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RESEARCH

Exploring uncharted waters of future crop systems: Pioneering *Ulva intestinalis* seedling development for a sustainable full-life-cycle offshore aquaculture in the wider Baltic Sea area

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Abstract

Ulva intestinalis has been proposed as a promising candidate for seaweed aquaculture in the Baltic Sea due to its wide environmental tolerance and fast growth. This study evaluates the full life-cycle cultivation potential of *U. intestinalis*, from strain selection, fertility induction and seedling development to offshore biomass production, using 40 strains from ecologically distinct Baltic locations. Fertility was successfully induced in only 10% of the strains, underscoring the need for targeted screening and optimized induction protocols for potential aquaculture strains combined with subsequent biobanking strategies. In successfully induced strains, gametogenesis proceeded in a synchronized three-day cycle, with rapid and uniform ontogenetic development observed across salinity origins. Offshore cultivation trials at two sites (Koster archipelago, Sweden and Kriegers Flak, Denmark) confirmed the feasibility of nursery-based pre-cultivation in combination with sea-based farming for biomass production. However, the lower biomass yield but relatively faster growth of this species compared to foliose *Ulva* spp. may require more frequent harvesting, which must be evaluated against the operational constraints of offshore sites. Although co-location with existing offshore infrastructure could mitigate spatial competition, the economic feasibility of *U. intestinalis* cultivation ultimately depends on aligning biological performance with efficient nursery production and practical harvesting strategies. Strain-specific characteristics relevant to intended markets may support an advantage for nearshore production sites. The here developed techniques demonstrate that *U. intestinalis* can be successfully cultivated from gametes to seeded crops in Baltic sea-based environments, establishing a proof-of-concept for its integration into Baltic aquaculture systems.

Keywords Aquaculture · Baltic Sea · Blue Economy · Gutweed · Low salinity crop · Chlorophyceae

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Introduction

Future projections indicate a potential inadequacy of terrestrial crop yields to meet the escalating global food demands due to the growing world population by the year 2050 (Ray and Foley 2013). At the same time, it is expected that the expansion of agricultural activities, focusing on sustainable mariculture practices, could serve as a future oriented way to amplify food and general resource production on a broader scale (Duarte et al. 2009). Hence, the urgent need for sustainable and novel resources that can be converted to nutritious food, renewable materials and novel biomolecules was emphasized by the sustainability goals of the United Nations (UN General Assembly 2015).

The increasing interest in seaweed biomass, particularly as a sustainable and renewable reservoir of high-value compounds, is gaining prominence as a prospective solution to confront these challenges especially as it addresses circularity in production systems by its wide applicability in different economic sectors (Duarte et al. 2009; Holdt and Kraan 2011; Spillias et al. 2023). In contrast to conventional terrestrial crops, seaweeds present a widely under-used resource that reduces competition for land utilization or freshwater stocks, thus potentially alleviating global pressures on arable land as well as freshwater resources (Spillias et al. 2023). While seaweed aquaculture and the use of seaweeds in daily commodities have a long history and tradition in many Asian countries as well as in ancient Europe (Buckley et al. 2023), the European Union is now also aiming to foster and support a growing seaweed industry as part of a sustainable European Blue Economy. By recognizing its cultivation as a pivotal sector for fostering sustainable practices, the EU has emphasized its importance in various recent strategic documents – not at least in the Farm-to-Fork strategy, the Commission's Green Deal, through the EU Biodiversity Strategy for 2030, and the EU Algae Action Plan including the EU4Algae Working Group (EU Commission 2019, 2020a, 2020b, 2024).

Within Europe, primary cultivation efforts were directed towards euhaline environments, emphasizing the preference and development initiatives for almost solely euhaline seaweed crop species – especially for the widely distributed seaweed crop sugar kelp, *Saccharina latissima*. Lower-salinity environments are unsuitable for the industrial application of sugar kelp, as growth and performance patterns strongly diverged from the favorable high salinity environments (Bruhn et al. 2016; Nielsen et al. 2016; Monteiro et al. 2021). Therefore, diversifying European seaweed crop species by including meso- and oligohaline tolerant strains becomes imperative when aiming to include low salinity environments – such as estuaries, saline streams, or the wider Baltic Sea – in future cultivation endeavors. Recent research revealed how especially meso- and oligohaline conditions indeed can be used as a tool for strain selection and optimization of functional traits in novel crop species (Cardoso et al. 2023; Steinhagen et al. 2025a, b) while simultaneously providing high-value low-salinity crop strains with desired biochemical composition that can be supplied to a circular bioeconomy (Steinhagen et al. 2021, 2022a, b).

The extensive Baltic Sea region, which is bordered by nine countries, exhibits a pronounced salinity gradient, ranging from fully marine conditions in the Skagerrak (28–32 PSU) to an almost freshwater state in the Bothnian Bay (0–2 PSU) (HELCOM 2018). Although the Baltic Sea constitutes one of the best researched waterbodies (Reusch et al. 2018), its different ecosystems currently stand as an underutilized resource for macroalgae cultivation (Weinberger et al. 2020) and therefore present an untapped reservoir with substantial potential for specific macroalgae species´ cultivation (Kotta et al. 2022; Steinhagen et al. 2025a, b).

Ecologically, introducing low-salinity seaweed farming to the Baltic Sea could have positive impacts, as seaweeds play vital roles in nutrient cycling, carbon sequestration, and maintaining water quality (Fox et al. 2016; Duarte et al. 2022; Pessarrodona et al. 2023). This cultivation could contribute to ecosystem restoration, mitigating the effects of eutrophication and potentially promoting biodiversity (Kotta et al. 2022). Beyond environmental considerations, the economic aspect is crucial, as the cultivation of low-salinity seaweed species could significantly contribute to the regional economy and economical independence after, for example, strong declines in fish populations resulted in insufficient catch for commercial fishing, leading to a high rate of resignation of local fishermen. The emerging seaweed sector could generate employment opportunities, foster growth, and revive the European Blue Economy of the region.

Fluctuating environmental conditions in the Baltic Sea (HELCOM 2018; Reusch et al. 2018) have been identified to make it an ideal habitat for certain sea lettuce (*Ulva*) species (Kotta et al. 2022), which are known for their adaptability to the region's specific characteristics underlined by the wide distribution of certain *Ulva* species in the full Atlantic-Baltic Sea transect (Larsen and Sand-Jensen 2006; Steinhagen et al. 2019a, b, 2023). However, *Ulva* species exhibit variations in their distribution patterns within this dynamic environment (Steinhagen et al. 2019a, 2023) and it has been outlined that especially *Ulva intestinalis* stands out as a noteworthy example, demonstrating a remarkable adaptability by thriving across the entire salinity gradient of the Baltic Sea (Steinhagen et al. 2019a, 2023; Kotta et al. 2022) which imparts it a unique ecological resilience (Björk et al. 2004; Rybak 2018; Steinhagen et al. 2019b; Kotta et al. 2022). Especially within

the past years, *Ulva* representatives gained immense interest by the aquaculture sector due to their many beneficial traits such as high productivity besides their environmental tolerance (Bolton et al. 2016; Nardelli et al. 2019; Steinhagen et al. 2021, 2022a, b), and their efficient bioremediation of nutrients (Sode et al. 2013; Al-Hafedh et al. 2015; Andersson et al. 2025; Larsen-Ledet et al. 2025), while simultaneously providing valuable biochemical compounds which can be applied in diverse economic sectors, including the food industry (Hofmann et al. 2025b).

First models calculated high production levels in *U. intestinalis* farms along the southern and eastern Baltic Proper coasts presenting promising prospects for farming initiatives in less saline Baltic Sea areas (Kotta et al. 2022). The broad salinity tolerance of *U. intestinalis*, capable of withstanding salinities near 0 and actively growing from 5–10 PSU, positions it as an ideal candidate for low salinity water farming, distinguishing it from commonly farmed macroalgae (Kotta et al. 2022). Hence models provided by Kotta et al. (2022) revealed that light, nitrate availability, and temperature exert greater influence on *U. intestinalis* biomass production under farming conditions than salinity and it has been suggested, that nitrogen enrichment – which is widely present in the eutrophicated waterbodies of the Baltic Sea – mitigates salinity-related impacts, enabling *U. intestinalis* proliferation in brackish systems.

While the prognoses for high *U. intestinalis* production in Baltic Sea are promising (Kotta et al. 2022), it is essential to acknowledge the current absence of specific cultivation protocols, particularly for the critical seedling nursery stage. While there is an established market for the foliose (leaf-like) species of *Ulva* (e.g., Steinhagen et al. 2021; Hofmann et al. 2025b; Wendin et al. 2024) in the EU, the tubular forms such as *U. intestinalis* still require significant market development — yet multiple studies show its suitability in e.g. the food sector and it has been well-received in sensory tests (Thunyawanichnondh et al. 2020). Further, tubular *Ulva* species have long been cultivated and consumed in East Asia, particularly in Japan where they are marketed as *Aonori*, indicating an established food use and cultural acceptance outside the European market (Kuda et al. 1997).

Mostly, the success of large-scale cultivation efforts depends on well-established protocols that address key stages of the algal life cycle, including the vulnerable seedling phase (Steinhagen et al. 2022a, b; Stévant et al. 2023; Visch et al. 2023). Moreover, the unique characteristics of the Baltic Sea, harboring numerous clonal strains of seaweeds (Pereyra et al. 2023) that have secondarily lost sexual reproduction, pose a challenge to conventional cultivation methods relying on viable offspring generation. Therefore, despite the optimistic projections, advancing *Ulva* cultivation in the Baltic Sea necessitates the development of targeted and adaptive cultivation protocols, addressing specific challenges associated with the critical seedling nursery stage and accounting for the prevalence of clonal strains with limited sexual reproductive capacity.

To support the growing aquaculture sector of the region, the overall aim of our study was to investigate the potential for full life-cycle aquaculture of different Baltic Sea strains of *U. intestinalis* and hence establish cultivation protocols for this low-salinity future crop species. We investigated the fertility inducibility of different *U. intestinalis* strains, originating from four different localities in the Baltic Sea, reflecting various source salinities. Additionally, we examined if changes in population source material affect the early ontogenetic development (growth and time of developmental stage) in *U. intestinalis* seedlings. Furthermore, we conducted sea-based cultivation of hatchery raised *U. intestinalis* seedlings, and examined survival and crop performance based on growth and biomass yield through a growth season to complete the closed life-cycle biomass production of Baltic Sea *U. intestinalis* strains.

Materials and methods

Ulva source material and taxonomic identification

Algal material for this study was collected at ten sites representing 40 strains across the Atlantic-Baltic Sea transect including *Ulva intestinalis* populations from different source salinity regimes. All collection data and experimental set up are summarized in Table 1 and Figure 1. At each of the sites > 100 g fresh biomass of tubular *U. intestinalis* (reflecting > 100 individuals from the same population) for subsequent fertility induction trials was collected and transferred into a plastic bag containing seawater from the respective collection site. Biomass bulk samples were transported in a chilled container (c.a. 10 °C) to the laboratory within < 24 h. Further, representative and epiphyte free specimens of each population ($n = 3$) were collected in micro-reaction tubes for DNA barcoding and were stored in a portable freezer (−20 °C) until transferred to the laboratory. All sampled biomass of the respective strains was each transferred to 14-L aquaria (40 aquaria in total), obtaining seawater with the respective source salinity, permanent aeration, and nutrient addition (PES [Provasoli 1968]) were maintained at previously defined favorable conditions (Steinhagen et al. 2024) at an average irradiance of 80–100 µmol photons m^{-2} s^{-1} under a 16:8 h L:D light regime (light source: OSRAM Lumilux Cool daylight L 58W/865) at 12 °C in a climate-controlled room.

Due to the appearance of many cryptic species and a high morphological plasticity within the genus *Ulva*, all strains were molecularly identified by barcoding the *tuf*A marker

Table 1 Overview of *Ulva intestinalis* strains examined in the present study with respective collection sites, environmental parameters and information on fertility inducibility and subsequent cultivation sites in Baltic offshore trials (n.a. = not available)

Strain ID	Species ID (GenBank accession number)	Collection site (and number in map)	Coordinates	Salinity [PSU]	Life history stage	Fertility inducible by chopping	Fertility inducible by drying	Viable F1 generation	Farm site
1	*U. intestinalis* (OP267898)	Tjärnö, SE (1)	58°52′33.7″ N 11°08′44.9″ E	30	Gametop.	Yes	yes	yes	1 Koster archipelago
2	*U. intestinalis*	Tjärnö, SE (1)	58°52′33.7″ N 11°08′44.9″ E	30	n.a	no	no	n.a	n.a
3	*U. intestinalis*	Tjärnö, SE (1)	58°52′33.7″ N 11°08′44.9″ E	30	n.a.	no	no	n.a.	n.a.
4	*U. intestinalis*	Lindholmen, SE (2)	58°53'22.0"N 11°07'12.7"E	30	n.a.	no	no	n.a.	n.a.
5	*U. intestinalis*	Lindholmen, SE (2)	58°53'22.0"N 11°07'12.7"E	30	n.a.	no	no	n.a.	n.a.
6	*U. intestinalis*	Lindholmen, SE (2)	58°53'22.0"N 11°07'12.7"E	30	n.a.	no	no	n.a.	n.a.
7	*U. intestinalis*	Lindholmen, SE (2)	58°53'22.0"N 11°07'12.7"E	30	n.a.	no	no	n.a.	n.a.
8	*U. intestinalis*	Falkenberg, SE (3)	56°52'32.2"N 12°30'48.3"E	18	n.a	no	no	n.a	n.a
9	*U. intestinalis*	Falkenberg, SE (3)	56°52'32.2"N 12°30'48.3"E	18	n.a.	no	no	n.a.	n.a.
10	*U. intestinalis*	Falkenberg, SE (3)	56°52'32.2"N 12°30'48.3"E	18	n.a.	no	no	n.a.	n.a.
11	*U. intestinalis*	Falkenberg, SE (3)	56°52'32.2"N 12°30'48.3"E	18	n.a.	no	no	n.a.	n.a.
12	*U. intestinalis*	Devin, DE (7)	54°16'07.5"N 13°08'38.5"E	9	n.a.	no	no	n.a.	n.a.
13	*U. intestinalis* (PP354977)	Devin, DE (7)	54°16'07.5"N 13°08'38.5"E	9	Gametop.	Yes	Yes	yes	3 Danish Kriegers Flak
14	*U. intestinalis*	Devin, DE (7)	54°16'07.5"N 13°08'38.5"E	9	n.a	no	no	n.a	n.a
15	*U. intestinalis*	Devin, DE (7)	54°16'07.5"N 13°08'38.5"E	9	n.a.	no	no	n.a.	n.a.
16	*U. intestinalis*	Devin, DE (7)	54°16'07.5"N 13°08'38.5"E	9	n.a.	no	no	n.a.	n.a.
17	*U. intestinalis*	Devin, DE (7)	54°16'07.5"N 13°08'38.5"E	9	n.a.	no	no	n.a.	n.a.
18	*U. intestinalis*	Sassnitz, DE (8)	54°30'46.9"N 13°38'46.6"E	9	n.a.	no	no	n.a.	n.a.
19	*U. intestinalis*	Sassnitz, DE (8)	54°30'46.9"N 13°38'46.6"E	9	n.a.	no	no	n.a.	n.a.
20	*U. intestinalis* (PZ180039)	Sassnitz, DE (8)	54°30'46.9"N 13°38'46.6"E	9	Gametop.	no	yes	yes	4 FINO2
21	*U. intestinalis*	Sassnitz, DE (8)	54°30'46.9"N 13°38'46.6"E	9	n.a.	no	no	n.a.	n.a.
22	*U. intestinalis*	Sassnitz, DE (8)	54°30'46.9"N 13°38'46.6"E	9	n.a.	no	no	n.a.	n.a.
23	*U. intestinalis*	Sassnitz, DE (8)	54°30'46.9"N 13°38'46.6"E	9	n.a.	no	no	n.a.	n.a.
24	*U. intestinalis*	Sassnitz, DE (8)	54°30'46.9"N 13°38'46.6"E	9	n.a.	no	no	n.a.	n.a.
25	*U. intestinalis*	Nynäshamn, SE (10)	58°53'27.6"N 17°56'51.1"E	7	n.a.	no	no	n.a.	n.a.

Table 1 (continued)

Strain ID	Species ID (GenBank accession number)	Collection site (and number in map)	Coordinates	Salinity [PSU]	Life history stage	Fertility inducible by chopping	Fertility inducible by drying	Viable F1 generation	Farm site
26	*U. intestinalis*	Nynäshamn, SE (10)	58°53'27.6"N 17°56'51.1"E	7	n.a	no	no	n.a	n.a
27	*U. intestinalis*	Närshamn, SE (9)	57°13'30.9"N 18°39'43.6"E	7	n.a.	no	no	n.a.	n.a.
28	*U. intestinalis*	Närsshamn, SE (9)	57°13'30.9"N 18°39'43.6"E	7	n.a.	no	no	n.a.	n.a.
29	*U. intestinalis*	Halmstad, SE (4)	56°39'44.8"N 12°49'32.4"E	18	n.a.	no	no	n.a.	n.a.
30	*U. intestinalis*	Halmstad, SE (4)	56°39'44.8"N 12°49'32.4"E	18	n.a.	no	no	n.a.	n.a.
31	*U. intestinalis*	Halmstad, SE (4)	56°39'44.8"N 12°49'32.4"E	18	n.a.	no	no	n.a.	n.a.
32	*U. intestinalis*	Halmstad, SE (4)	56°39'44.8"N 12°49'32.4"E	18	n.a	no	no	n.a	n.a
33	*U. intestinalis*	Mönkeberg, DE (6)	54°21'07.5"N 10°10'40.3"E	14	n.a.	no	no	n.a.	n.a.
34	*U. intestinalis* (PZ180039)	Mönkeberg, DE (6)	54°21'07.5"N 10°10'40.3"E	14	Gametop.	no	yes	yes	2 Kieler Meeres-farm
35	*U. intestinalis*	Mönkeberg, DE (6)	54°21'07.5"N 10°10'40.3"E	14	n.a.	no	no	n.a.	n.a.
36	*U. intestinalis*	Mönkeberg, DE (6)	54°21'07.5"N 10°10'40.3"E	14	n.a.	no	no	n.a.	n.a.
37	*U. intestinalis*	Mönkeberg, DE (6)	54°21'07.5"N 10°10'40.3"E	14	n.a.	no	no	n.a.	n.a.
38	*U. intestinalis*	Strande, DE (5)	54°27'13.3"N 10°11'50.4"E	14	n.a.	no	no	n.a.	n.a.
39	*U. intestinalis*	Strande, DE (5)	54°27'13.3"N 10°11'50.4"E	14	n.a.	no	no	n.a.	n.a.
40	*U. intestinalis*	Strande, DE (5)	54°27'13.3"N 10°11'50.4"E	14	n.a.	no	no	n.a.	n.a.

gene following the protocol described by Steinhagen et al. (2019a). For GenBank accession numbers see Table 1.

Fertility induction in *Ulva intestinalis* and selection of aquaculture strains

To induce fertility and thus obtain viable swarmers of the 40 strains of *U. intestinalis*, two methods were employed using three replicates of 25 g biomass from the respective strains for each test. The first method relied on an amendment of the protocol described in Kessler et al. (2018). Mature thalli of *U. intestinalis* (> 10 cm thallus length) were chopped and thoroughly washed with sterile seawater to remove possible sporulation inhibitors widely present in vegetative thallus tissue of *Ulva* species (Stratmann et al. 1996; Kessler et al. 2018). The thallus fragments were transferred into a 1-L beaker which was placed at above-described cultivation conditions in a temperature regulated room. Potential swarming inhibitors were removed at day three and four after induction by re-washing the material as described by Wichard and Oertel (2010).

The second method was amended from Carl et al. (2014). First, excess water of the mature thalli of *U. intestinalis* (> 10 cm thallus length) was removed with a salad spinner after which the individuals were dried with paper towel. The thalli remained dehydrated at room temperature for one hour, receiving daylight. Subsequently, the algae were re-hydrated in seawater (25 g biomass per L seawater) and formation of fertile tissue was checked for twice per day over a course of five days. For both methods, continuous microscopic observations of the fertility status (formation of gametangia/sporangia) and additional phototaxis tests determined the life stage of released swarmers (gametophytic or sporophytic). Swarmers with positive phototactic behaviour were assumed to indicate gametophytic strains (see also Wichard 2015; Steinhagen et al.

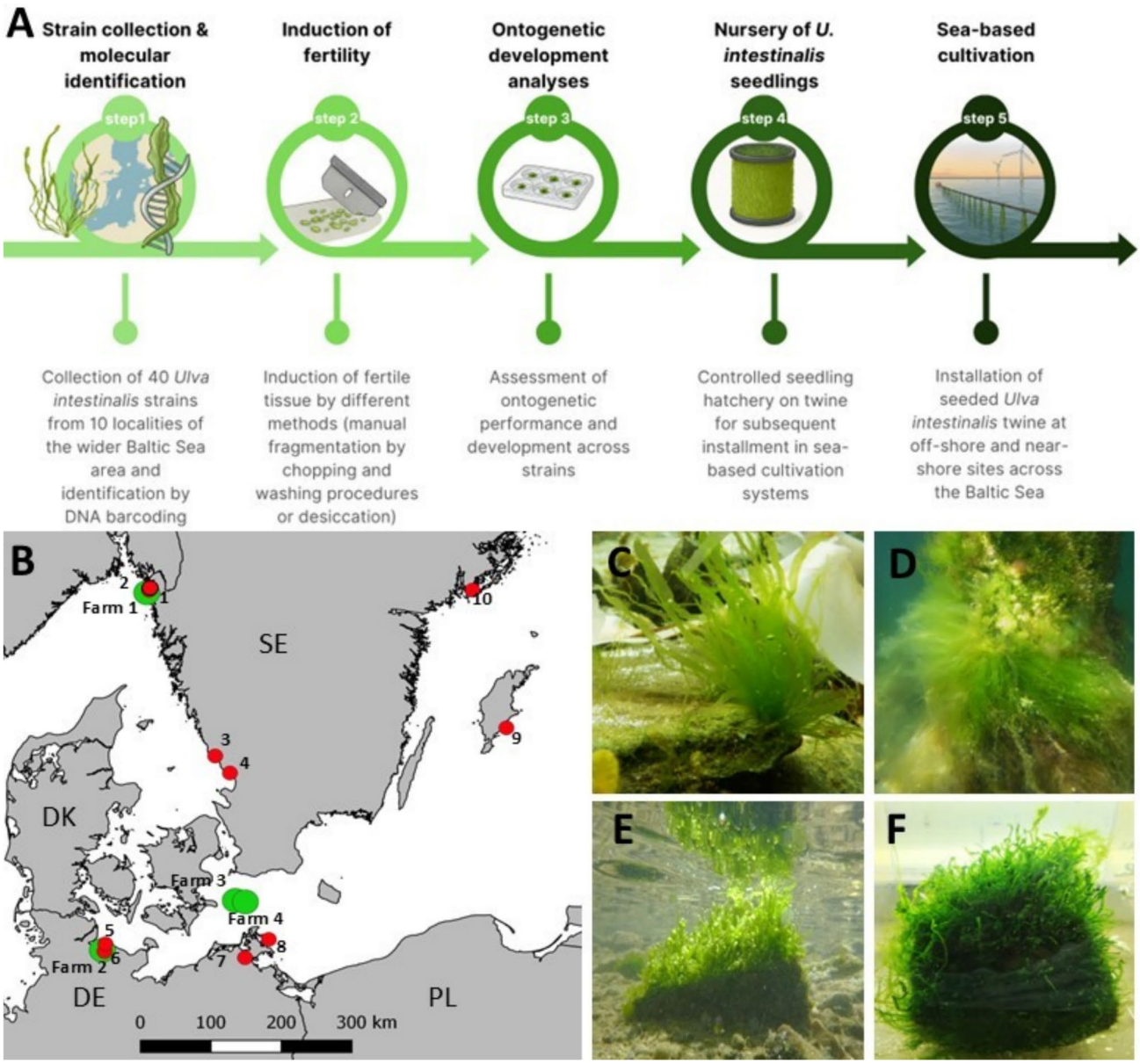


Fig. 1 Overview about the experimental cultivation steps and collection as well as farming sites of *Ulva intestinalis* in the wider Baltic Sea region, including the Skagerrak and Kattegat. **A**) The different experimental steps (1–5) from initial strain selection and hatchery establishment to the successful implementation of controlled cultivation and final deployment of *Ulva intestinalis* seedlings in sea-based cultivation units are shown. **B**) The ten collection sites (red circles) of *Ulva intestinalis* populations spread across the Atlantic-Baltic Sea transect and represent different ecosystems present in the wider Baltic Sea region. Further the four different farm sites (green circles) are indicated. *Ulva intestinalis* strains successfully used in cultivation experiments stem from **C**) the Swedish west coast, Tjärnö (1) and the German sites in **D**) Mönkeberg (6), **E**) Devin (7), and **F**) Sassnitz (8) and thallus size ranged from 3–12 cm

2019c) and were selected for the subsequent experiments. Note that fertility induction was only possible in four out of 40 strains, namely in strains of the Skagerrak (Tjärnö Marine Laboratory, Sweden), the Kiel bight (Mönkeberg, Germany), and in those originating from the margins of the Arkona Basin (Devin and Sassnitz, Germany) (Table 1, Fig. 1). Hence, following descriptions of investigations are only conducted for the respective strains.

Ontogenetic development and seedling nursery

Induction and collection of viable swarmers was successful in only four of the 40 sampled strains. The swarmer solutions were kept in absolute darkness for 24 h to allow the gametes to shed their flagella resulting in immobilization. Subsequently, the hatchery performance assessments of gametes of the different *U. intestinalis* strains was performed

(Fig. 1A) in 10-mL six-well-plates (Sarstedt, Germany) in thermostatic culture cabinets (Liebherr, Germany) where temperature (12 °C), swarmer density (1 000 swarmers mL^{-1}, counted in a Neubauer counting chamber), the concentration of Provasoli Enriched Seawater (Provasoli 1968) and a 16:8 h (L:D) photo regime at an irradiance of 110 µmol photons m^{-2} s^{-1} (light source: LED white light) were constant in all ontogenetic trials. To prevent diatom growth 1 mg L^{-1} GeO_2 was added to each replicate well (n=3) and the medium was changed weekly. Throughout the experiment, the growth of seedlings was monitored – daily in the first week and afterwards weekly – by microscopy and documented via photographs from haphazardly chosen locations across the well. The photographs were used to determine the development stage and quantify the length and width after six weeks of the ten randomly selected thalli per replicate well. Subsequent measurements were carried out in ImageJ (Schneider et al. 2012). The early development of *U. intestinalis* was categorized as five different phases a seedling has to undergo to proceed from swarmer (only gametes used in this experiment) until juvenile thallus stage is reached and followed – with small amendments implemented for tubular *Ulva* individuals – the universal concept for *Ulva* ontogenetic development introduced by Steinhagen et al. (2021). The phases were defined as: I) attached, germinating cell, II) germinating cell with an apparent germination tube, III) beginning of distal cell division IV), beginning of tube formation, V) juvenile thallus with clear growth by distal and lateral cell divisions (Fig. 3A-F).

In preparation for future offshore cultivation, development and growth of swarmers attached to twine was assessed simultaneously. For this, the residual gamete solutions (1000 swarmers mL^{-1}) were applied by pipetting to three replicate PVC spools coiled with 10 m (±50 cm) of nylon cord (ø = 2–3 mm) which had an absorbance of 7 AU. After 30 min of gamete settlement the spools were submersed in 1-L aerated aquaria supplied with sterile filtered (0.2 µm) seawater of the respective source salinity of the strains, following the same cultivation conditions as described for the ontogenetic development in 6-well plates. The settled gametes were allowed to grow in the spool hatchery for six weeks and similar measurements on development and growth were conducted for seedlings inoculated on spools. However, due to challenging sample acquisition within the first week of growth, measurements on thallus growth were only possible from the second week onwards and as growth patterns followed observations made on individuals planted in 6-well plates, results are only shown for week 6 and as photographs of the developing spools.

Parental laboratory strains retained reproductive competence following more than five successive clonal propagation cycles, enabling repeated seedling production throughout the experimental period.

Trials of offshore and nearshore cultivation of *Ulva intestinalis*

To establish a proof of concept for sea-based *U. intestinalis* cultivation using a full-life-cycle methodology, outplanting trials were conducted at four different farm sites along the Atlantic–Baltic Sea salinity gradient. The selected sites represented distinct salinity regimes:

- Farm 1: Koster Archipelago, Skagerrak, Sweden (N58.859901, E11.068660; 28–30 PSU; see Steinhagen et al. 2021);
- Farm 2: Kiel Bight, Kiel, Germany (54.368500, 10.132250; 14 PSU; see Weinland et al. 2021);
- Farm 3: Danish Kriegers Flak (Vattenfall), Arkona Basin, Denmark (N54.977233, E12.786533; 8 PSU; see Mueller et al. 2011);
- Farm 4: FINO2 site, southern Baltic Sea (55.006917, 13.154069; 9 PSU; see Hübler et al. 2017; BSH 2025).

Farm 1 and Farm 3 employed a classical long-line cultivation approach, while Farm 2 and Farm 4 used 1.5 × 1 m frame systems. In the latter, nylon twine bearing seedlings was coiled around 1 m rope segments and fixed to the frames at 20 cm intervals.

To minimize ecological risk and avoid the spread of non-native strains or genetic material across distinct marine ecosystems, only *U. intestinalis* strains that had their origin within an 80 km radius from the respective farm locations were used (see also Table 1, Fig. 1).

It is important to note that the objective of this trial was to evaluate the general feasibility of targeted sea-based outplanting of nursery-cultivated *U. intestinalis* seedlings across environmentally contrasting locations, rather than to compare different farm systems or to assess strain-specific performance in different environments — the latter will be addressed in a forthcoming study.

Due to differences in strain origin, cultivation design and site-specific conditions, results among farms are not directly comparable.

After six weeks nursery rearing under standardized hatchery conditions, seedling-bearing spools ($n = 3$) of the respective strain were transported to the respective farm site in chilled containers (approx. 10–12 °C) and deployed within 48 h of arrival.

Deployment of the seeded spools ($n = 3$ per farm site) was conducted in fall (Oct-Nov) 2024, corresponding to the typical winter out-planting period for seaweed cultivation in the Northern Hemisphere. The growth of the algae was checked based on ship availability at the offshore sites and prevailing weather conditions. For growth measurements either a grid was placed underneath the algae bearing rope and photographs were taken of ten randomly chosen

individuals per replicate spool and the average length and width of the thalli was quantified using ImageJ (Schneider et al. 2012), or the measures were taken at harvested individuals. As no fouling organisms were detected directly on the biomass, quantification of epibionts was not performed. To assess growth in terms of biomass, fresh weight was determined per meter of cultivation rope at three random locations per replicate spool. Accurate assessment of fertility was impeded by the cyclical degeneration and regeneration of the thallus following swarmer release, thereby complicating reliable fertility predictions.

Statistical and data analyses

All analyses were conducted in R version 4.4.1 (R Core Team 2020). For convenience, all statistical tables are included in the supplementary appendix (Supplement Tables S1-S6).

All data were checked for normality (Shapiro-Wilk test) and variance homogeneity (Levene's test). To assess differences between strains in seedling development during the nursery phase, the percentage of seedlings that reached stage 5 after three weeks was analyzed with a one-way ANOVA with strain as the fixed factor. Additionally, seedling length after six weeks of growth on the spools were analyzed using a linear mixed model (lmer-function in lme4 package, Bates et al. 2015) with strain as a fixed factor and the 10 subsamples nested within each spool. Degrees of freedom and F-tests were calculated using Kenward-Roger approximation via the lmerTest package (Kuznetsova et al. 2017). Post hoc pairwise comparisons between strains were performed using the emmeans-function (emmeans package, Lenth 2014) with Tukey´s method for p-value adjustment. The length data was log-transformed to increase normality and variance homogeneity.

To assess difference in growth between the samplings at the Koster Farm, biomass (gram fresh weight per meter rope) was analyzed using a linear mixed model (lmer-function in lme4 package, Bates et al. 2015) with sampling as the fixed factor and spool-ID as a random factor to account for repeated measures of the spools during sampling. Thallus length was analyzed using a linear mixed model with sampling as the fixed factor, a random factor accounting for the repeated measures of the spools and a random factor accounting for the variability of the subsamples within each spool and sampling time. Degrees of freedom and F-tests were calculated using Kenward-Roger approximation via the lmerTest package (Kuznetsova et al. 2017). The length data was log-transformed to increase normality and variance homogeneity. Post hoc pairwise comparisons were performed using the emmeans-function (emmeans package; Lenth 2014) with Tukey´s method for p-value adjustment.

Due to a different sampling design for the Danish Kriegers Flak farm where samples have been randomly taken from the line with the three spools attached, differences in biomass between the samplings were analyzed with a one-way ANOVA with sampling as a fixed factor. Thallus length was analyzed with a linear mixed model with sampling as a fixed factor and a random factor to account for possible non-independence of the length measurement within a sample. Degrees of freedom and F-tests were calculated using Kenward-Roger approximation via the lmerTest package (Kuznetsova et al. 2017). The data on length was log-transformed to improve normality and homogeneity of variances.

Results

Fertility induction in *Ulva intestinalis* strains

All *U. intestinalis* populations used in this study were identified by molecular methods using the plastid-encoded *tuf*A gene as DNA barcoding marker, with resulting sequences made publicly available (GenBank accession numbers; Table 1). The species was consistently found across all sampled sites, representing natural populations spanning the full salinity gradient investigated (7–30 PSU). Only healthy populations with thalli of similar size (>10 cm), indicative of comparable age, were selected at the time of collection to ensure uniformity of parental material. A small number of individuals that spontaneously released gametes upon transfer to fresh laboratory media – present in culture 1 from Tjärnö and 34 from Mönkeberg - were removed prior to experimentation. Fertility induction of the 40 populations was achieved following established protocols, and the progression to gametangia formation was monitored microscopically (Fig. 2).

Out of 40 populations examined, only four were successfully induced to form fertile tissue (Table 1). These fertile strains originated from ecologically distinct sites: Tjärnö (Skagerrak, 30 PSU), Mönkeberg (Kiel Fjord, 14 PSU), and both Devin and Sassnitz (Arkona Basin, 9 PSU). Following fertility induction, all four strains were confirmed as gametophytes based on the morphology of biflagellate gametes (see also Figs. 2, 3A). While fertility could be induced in all four strains via desiccation (1 hour drying), mechanical fragmentation (chopping) proved effective in only two of the four strains – strain 1 from Tjärnö and strain 13 from Devin (Table 1).

All four responsive strains exhibited a conserved developmental timeline and morphological progression during gametogenesis (Fig. 2). Already in the evening of the day of induction, the parietal chloroplast appeared grainy and visible color changes from light green to an olive color appeared. Furthermore, the prominent pyrenoid was no

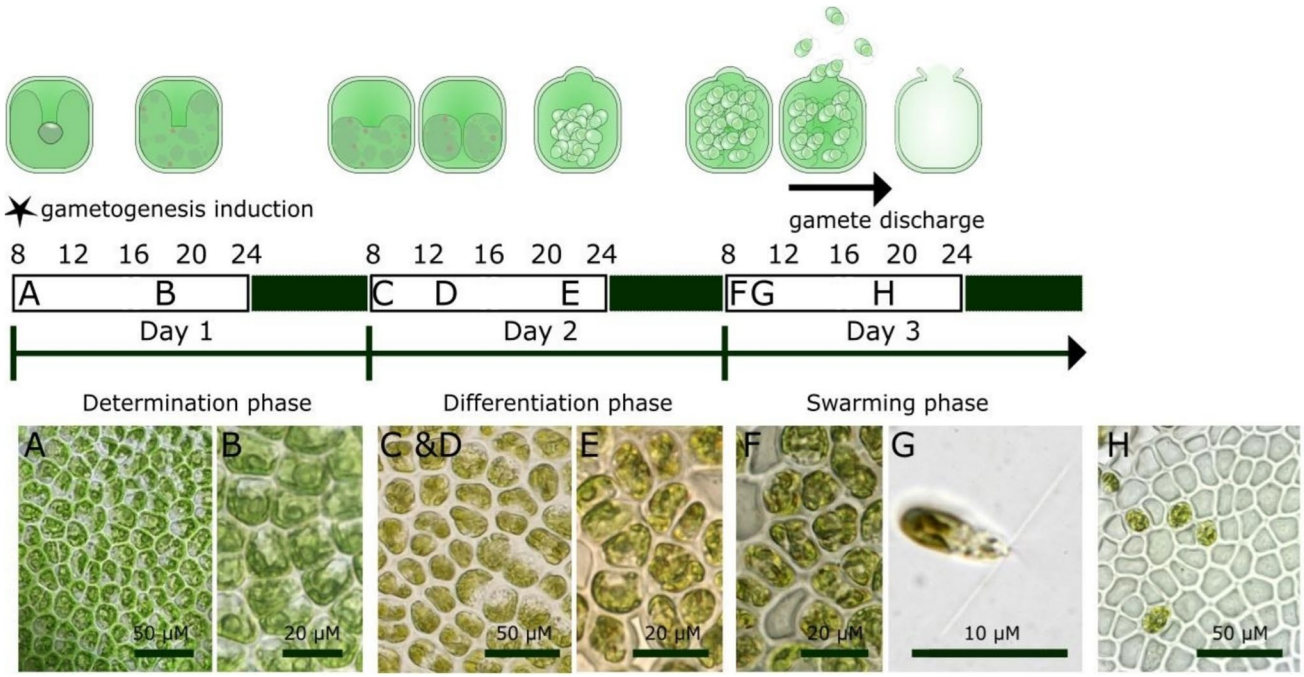


Fig. 2 Overview on the time course of induced gametogenesis in Baltic strains of *Ulva intestinalis* shown from gametogenesis induction until discharge of gametes. Gametogenesis was induced in various strains from the wider Baltic Sea region and followed a conserved developmental progression which could be divided into determination, differentiation, and swarming phase as described by Katsaros et al. (2017). **A**) Vegetative cells with a parietal chloroplast and one pyrenoid irreversibly proceed into **B**) gametangium differentiation and increased accumulation of granules is visible until **C**) the chloroplast and pyrenoid disintegrates completely and the stroma is granular. **D**) Progametes begin to emerge and **E**) progamete duplication is visible by the continuous reconstructing of the cell´s stroma, until **F**) mature gametangia become visible. **G**) Viable biflagellate gametes are being discharged asynchronously through a pore by the mature gametangia and subsequently leave **H**) empty cells and dead tissue

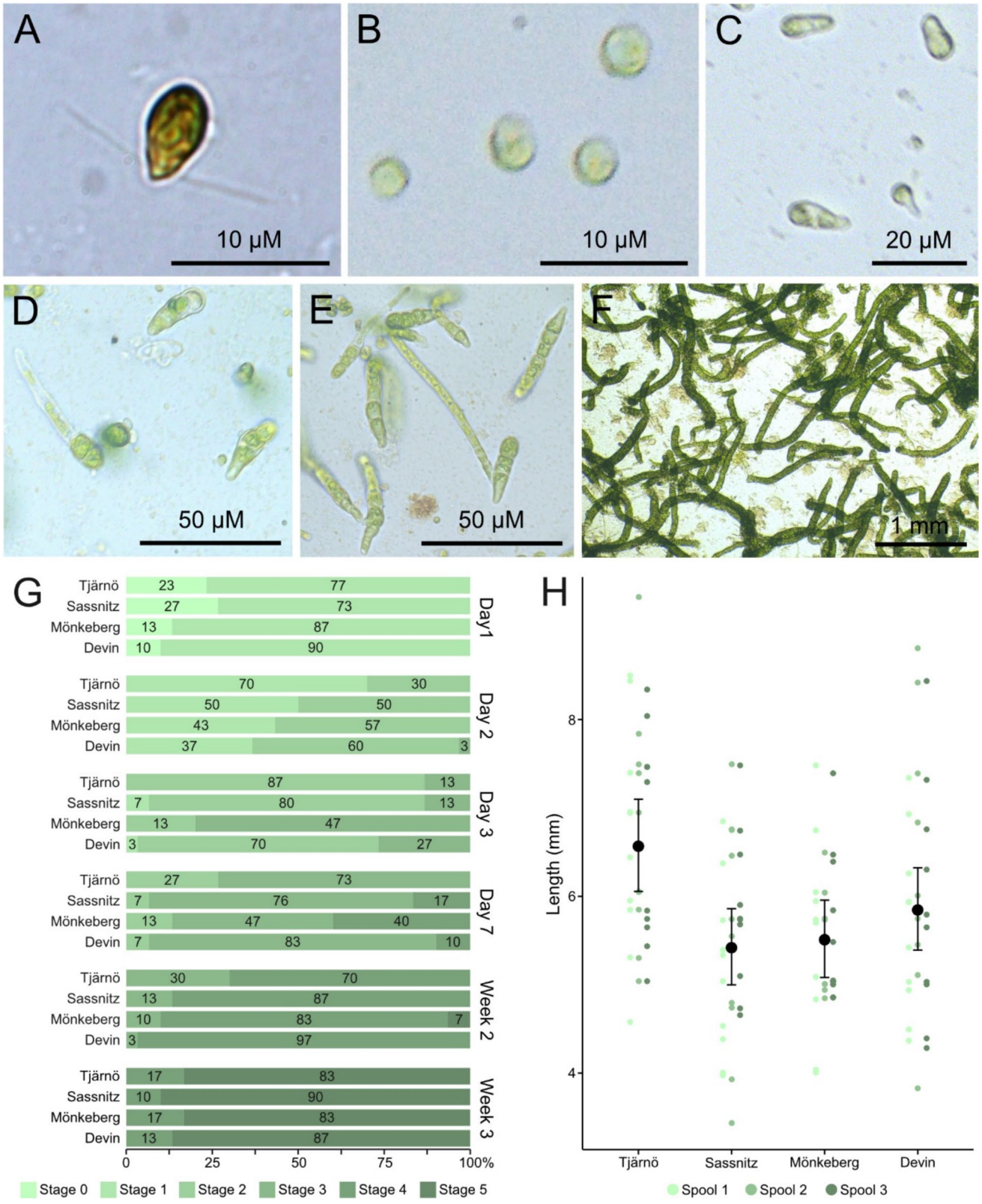
longer visible and smaller granules appeared. By the morning of the second day post-induction (either induced through chopping and washing or through desiccation and medium refreshment), vegetative cells with parietal or cell-filling chloroplasts (usually 1 pyrenoid), showed irreversible commitment to gametangial differentiation, accompanied by chloroplast reorientation and visible restructuring of the stroma under light microscopy. By late afternoon of the second day, the cytoplasm appeared granular and original cellular structures were no longer discernible. In the evening of the second day, progametes were visible. On the morning of the third day, mature gametes were clearly visible within the gametangia. At this stage, induced biomass was subjected to a standardized washing procedure to eliminate potential swarming inhibitors. Upon submersion in fresh medium, the majority of gametes was asynchronously discharged within the first 30 min, although a subset of cells continued releasing gametes over a period of up to 4 hours.

Ontogenetic development

All four strains of *U. intestinalis* successfully developed from the gamete stage to the juvenile stage (Fig. 3A-H). A continuous, relatively conserved development was observed between all-time points over three weeks (Fig. 3G), indicating comparable developmental speeds and relatively stable phase transitions. Even though there was some variation in the speed of transitioning between development stages (Fig. 3G), 83–90% of the individuals reached the juvenile stage after three weeks with no differences between strains (ANOVA, $F_{3,8}$=0.2, p=0.89, Table S1). However, after six weeks in the nursery, the average thallus length of individuals grown on nylon twine, coiled around PVS spools, differed between strains ($F_{3,8}$=6.3, *p=0.016*, Table S2). Pairwise comparisons of estimated marginal means (Tukey adjusted) indicated that individuals of the Tjärnö strain were with a length of 6.6 mm slightly but significantly longer than the Sassnitz (5.4 mm, *p=0.018,* Table S2) and Mönkeberg (5.5 mm, *p=0.029*, Table S2) strain.

Growth at the sea farm

The sea-based cultivation of the four strains of *U. intestinalis* was successful at their respective farm and is exemplified for the offshore sites Danish Kriegers Flak, Denmark and Koster archipelago, Sweden (Fig. 4A-G). Out



of the four sea-based cultivation sites for *U. intestinalis*, two experienced infrastructure loss due to heavy storm events, namely cultivations in Kiel, Germany (Farm 2) and at FINO2, Germany (Farm 4). Consequently, subsequent analyses were limited to material from the Koster archipelago, Sweden (Farm 1) and Danish Kriegers Flak, Denmark

◂**Fig. 3** Illustration of the progression from gamete stage to seedling of *Ulva intestinalis* of Baltic Sea strains. **A**) Gamete (swarmer, developmental stage [ds] 0); **B**) rounded cell after settlement (ds 1); **C**) cell with emerging germination tube (ds 2); **D**) first cell division (ds 3); **E**) distal cell divisions (ds 4); and **F**) juvenile individuals (ds 5) developing into seedlings of *Ulva intestinalis*. **G**) Ontogenetic development of 4 strains of *U. intestinalis* (Tjärnö, Sassnitz, Mönkeberg, Devin) over 3 weeks. Developmental stage defined as 0 = gamete, 1 = zygote/germination cell, 2 = germination tube, 3 = distal cell division, 4 = lateral cell division, 5 = juvenile. **H**) Thallus length (mm) of *U. intestinalis* seedlings after 6 weeks of development for all 4 Baltic Sea strains of the present study. Shown are mean values and error bars indicate 95 % confidence intervals (**G**-**H**)

(Farm 3). Nevertheless, positive growth was observed at all sites prior to storm impact, highlighting the general feasibility of cultivating *U. intestinalis* in sea-based systems. However, due to differences in deployment times and experimental conditions at the respective farms, the growth of the strains and biomass yields are not directly comparable. For the Koster farm, biomass (Fig. 4D) and thallus length (Fig. 4E) significantly varied over time ($F_{3,6}$=335.5, $p<0.001$, Table S3; $F_{4,8}$=299.9, $p<0.001$, Table S4). The average biomass and length significantly increased from under 2 g m^{-1} and 1.3 cm to 58.3 g m^{-1} and 24.5 cm from October to December but dropped significantly to values of 5.9 g m^{-1} and a thallus length of 4.5 cm in January (Table S3 + S4). Both biomass and thallus length slightly recovered to values of 21.7 g m^{-1} and 13.2 cm in February (Fig. 4D-E, Table S6). The outplanting of *U. intestinalis* at Danish Kriegers Flak showed a significant increase in the average length from 28.0 cm in February to 89.7 cm in April (ANOVA, $F_{1,3}$=63.8, $p=0.0041$, Table S6; Fig. 4F), as well as an increase of 41.97 g FW m^{-1} in yield between February and April ($F_{1,4}$=23.1, $p=0.0086$, Table S5; Fig. 4G). From April onward, residual biomass on the spools was minimal.

It should be mentioned that all four strains were maintained by clonal propagation of gametophytes and that the offspring generated from each strain maintained inducible for gametogenesis after maturation.

Discussion

To advance sustainable seaweed aquaculture in the Baltic Sea region, this study provides a comprehensive assessment of the full life-cycle cultivation potential of *U. intestinalis* by investigating strain-specific fertility inducibility, early seedling development across varying salinity origins, and the performance of in nursery–raised seedlings under offshore cultivation. Our results establish the feasibility of sea-based cultivation of *U. intestinalis* based on four key lines of evidence.

1) We show that fertility induction in *U. intestinalis* is possible, albeit at relatively low inductive rates, defined here as the proportion of isolates that successfully underwent gametogenesis and released swarmers following induction.
2) Our study elucidates the developmental timeline of gametogenesis in *U. intestinalis*, revealing a conserved and predictable sequence across Baltic Sea strains, following a three-day cycle.
3) We describe in detail the ontogenetic stages and developmental speed from gamete to juvenile thallus, offering a reproducible framework for seedling nursery development.
4) Our study demonstrates the successful offshore cultivation of *U. intestinalis* seedlings, achieved using four reproductively induced strains originating from distinct locations across the Baltic Sea region, confirming the species' broad adaptability and cultivation potential under full-life-cycle, sea-based farming conditions.

For industrial-scale seaweed aquaculture, the development of a reliable nursery system or an efficient direct seeding technique is crucial to ensure uniform seedling establishment and sustained biomass production. While *Ulva* species have been increasingly recognized as promising candidates for large-scale cultivation in low-salinity environments (Kotta et al. 2022; Cardoso et al. 2023; Steinhagen et al. 2025a, b), the realization of full life-cycle cultivation remains limited. To date, no successful large-scale seaweed farming operations have been established in the Baltic Sea. This underscores the urgent need for sustainable and innovative cultivation strategies to support blue growth and the renewable bioeconomy in this region. This limitation primarily arises from challenges in controlled fertility induction, incomplete understanding of life-cycle regulation, and underdeveloped nursery techniques tailored to Baltic crop strains such as *U. intestinalis,* which is known to spread with its occurrence throughout the full Atlantic-Baltic Sea transect (Steinhagen et al. 2023). In the present study, only 10 % of the 40 *U. intestinalis* strains tested could be reliably induced to undergo gametogenesis under laboratory conditions. This low inducibility highlights a major bottleneck for scaling up *Ulva* cultivation and emphasizes the necessity of broad strain screenings to identify genotypes with consistent reproductive responses. Although the causal mechanisms underlying the failure of most strains to initiate gametogenesis were beyond the scope of this study, persistent vegetative propagation, and clonal reproduction—well-documented in other Baltic Sea macroalgae (Pereyra et al. 2023, 2025)—may partly explain the observed lack of fertility induction. These factors, if prevalent in *U. intestinalis*, would require careful consideration in strain selection and breeding strategies for aquaculture.

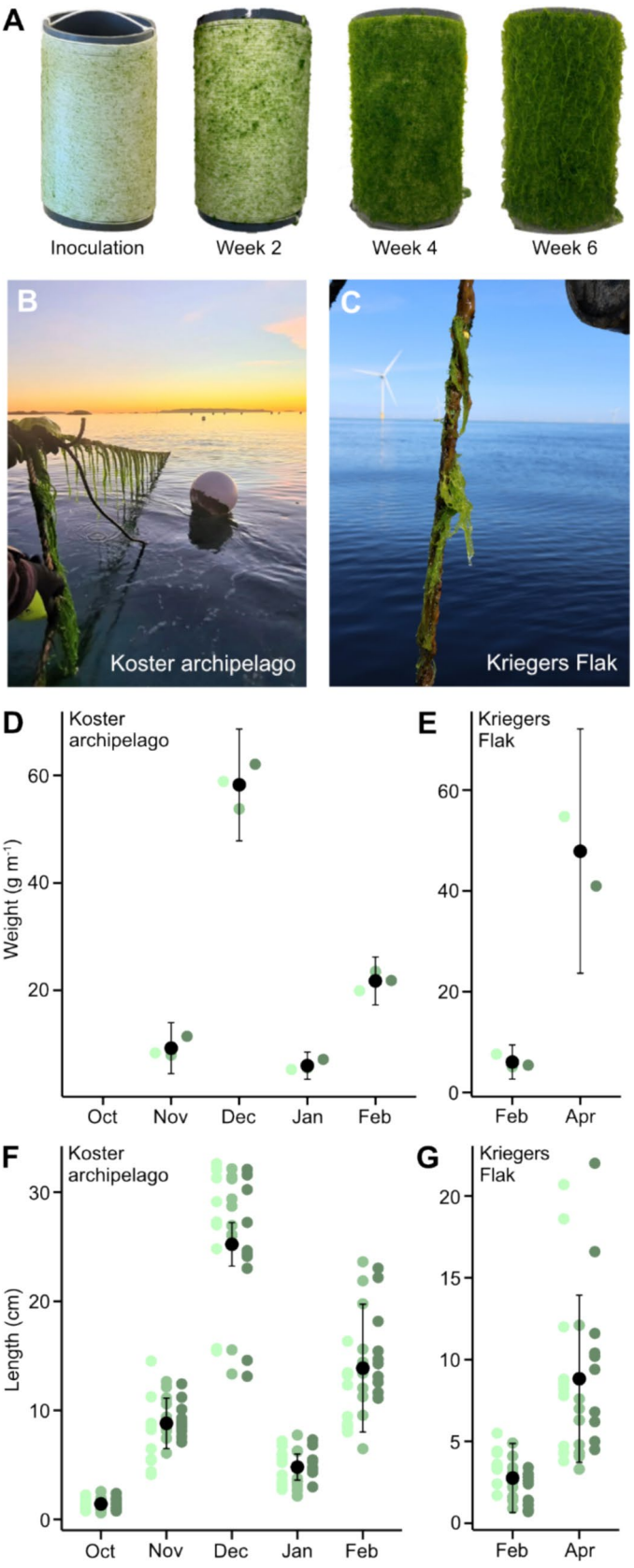


Fig. 4 Illustration of the seedling development on spools and final sea-based cultivation of *Ulva intestinalis* in the Baltic Sea area. **A**) PVC spools coiled with nylon twine, shown immediately after inoculation with *U. intestinalis* gametes and seedling growth after 2, 4, and 6 weeks (spool size, ⌀ = 7 cm, height = 16 cm). Successful sea-based cultivation of these strains is exemplified at **B**) offshore farms in the Koster archipelago, Sweden, and at **C**) Danish Kriegers Flak, Denmark. **D**) Average yield of fresh weight (g m^{-1}) of outgrown *U. intestinalis* in the Koster archipelago from harvests over a course of five months (Oct-Feb) and **E**) respective yield of fresh weight (g m^{-1}) at Danish Kriegers Flak (outlier in April was removed from dataset). **F**) Average length (cm) of outgrown *U. intestinalis* in the Koster archipelago from harvests over a course of five months (Oct-Feb) and **G**) respective average length (cm) of outgrown *U. intestinalis* from harvests in February and April at Danish Kriegers Flak. Different colored dots represent replicate spools (Koster archipelago) and random samples (Danish Kriegers Flak). Shown are mean values (**D**-**G**) and error bars indicate 95 % confidence intervals

Desiccation followed by washing proved to be more effective than chopping and washing, indicating that the physiological stress of dehydration may more effectively trigger reproductive development in *U. intestinalis* which is known to be a main component of the intertidal flora of the Baltic Sea area (Pankow 1990; Schories et al. 2009; Afanasyev et al. 2022). Numerous studies on *Ulva* have demonstrated that fertility induction requires testing of multiple approaches, as no single method has proven universally effective across species—or even among different strains within a species (Carl et al. 2014; Balar and Mantri 2019). Our results demonstrated that, in all four strains, the ability to induce gametogenesis via desiccation was retained in both the F_1 generation and subsequent gametophytic clones. This highlights the importance of targeted strain selection and preservation to enable consistent cultivation and reduce reliance on wild populations and omit low induction rate bottlenecks.

In the strains that responded positively to induction, gametogenesis proceeded in a highly synchronized and predictable manner under standardized light–dark conditions. The full sequence from commitment to gametangia formation to the release of motile gametes was completed within three days, offering a clearly defined temporal framework for hatchery operations. Notably, this developmental timeline is similar to that of *Ulva mutabilis* (Wichard and Oertel 2010) but shorter than that observed in the Northern Hemisphere crop *Ulva fenestrata* (Steinhagen et al. 2021), which typically follows a five-day gametogenic cycle. Additionally, the early post-zygotic development from gamete to juvenile thallus in *U. intestinalis* occurred at a faster rate compared to foliose *Ulva* strains used in cultivation (Steinhagen et al. 2021). These findings suggest that *U. intestinalis* holds promise for rapid and synchronized seedling production, a critical advantage for scaling up biomass cultivation in offshore or land-based systems. Further, the sustained reproductive capacity observed over multiple clonal propagations indicates that *U. intestinalis* can be maintained as a stable laboratory stock for repeated seedling production, although potential changes in productivity or reproductive output across generations remain to be investigated in future studies, as previous studies have shown that these traits can vary (Carl et al. 2016). In this context, the observed reduction in biomass between December and January is likely attributable to the onset of reproductive development and associated tissue degradation following swarmer release, a process commonly reported for *Ulva* species, although direct confirmation under offshore conditions was not possible.

Particular care must be taken when handling reproductively active *Ulva* thalli in large-scale aquaculture settings, as certain species and ecotypes—including *U. intestinalis*—are known contributors to green tide events present in the Baltic (Blomster et al. 2002). However, individuals associated with such proliferations are typically foliose morphotypes (Blomster et al. 2002), which were explicitly excluded from this study to avoid the unintended propagation of potentially nuisance genotypes within natural ecosystems. Independent of *Ulva´*s blooming potential, to further minimize the risk of uncontrolled reproduction and to optimize biomass yields, harvesting schedules should be carefully aligned with the thalli's reproductive cycle. Results on foliose temperate *Ulva* crop species have shown that seasonality and underlying environmental factors strongly determine growth, biomass yield, and biochemical composition of the *Ulva* biomass (Steinhagen et al. 2021, 2022a, b, 2025a, b). Regular clipping or mowing of mature tissue could serve as an effective cultivation strategy, promoting regrowth from juvenile parts while simultaneously reducing the accumulation of fertile biomass in the cultivation system (Carl et al. 2016).

The offshore cultivation of *U. intestinalis* in the Baltic Sea presents both promise and limitations that must be critically evaluated in the context of industrial-scale production. While our study demonstrates the biological feasibility of full life-cycle cultivation and successful offshore deployment, *U. intestinalis* typically produces lower biomass compared to foliose *Ulva* species, and its filamentous morphology may necessitate modified harvesting strategies, such as more frequent clipping cycles, optimization of seasonal harvest schedules, and fertility assessments. These adjustments can increase operational costs and complicate logistics, especially given offshore constraints such as limited accessibility under sea states exceeding 1 m wave height. Moreover, the yield-to-labor ratio and return on investment remain key challenges, particularly in exposed sites where work is seasonal and infrastructure demands are high. From a production standpoint, cultivation capacity should be carefully assessed against species alternatives; in regions with higher native *Ulva* biodiversity, selection of faster-growing or higher-yielding species may be more advantageous. In addition, strain-specific characteristics such as biochemical content, organoleptic properties (e.g. taste), and post-harvest quality will play a decisive role in determining whether *U. intestinalis* is a suitable candidate for targeted food, feed, or biomaterial markets. While offshore spaces — particularly those shared with existing infrastructure such as wind farms — offer promising alternatives to nearshore areas often constrained by tourism and coastal development, the economic feasibility of such co-location strategies must be carefully weighed against the increased costs of offshore operations and maintenance. In this context, multi-use nearshore options are being tested and are currently being scaled up. Although tubular *Ulva* species have not yet entered the European market at full scale, they represent an important and well-established food commodity in e.g., Japan, where they are cultivated and marketed as e.g., *Aonori*. Furthermore, studies from tropical regions

have demonstrated that commercially relevant yields of *Ulva* can be achieved through targeted adaptation of cultivation strategies, underscoring the substantial production potential of this genus (Carl et al. 2014, 2016).

Finally, as underlined by our findings—where only 10% of the 40 screened strains proved viable for full-life-cycle large-scale aquaculture, and even these require further selection and breeding—there is a pressing need, as also emphasized by Hofmann et al. (2025b), to systematically document the genetic, ecological, and functional characteristics of each strain in a dedicated biobank. Such coordinated efforts are essential for aquaculture, where the repeated duplication of work remains a major barrier to the growth of the Blue Economy.

Conclusion

This study provides a comprehensive assessment of the full life-cycle cultivation potential of *U. intestinalis* in the Baltic Sea region. We demonstrate that reproductive induction, seedling development, and successful offshore cultivation are feasible using selected strains from ecologically distinct locations. Despite the overall low inducibility rate (10%) among tested strains, the conservation of reproductive capacity across F_1 and clonal generations underscores the importance of targeted strain selection and preservation.

Our results reveal a fast and synchronized gametogenic cycle, enabling predictable nursery timing, and a rapid post-gametic development, making *U. intestinalis* a promising candidate for seedling-based aquaculture. Although exhibiting a faster ontogenetic development and biomass growth compared to other Northern Hemisphere *Ulva* crops, its lower biomass yield, filamentous morphology, and strain-specific inducibility demand optimization of *U. intestinalis* aquaculture in large-scale offshore settings.

While *U. intestinalis* holds potential for integration into Baltic aquaculture systems—especially in low-salinity zones—industrial application will require strain selection and refined induction protocols, efficient harvesting strategies in sea-based cultivation units, and careful economic evaluation of offshore operations. Co-location with existing offshore infrastructure may offer opportunities, but feasibility depends on balancing biological performance with operational costs and accessibility of infrastructure.

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Author contributions SST: conceptualization of the study, implementation of experiments, investigation, data analyses, visualization, funding acquisition, and original draft; SE: implementation of experiments, data analyses, visualization, and refining of draft; ESB: implementation of experiments, data analyses and refining of draft; IH: data analyses and refining of draft; IJ: implementation of experiments, data analyses and refining of draft; GN: funding acquisition, and refining of draft; AO: implementation of experiments, data analyses and refining of draft; KR: investigation and refining of draft; ES: investigation, funding acquisition, and refining of draft; JB: investigation and refining of draft; TS: investigation, funding acquisition, and refining of draft. MK: investigation, funding acquisition, and refining of draft; TB: implementation of experiments, data analyses and refining of draft; AB: investigation, funding acquisition, and refining of draft; All authors contributed to the article and approved the submitted version.

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Data availability Data are available from the corresponding author upon reasonable request.

Declarations

Competing interests The authors declare no competing interests.

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