesis

Macrocystis spores seeded on ropes and transferred to the field. Laboratory conditions on the other hand are less harsh than field conditions, e.g., excluding grazing and resulted in lower mortality rates. Survival rates of juvenile sporophytes of *A. esculenta* and *Saccharina latissima* were 20–100 times higher in the laboratory compared to field experiments despite similar initial spore densities (Messingfeld 2016). Similarly, the sporophyte survival rates in our experiments are higher compared to field experiments, which is in accordance with the results given by Messingfeld (2016). Direct comparison to other studies is difficult due to different methodologies and time spans for recruitment applied (e.g., Chapman 1984; Reed 1990). However, spore settlement in kelps needs to occur in high densities, because the fertilization process takes place after spore release, requiring a close proximity of spores and resulting gametophytes (minimum density of 1 spore mm^{-2}, Reed 1990). A density-dependent mortality during recruitment and sporophyte growth is, therefore, a logical consequence given the size differences between an adult kelp of several meters length and spores of ~ 4 µm length (Reed 1990).

Temperature effects on different ontogenetic processes of *A. esculenta* and *L. digitata*, irrespective of culture treatment

In addition to a sufficient supply of propagules, successful recruitment in kelps requires ideal abiotic conditions as shown in other studies (Deysher and Dean 1986; Reed 1990; Ladah and Zertuche-González 2007). In general, early ontogenetic processes (spore germination, gametogenesis of gametophytes, and sporophyte development) and growth of juvenile sporophytes were faster in *A. esculenta* than in *L. digitata* at present summer temperatures in the Arctic (4–5 °C) and at projected future summer temperatures (9–10 °C), but not at temperatures simulating the southern distribution boundary (15 °C). At 15 °C, gametogenesis of *A. esculenta* was extremely limited and no sporophytes developed up to 64 days of cultivation. These results are consistent with a study on *A. esculenta* from Kongsfjorden performed by Park et al. (2017) who showed that more sporophytes were produced at 5 °C than at 10 °C and no sporophytes developed at 15 °C in 24 days of cultivation. Not only was sporophyte development faster in our study, but sporophyte growth of *A. esculenta* was also 2–3 times higher than growth of *L. digitata* at 4° and 10 °C. Icelandic *A. esculenta* sporophytes which were raised at Helgoland (North Sea) grew fine in the field when temperatures ranged between 3.3 and 8.5 °C, while blades died at 16–17 °C (Sundene 1962; Munda and Lüning 1977). Thus, the observed temperature responses seem to be characteristic for *A. esculenta* in general.

Each ontogenetic stage and developmental process has a particular temperature range for optimal development as has already been observed among different kelp species (Martins et al. 2017; tom Dieck 1992, 1993) and was confirmed in this study. Spore germination, gametogenesis, and sporophyte development of both species were positively stimulated by an increase in temperature from present Arctic summer seawater temperatures of 4–5 °C to forecasted seawater temperatures by the end of this century of 9–10 °C (IPCC 2012). Sporophyte growth of *A. esculenta*, however, was slower at 10 °C than at 4 °C, whereas sporophyte growth of *L. digitata* was similar at both temperatures. Former studies on both kelp species from lower latitude populations already indicated that *A. esculenta* is better adapted to colder temperatures than *L. digitata* (e.g., Lüning 1980; tom Dieck 1992, 1993). Adult sporophytes of *A. esculenta* have been reported to die at 16–17 °C (Munda and Lüning 1977), whereas juvenile *L. digitata* sporophytes from southern populations may survive up to 21 °C in the laboratory (tom Dieck 1992). While the upper survival temperature for male and female gametophytes of *A. esculenta* from strains from Iceland is 19–20 °C and 20–21 °C, respectively (tom Dieck 1993), the upper fertility temperature was approx. at 15 °C for the investigated Arctic populations in our study. Although populations from lower latitudes may be adapted to slightly higher temperatures, it became evident that the limit for gametophyte and sporophyte reproduction in *L. digitata* is a few degrees lower than the survival temperature of the respective life cycle stage (Bartsch et al. 2013; Martins et al. 2017). In our study, gametogenesis of *L. digitata* was considerably slower and sporophyte recruitment was much lower

at 15 °C than at 5 °C. This is slightly different to results from a southern population of *L. digitata* from Helgoland (North Sea) where gametogenesis was fastest at 10–15 °C, but sporophyte recruitment was also highest at 5 °C (Martins et al. 2017). This indicates that the Arctic population may have adapted to local conditions with year-round low temperatures. This is supported by the growth performance of sporophytes. Juvenile sporophytes of our Arctic *L. digitata* population showed similar high growth rates at 4° and 10 °C, while the optimum growth temperature for strains from Helgoland and Canada was 10 °C and reduced growth was observed at 5° and 15 °C (Bolton and Lüning 1982; tom Dieck 1992). Even though the Arctic strains used in our experiments may represent genotypes specifically adapted to low temperatures, the predicted temperature change until the end of this century itself will not be detrimental for either of the two species in Arctic regions, but rather accelerate developmental processes.

Co-cultivation effects on different ontogenetic processes of *A. esculenta* and *L. digitata*, and interactive effects of co-cultivation and temperature

The co-cultivation treatments indicated that interactions between the microscopic stages of the two species of kelp significantly influenced patterns of their macroscopic recruitment. Furthermore, it became evident that altered physical conditions shifted the balance of interactions between the two species. However, the underlying mechanisms probably differed depending on the developmental stage and investigated process, but cannot conclusively answer by our experimental design.

Irrespective of temperature, *A. esculenta* outcompeted *L. digitata* during several developmental processes leading to higher sporophyte recruitment and growth (experiments 2 and 3b; Fig. 8). As *A. esculenta* developed sporophytes faster during gametogenesis and sporophytes grew faster in general, they may have experienced an early competitive advantage over *L. digitata,* most likely because of a higher nutrient uptake rate of *A. esculenta* compared to *L. digitata* sporophytes. Thereby *A. esculenta* may have been able to exploit nutrients more efficiently at an earlier age and so outperforming *L. digitata* (exploitative competition). *Alaria esculenta* in the co-culture could then grow better than in the monoculture, because the intraspecific competition for nutrients was possibly higher in the monoculture (30 *A. esculenta* individuals competing) than the intra- and interspecific competition with *L. digitata* in the co-culture (15 individuals of each species, with *L. digitata* slow growing). *Laminaria digitata*, on the other hand, grew better in monoculture, because the slow growth of the species did not lead to a competition for nutrients as it did in the co-culture with *A. esculenta*. This observation suggests that *A. esculenta* may be a species with a potentially higher nutrient uptake rate than *L. digitata*, finally leading to outcompetition of *L. digitata*. As we did not follow nutrient dynamics of the seawater or the CN ratio of sporophytes during the experiment, this is only an assumption. Lubsch and Timmermanns (2019) showed that dissolved inorganic phosphate (DIP) and dissolved inorganic nitrate (DIN) uptake kinetics of young sporophytes of *L. digitata* was much slower than those of the kelp *S. latissima.* Furthermore, young sporophytes of *S. latissima* took up twice as much nitrogen as older sporophytes indicating life stage-dependent uptake kinetics (Harrison et al. 1986; Roleda and Hurd 2019). As the nutrient uptake kinetics of *A. esculenta* are unknown, we can only speculate that this species behaves similar as *S. latissima.* The latter species has similarly high growth rates and sporophyte recruitment patterns as *A. esculenta* (Messingfeld 2016). Similarly, changing nutrients and salinity (Fong et al. 1996), temperature and nutrients (Steen and Scrosati 2004; Alestra and Schiel 2014; Brooks and Crowe 2018), or sediment cover and timing of settlement (Traiger and Konar 2017) altered the outcome of competition between macroalgae. In another study, Steen (2004) showed that elevated temperature increased the competitive impacts of an ephemeral species (*Ulva compressa*) on germlings of two *Fucus* species. Also Armitage et al. (2017) found interspecific competitive interactions between three adult macroalgal species including one kelp (*S. latissima*) which changed under higher temperatures. These experiments did not assess which resource was being competed for, but competition for light and nutrients were discussed and also interference competition as a possible explanation mentioned.

Increased temperatures, mimicking future modeled Arctic summer temperatures affected germination (after 3 days) and formation of *A. esculenta* sporophytes (after 16 days) in our experiment positively when co-cultivated with *L. digitata.* On the other hand, less sporophytes were formed in *L. digitata* co-cultured with *A. esculenta* compared to its monoculture at 9 °C (experiment 1; Fig. 8). Exploitative competition for common resources at this stage of kelp development is very unlikely as the spores and early sporophytes are still very small (µm scale), and there is no shading and the amount of nutrients is assumed to be sufficient for all individuals as the PES is saturated with nutrients. Furthermore, the interaction cannot be explained by different temperature optima as *A. esculenta* is adapted to lower temperatures than *L. digitata* (see above). Thus, a temperature-independent mechanism involving interference through allelopathic substances (Nabivailo and Titlyanov 2006; Begon et al. 2006; Xu et al. 2013) such as alkaloids, terpenes, volatile organic compounds, or pheromones (Leflaive and Ten-Hage 2007) may also explain inhibition of one species by the other as observed by Reed (1990) and as hypothesized for our study.

The pheromone Lamoxirene that induces sperm release and attracts sperm to oogonia in kelps is the same in all kelp species (Lüning and Müller 1978; Müller et al. 1985). It has been suggested that faster female fertility may attract sperm of the same and co-occurring kelp species at the same time, thereby reducing the reproductive success of the slower species, and, more importantly, could stimulate the release of gametes from the competitor before its females were mature (Müller 1981; Reed 1990). Interference competition may also inhibit or facilitate the performance of a macroalga by its competitor (Friedländer et al. 1996; Nelson et al. 2003; Xu et al. 2013). Allelochemicals released by ulvoids were shown to have negative effects on competitors, e.g., on *Fucus gardneri* zygotes (Nelson et al. 2003) or on growth of *Hormosira banksii* and *Gracilaria* spp. (Friedländer et al. 1996; Alestra and Schiel 2014). On the other hand, some positive interactions facilitating macroalgae recruitment have been described (Santelices 1990).

This study compared competitive abilities of sympatric kelp species in co-culture with their growth abilities in monoculture under different temperatures. However, as no other data, e.g., allelochemical production and species-specific nutrient uptake rates in both mono- and co-cultivation treatments were measured, the results cannot be appropriately attributed to competition. In kelps, additional experiments are necessary to further elucidate the underlying mechanisms of the competition in early life-history phases. For example, measurements of nutrient uptake rates in monoculture would allow to identify which species possibly were a better competitor for nutrient uptake during co-cultivation. Another option would be to analyze metabolites or observing the development of one species in a medium which was pre-used by the other species (Bollen 2017).

Our study, however, indicates that the outcome of interactions between the early life phase of *A. esculenta* and *L. digitata* is mediated by temperature. This effect on early life stage performance will ultimately have consequences at higher levels of organization in the marine macroalgae community. Rising temperatures could, therefore, cause a change in the community structure of Arctic kelp populations in the future with implications for ecosystem functioning as suggested for an NE Atlantic kelp forest (Pessarrodona et al. 2019). Our results suggest an increase in *A. esculenta* and a decrease of *L. digitata* presence in the future as a response of altered competition mediated by increasing temperatures. At our study site, *A. esculenta* has become more common in depths > 8 m during the last 20 years, but is also present at 0 m, while *L. digitata* biomass increased at shallow depths and is dominant there (Bartsch et al. 2016). This pattern is not totally consistent with our results and probably not only a consequence of the warming of the fjord. Temperature is not the only environmental condition that affects the recruitment and interaction of kelps in the field; other factors such as irradiance level, sedimentation, substrate type, and wave exposure may also affect species interactions (Hop et al. 2012, 2016; Bartsch et al., 2016; Zacher et al. 2016; Traiger and Konar 2017). Along the fjord axis, *A. esculenta,* e.g., was more dominant than *L. digitata* in highly wave-exposed sites (outer fjord), while it only became dominant at deeper sites at less wave-exposed sites (middle and inner fjord) (Hop et al. 2016). Overall, a multitude of factors affect community structure of kelps and kelp–kelp interactions (e.g., Kroeker et al. 2013; Gaitán-Espitia et al. 2014), and hence, it is very difficult to predict the future of coastal communities under a changing climate. However, future global warming may not only induce a large poleward shift of kelps species as has been predicted (Assis et al. 2018), but also has the potential to influence species interactions which should be considered when calculating future projections.

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Compliance with ethical standards

Conflict of interest All authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for sampling, care, and experimental use of organisms for the study were followed.

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