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RESEARCH

Hatchery development for aquaculture of the southern bull kelp *Durvillaea potatorum* (Fucales): gamete release, fertilisation rate, and juvenile growth

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Abstract

Durvillaea spp. (Fucales) occur on wave-exposed coasts in parts of the southern hemisphere. In Tasmania, Australia, a small but economically valuable industry (> US$1.5 million GVP) harvests beach-cast *Durvillaea potatorum*, primarily for alginates and liquid plant biostimulants. Currently, demand for *D. potatorum* biomass exceeds supply, prompting interest in aquaculture to sustainably increase production. However, fundamental hatchery methods required for its cultivation are not well understood. We conducted a series of experiments to determine optimal conditions for gamete release, fertilisation, and juvenile growth in a hatchery setting. Releasing gametes for 10 min at 14 °C produced consistently high egg densities (mean ± SE: 12,720 ± 1020 cm^{-2} tissue) and fertilisation rates peaked (89 ± 4%) when reproductive tissue was held overnight and gametes were released at 14 °C. Moreover, ~ 50% of male and female gametes were released within 10 min and > 90% within one hour. Three growth experiments showed that: (i) the highest growth rate was found by first holding the samples in the dark overnight at 14 °C and then using a gamete-release temperature of 18 °C, with juveniles reaching a mean length of 1.2 mm ± 0.1 SE and width of 0.29 mm ± 0.02 SE after 60 days at 14 °C and a light level of 35 µmol photons m^{-2} s^{-1} (12 h light: 12 h dark photoperiod); (ii) an irradiance level of 95 µmol photons m^{-2} s^{-1} for maximise growth of juveniles; and (iii) nutrient medium and temperature influenced growth, with the best performance in F/2 medium at 15 °C after 30 days (mean length 0.9 ± 0.2 mm; width 0.38 ± 0.01 mm). Growth of juvenile *D. potatorum* was poor in media containing ammonium (NH_4^+), such as Provasoli's Enriched Seawater (PES) and seawater enriched with N and P, at similar concentrations to PES, suggesting NH_4^+ toxicity for early life stages at high concentrations. These results represent a significant step toward establishing effective hatchery methods for *Durvillaea spp*. and other Fucales more broadly, supporting future at-sea cultivation.

Keywords Phaeophyceae · Australia · Cultivation · Kelp · Fucoid · Mariculture · Nursery · Seaweed

Introduction

Global seaweed aquaculture has increased rapidly over the past three decades with a total harvest of 36.5 million tonnes wet weight in 2022 (FAO 2024). This production is dominated by Asian countries, which produce around 97% of aquaculture seaweeds concentrated on just 8 major genera (Nayar and Bott 2014; Chopin and Tacon 2020; FAO 2024). Western nations such as the USA, Norway and other European nations have begun domestic aquaculture in response to an increasing demand for seaweed (Stévant et al. 2017; Kim et al. 2019; FAO 2024). In comparison, seaweed aquaculture in Australia is limited, and the industry largely relies on imports and collecting beach-cast seaweeds to meet its needs (Kelly 2020; Steven et al. 2020; FAO 2024). Nonetheless,

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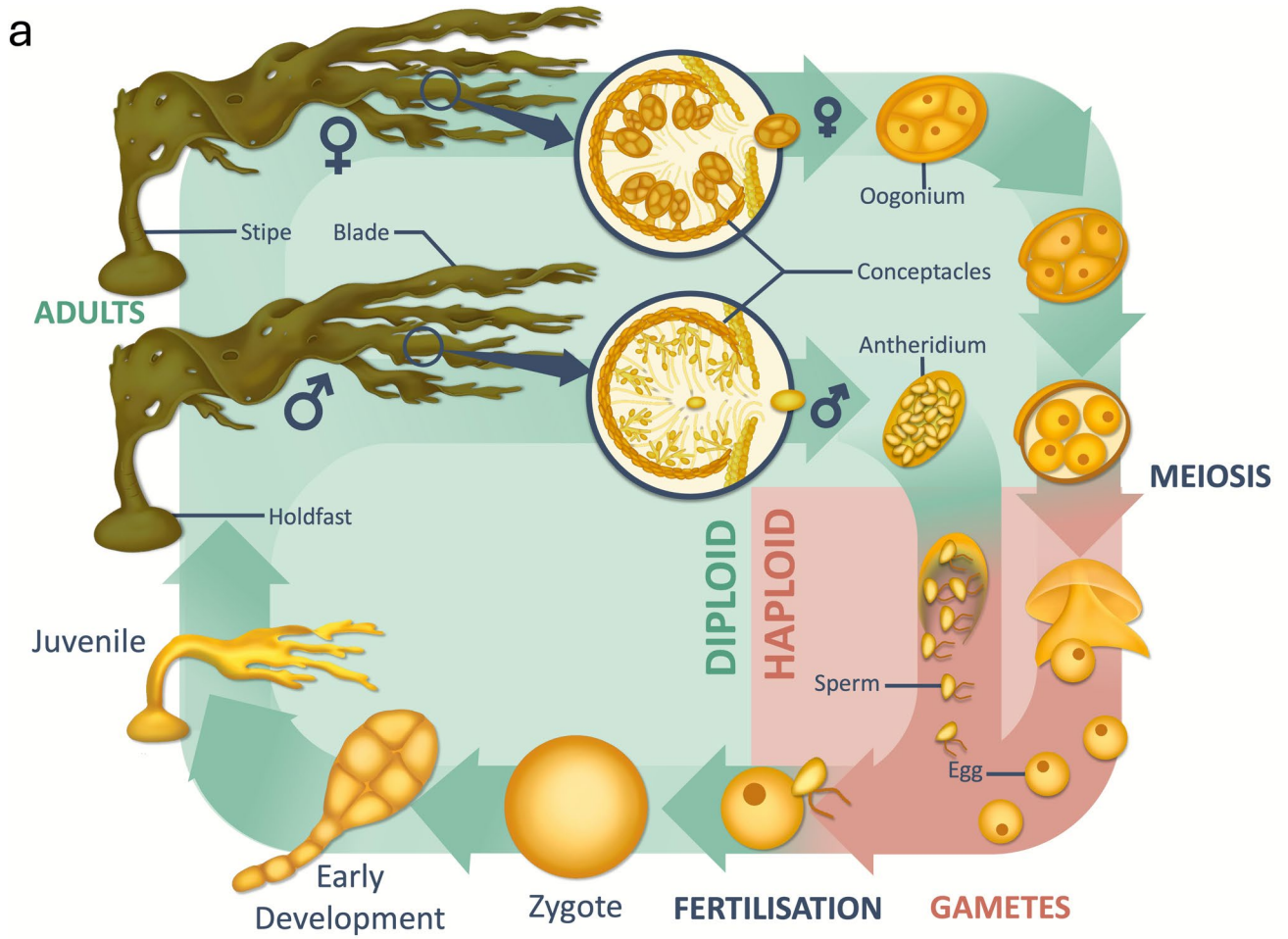
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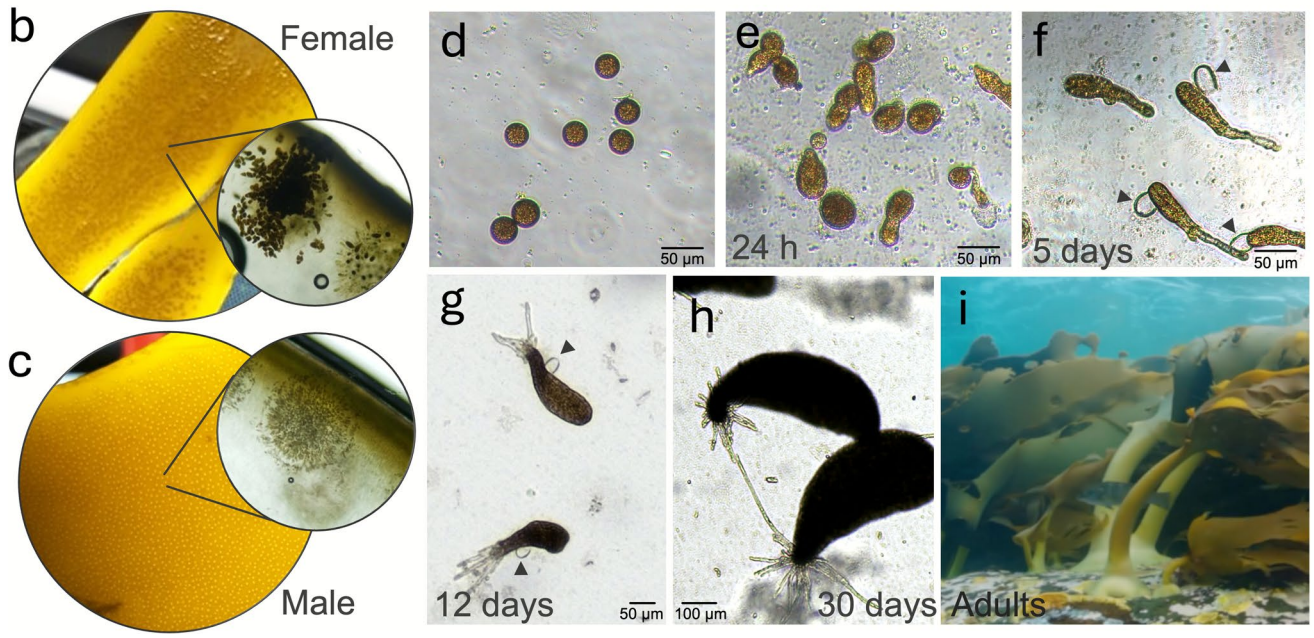
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◂**Fig. 1** Life cycle stages of *Durvillaea potatorum*. (**a**) Diplontic life cycle of the genus *Durvillaea* (Fucales, Ochrophyta). Macroscopic dioecious sporophytes (2n) produces gametes (n) via meiosis within conceptacles distributed across the blade of mature reproductive individuals. Male and female gametes develop in antheridia and oogonia, respectively, and are released into the water column. Negatively buoyant eggs settle on suitable substrates, are fertilised, and form zygotes that develops into the next sporophyte generation (2n). Reproduction peaks in winter, most individuals remain non-reproductive from late spring to autumn. (b–c) Fertile regions on adult sporophytes showing conceptacles: (**b**) female thallus with oogonia; (**c**) male thallus with antheridia. (**d**) Released gametes (eggs and sperm) under light microscopy. (**e**) Zygotes 24 h after fertilisation, beginning germination. (**f**) Germlings at 5 days showing initial rhizoid development and zygote wall shedding (arrowheads). (**g**) Juvenile sporophytes at 12 days with elongated thallus and rhizoids, plus remnants of zygote walls (arrowheads). (**h**) Juveniles at 30 days showing further thallus growth and multiple unfused rhizoids. (**i**) Mature sporophytes with large discoid holdfasts and thick stipes forming dense stands in wave-exposed habitats. Life cycle diagram by Elise Hore; images (b-h) by Wouter Visch; and (i) courtesy by Great Southern Reef Foundation

Australian aquaculture stakeholders have expressed a strong interest in increasing domestic seaweed production, reflecting the diverse market opportunities and favourable environment (Steven et al. 2020; Visch et al. 2023).

A recent review identified *Durvillaea* spp. as the most suitable Australian seaweed for offshore aquaculture, due to its established market, high biomass, and tolerance to hydrodynamic stress (Visch et al. 2023). The genus *Durvillaea* (order Fucales) occurs in the southern hemisphere distributed across southern Australia, South America, New Zealand, and sub-Antarctic islands (Cheshire and Hallam 1985; Fraser et al. 2020; Velásquez et al. 2020). *Durvillaea* grows up to 10 m in length and has thick blades, robust stipes and large discoid holdfasts (Velásquez et al. 2020). It is abundant on wave-exposed rocky coasts where it grows in dense forests and achieves standing crops (mean 22.5 kg m^{-2}; max-value 108 kg m^{-2}) comparable to *Macrocystis* (Cheshire and Hallam 1988). In Tasmania, southern Australia, *D. potatorum* and *D. amatheia* co-occur along eastern, western, and southern coasts, differing mainly in genetics, subtle morphology, and with *D. potatorum* being more dominant in the intertidal and shallow subtidal (Weber et al. 2017). Despite its potential, *D. potatorum*. has never been commercially cultivated, and current supply relies on beach collected material (Hurd et al. 2023).

Market demand for *Durvillaea* spp. is driven by its exceptionally high alginate content (up to 50% of dry weight) and its plant biostimulant properties (Kelly and Brown 2000; Abraham et al. 2019; Arioli et al. 2024). Annual beach collection of *D. potatorum* on King Island, northwest of Tasmania, Australia peaked at 4,000 t dry weight in 1990 but has declined significantly since 2000 (André et al. 2009), underscoring the strong need for sustainable aquaculture. Prioritising *D. potatorum* cultivation in Australia represents a major opportunity to meet growing demand and develop resilient aquaculture systems.

Adult *Durvillaea* thalli have diffuse growth, producing new cells across the blade rather than in a distinct meristem, and have large discoid holdfasts. The genus is dioecious (Fig. 1), with male and female individuals producing gametes in conceptacles distributed across the blade (Fig. 1) (Clayton et al. 1987; Velásquez et al. 2020). Sperm and eggs are released into the water column where fertilisation occurs after which the zygote secretes an adhesive mucilage to attach to substrate and undergoes longitudinal cell divisions for the first 1–3 days (Hay 1977). By 4–5 days, the zygote wall begins to separate, allowing the embryos to widen (Kevekordes and Clayton 1999). Rhizoids develop shortly thereafter to further secure the germling to the substate (Hay 1977; Collantes et al. 2002; Dimartino et al. 2016), with multiple rhizoids forming over the following 2–3 weeks as germlings begins to orient upright (Velásquez et al. 2020). The peak reproductive period of *D. potatorum* along the southeastern coast of mainland Australia is the austral winter (June to October; Clayton et al. 1987). However, the specific environmental requirements and fine-scale timing of developmental stages for *Durvillaea* populations in Tasmania, Australia, remain to be determined.

Standard hatchery protocols for seaweeds typically involve sourcing wild seedstock, maintaining/holding reproductive tissue, inducing gamete or spore release through desiccation and immersion, fertilisation, seeding onto substrates, and rearing germlings to outplant size (Zhao et al. 2009; Kerrison and Le 2016; Pan et al. 2019; Largo et al. 2020). While protocols have been developed for some fucoid species, such as *Sargassum* spp. (Kerrison and Le 2016; Le et al. 2018; Largo et al. 2020; Liu et al. 2021; Magcanta-Mortos et al. 2025), they remain very limited for *Durvillaea* (Gutiérrez et al. 2016). For *D. potatorum*, the optimal conditions, such as duration and temperatures for optimal gamete release and fertilisation, as well as the light, temperature and nutrient requirements to maximise growth of hatchery-reared germlings are currently unknown.

The overall aim of this study was to develop hatchery methods to produce juvenile *Durvillaea* for subsequent cultivation at-sea. Specifically, we tested the effect of (1) gamete release duration on fertilisation; (2) holding and release temperature on gamete release, fertilisation success, and early growth of zygotes; (3) irradiance, temperature, and nutrient medium on early growth of juveniles; and (4) gamete release from reproductive tissue over time (> 10 days).

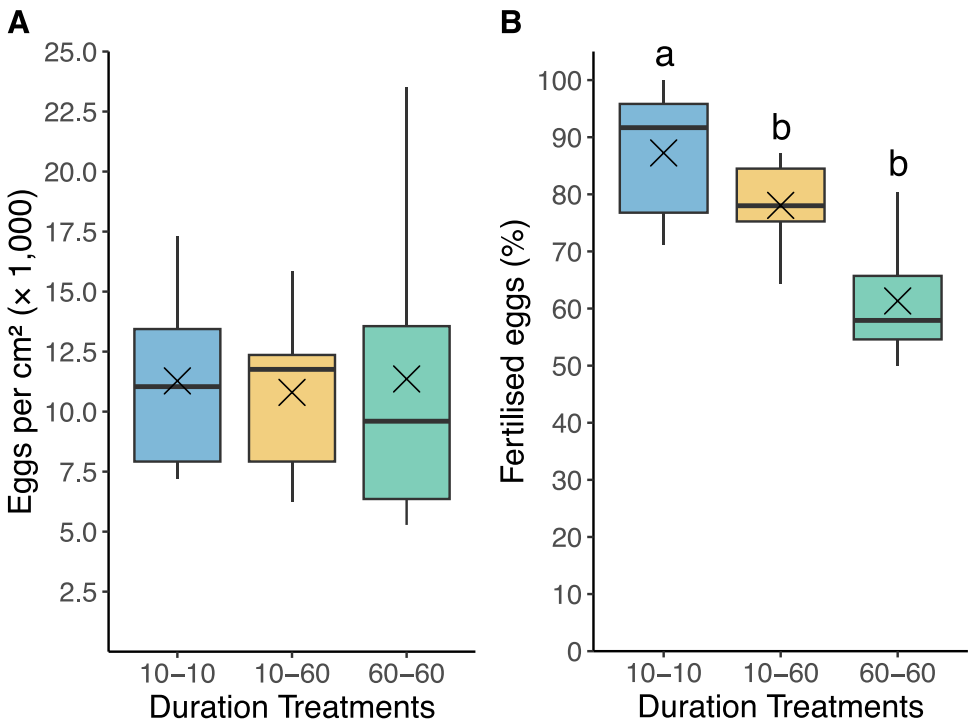

Fig. 2 Experiment 1: Egg release per cm^2 tissue (**A**) and the percentage of fertilised eggs after 72 h (**B**) under three release duration treatments (10:10, 10:60, 60:60 min release for sperm:eggs). The overnight and release temperatures were 4 and 14 °C, respectively. Boxes show the interquartile range, with whiskers from the first to the third quartiles; medians are lines, means are marked with an X (n = 6). Boxes sharing a letter are not significantly different (Tukey HSD, α = 0.05)

Material and methods

Study site and sample collection

We collected *Durvillaea potatorum* from Binalong Bay (41.2515° S, 148.3111° E) and Clyde's Island (43.0136° S, 147.9367° E) on the east-coast of Tasmania between June and July 2023. Both sites experience high wave-exposure primarily from the east. Reproductive tissue was collected from haphazardly selected reproductive male and female thalli in the lower intertidal/upper subtidal zone where *D. potatorum* occurs (Weber et al. 2017). For each experiment, a sample was cut from the frond tips of reproductive male and female thalli (n = 6 per sex). Male and female samples were stored separately in zip-lock bags with seawater and transported from the field site to the IMAS laboratory in Hobart in a cooler within 2 h of collection. On return to the lab, samples were cut to desired size (see below), rinsed twice in 5% iodine (Betadine solution) and then in filtered (0.2 µm) autoclaved seawater (hereafter; sterilised seawater). Samples were then wrapped in damp paper towel, sealed in Ziplock bags, and placed overnight in a cool dark room (sensu Visch et al. 2024). Overnight holding temperature, release temperature, tissue size (surface area of both sides) and number of replicates for gamete release varied between experiments and are specified below.

General procedures for gamete release, fertilisation, and early growth

Gametes were released by placing male and female reproductive tissue into sterilised seawater for a defined duration under controlled temperature conditions (determined in Experiment 1). Fertilisation was initiated by transferring equal volumes of sperm and egg suspensions into 10 mL wells containing enriched seawater medium. Well plates were maintained in darkness at 14 °C for 24 h, followed by a 12:12 h light:dark cycle (~ 35 µmol photons m^{-2} s^{-1}). Gamete density was counted at each time point using a haemocytometer (sperm) and a 1 mL Sedgewick rafter chamber (eggs). Fertilisation and egg densities were obtained from five evenly spaced microscope images (Nikon Eclipse TS2, 100 × magnification) per well, and fertilisation percentages were calculated (n = 5 per treatment). Fertilisation was identified by elongation of eggs, rhizoid development, or zygote wall shedding; unfertilised eggs remained circular with no signs of division (Clayton et al. 1987; Collantes et al. 2002). Early growth was assessed by photographing juveniles at specified time intervals and measuring length and width using ImageJ (Schindelin et al. 2012). An overview of the five experiments conducted in this study is provided in Table 1.

Table 1 Summary of experimental design, independent and dependent variables, and associated analysis

	Experiment 1	Experiment 2.1	Experiment 2.2	Experiment 3	Experiment 4	Experiment 5
Aim	Effect of gamete release duration on fertilisation	Effect of holding and release temperature on gamete release and fertilisation	Effect of holding and release temperature on early growth	Effect of irradiance on early growth	Effect of temperature and nutrient medium on density and early growth	Gamete release from reproductive tissue over time
Independent variables	Gamete release duration (male:female): 10:10 min, 10:60 min, 60:60 min	Holding – release temperatures: 4–10 °C, 4–14 °C, 14–14 °C, 14–18 °C	Growth after Exp. 2.1 treatments; best treatment (14–18 °C) over 60 days.	Irradiance: 0–240 µmol photons $m^{-2}s^{-1}$ (15 levels)	Temperature: 9, 12, and 15 °C; Nutrient medium: F/2, PES, SES, and seawater	Release time: 10 min - 252 h (10 levels)
Dependent variables	Egg density (cm^2), % fertilisation	Egg density (cm^2), % fertilisation	Length and width	Length	Length, width, density	Gamete density and release rate
Statistical analysis and Figures	One-way ANOVA (3 levels): Figure 2	One-way ANOVA (4 levels); Figure 3	One-way ANOVA (4 levels); Figure 4	Quadratic curve fitting (regression model); Figure 5	Two-way ANOVA (Temperature, 3 levels; Nutrient, 4 levels); Figure 6	Separate one-way ANOVAs for males and females (release time, 10 levels); Figure 7

Experiment 1: Effect of gamete release duration on fertilisation

Gametes were released (males:females) at 14 °C for three durations: 10:10 min, 10:60 min, and 60:60 min. Six replicate tissue samples (20 cm^2) per sex were placed in separate beakers containing 30 mL sterilised seawater. After release, 1 mL of sperm and egg solution was transferred into wells with 8 mL F/2 medium (Guillard and Ryther 1962; Guillard 1975). Fertilisation was quantified as described in the general procedures.

Experiment 2: Effect of holding and release temperature on gamete release, fertilisation, and early growth

Experiment 2.1. Gamete release and fertilisation

Samples of tissue (20 cm^2) were held as above overnight at either 4 °C or 14 °C. The following day, gametes were released into sterilised seawater at 10 °C, 14 °C and 18 °C creating four overnight holding-release combinations: 4–10 °C, 4–14 °C, 14–14 °C, 14–18 °C. Gametes were released for 10 min, and fertilisation was assessed following the general procedures.

Experiment 2.2. Early growth

Juveniles were maintained in 12 h light:12 h dark cycle at ~ 35 µmol photons m^{-2} s^{-1} at 14 °C and growth (length and width) was measured after 39 days for all treatments and at multiple time points (3, 12, 31, 29, 60 days) for the holding-release treatment (14–18 °C) with the most eggs released and highest fertilisation rate (determined in experiment 2.1). Length and width were recorded for haphazard selected individuals (n = 20) for each well (N = 6) using ImageJ.

Experiment 3. Effect of irradiance level on early growth

Gametes were released for 10 min, and conditions for fertilisation and early growth followed the general procedures. From a 5 L zygote stock solution, 1 mL was pipetted into wells of six-well plates, each topped up with 8 mL of F/2 medium (n = 6 per treatment). Plates were placed on shelves in a temperature-controlled room (14 °C) at progressively decreasing distances from an overhead light source (type etc.), creating 15 irradiance levels (0, 10, 22, 27, 32, 40, 47, 52, 63, 72, 84, 102, 144, 180, and 240 µmol photons m^{-2} s^{-1}). The 0 µmol photons m^{-2} s^{-1} treatment was established by wrapped the plate in aluminium foil. After 19 days, one haphazardly selected field of view (40 × magnification)

in each replicate well were taken using a camera (Canon EOS 5D) mounted on a dissecting microscope (Leica M165 C). From each image the mean length of 10 haphazardly selected juveniles was measured using ImageJ.

Experiment 4: Effect of temperature and nutrient medium on density and early growth

Gametes from males and females were released for 10 min into separate beakers (200 mL sterilised seawater). Wells (n = 6) contained 8 mL of four nutrient media (Table 2): F/2, Provasoli Enriched Seawater (PES) (Andersen 2005), Simple Enriched Seawater (SES; containing only nitrate, ammonium, and phosphate at similar concentrations as PES), and seawater only.

Plates with zygotes were placed in a temperature-controlled cabinet (Model F-FLI-350, Labec Pty Ltd, Australia) equipped with internal LED lighting (Cool White, 380–760 nm) under a 12:12 h light:dark cycle (100 µmol photons m^{-2} s^{-1}), at temperatures of 9, 12, or 15 °C. Medium was changed weekly. Density and growth were assessed after 30 days by photographing each well using a camera (Canon EOS 5D) mounted on a dissecting microscope (Leica M165 C) at 7.3 × magnification. Density was determined by counting all juveniles within each image, and growth by measuring their length and width using ImageJ.

Experiment 5: Gamete release from reproductive tissue over time

Replicate reproductive tissue (2.66 cm^2) was wrapped in damp paper towel inside a Ziplock bag, stored overnight at 14 °C, then placed in wells with 5 mL seawater for the following durations: 10 min, 30 min, 1 h, 3 h, 18 h, 24 h, 96 h, 144 h, 180 h and 252 h. After each time interval, the tissue was carefully transferred to a fresh well using sterilized tweezers to ensure separation of gamete release across time points. Gamete release was quantified by counting all the gametes (sperm or eggs) present in each well for each time-interval after the tissue was removed and converted to an hourly release rate (cells per hour) to enable comparing between time intervals. Although gametes were still being released after 252 h, the tissue started to become necrotic, and the experiment ceased.

Table 2 Nutrient media and their respective macro-nutrients

Component (µM)	F/2	Provasoli Enriched Seawater (PES)	Simple Enriched Seawater (SES)
Nitrate (NO_3^-)	882.5	823.6	823.6
Ammonium (NH_4^+)	-	187.0	187.0
Phosphate (PO_4^{3-})	36.2	32.7	32.7
Micro-nutrients	Present	Present	Absent

F/2 and Provasoli's Enriched Seawater are prepared as per the recipe in Andersen (2005), the Simple Enriched Seawater treatment was created using the macro-nutrients at identical concentrations as in Andersen (2005), with micro-nutrients omitted. Data is presented in µM.

Experimental design and statistical analysis

An overview of the experiments with their respective dependent and independent variables is provided in Table 1. All plots and statistical analyses were performed using R software (R Core Team 2025). Differences among treatments in the number of eggs released per cm^2 of tissue and percentage of fertilised eggs (experiments 1 and 2.1) were analysed with a one-way analysis of variance (ANOVA) while growth and density data were analysed with one-way ANOVA (experiment 2.2) or two-way ANOVA (experiment 4). Separate one-way ANOVAs were used to test the effects of time on the density of released gametes for females and males (experiment 5) using the *aov* function. When main effects were significant ($\alpha = 0.05$), a Tukey's Honestly Significant Difference (TukeyHSD) post-hoc test was used to determine differences between treatments of each experiment. Prior to analysis, data were checked for violations of ANOVA assumptions of normality of residuals (diagnostic plots and Shapiro–Wilk test; $\alpha = 0.05$) and heteroscedasticity (diagnostic plots and Bartlett test; $\alpha = 0.05$) and data were transformed when assumptions were violated. To determine the irradiance level associated with maximum early growth (experiment 3), a quadratic regression model was fitted to the relationship between irradiance level (µmol photons m^{-2} s^{-1}) and mean thallus length using the *lm()* function in R with a second-order polynomial term. Predicted values and 95% confidence intervals were generated using *predict()* and the irradiance corresponding to the maximum predicted length was identified by locating the peak of the fitted curve.

Results

Experiment 1: Effect of gamete release duration on fertilisation

There was no significant effect of release duration on the number of eggs released by female *Durvillaea* ($F_{2,15} = 0.02$; $p = 0.979$; Fig. 2A). In contrast, the percentage of fertilised eggs was significantly affected by the release duration treatments ($F_{2,15} = 8.91$; $p = 0.003$) with the highest fertilisation when both the sperm and eggs were allowed to release for 10 min (Fig. 2B). There was a noticeable decline in fertilisation when sperm were held for

60 min, and the decline was even greater when both eggs and sperm were held for 60 min.

Experiment 2: Effect of holding and release temperature on gamete release, fertilisation, and early growth

Experiment 2.1. Gamete release and fertilisation

There was no significant effect of the holding and release temperature treatments on the number of eggs released by female *Durvillaea* ($F_{3,20} = 1.86$; $p = 0.168$). Although not statistically significant, the overnight holding temperature of 14 °C tended to result in higher egg release, regardless of release temperature (Fig. 3A).

The percentage of fertilised eggs differed significantly across treatments ($F_{3,20} = 3.31$; $p = 0.041$; Fig. 3B), with the highest fertilisation in the 14–14 °C (holding – release) treatment. Post-hoc TukeyHSD tests revealed a significant difference between the 14–14 °C and 4–14 °C treatments ($p = 0.048$) and no significant differences between the 14–14 °C and either the 4–10 °C ($p = 0.082$) and 14–18 °C ($p = 0.119$) treatments.

Experiment 2.2. Early growth

There was a significant effect of the holding and release temperature treatments on juvenile *Durvillaea* growth after 39 days, for both length ($F_{3,72} = 6.32$; $p < 0.001$; Fig. 4A) and width ($F_{3,72} = 3.69$; $p < 0.016$; Fig. 4B). The length of the *Durvillaea* juveniles was significantly greater in the 14–18 °C (holding – release) treatment compared to in the 4–10 °C and 14 −14 °C treatments. Width of the juveniles was also greater in the 14–18 °C treatment compared to the 4–10 °C treatment. After 60 days, length in the 14–18 °C treatment increased to 1215 ± 100 µm and width to 286 ± 18 µm (mean ± SE, N = 6; Figs. 4C and 4 D, respectively).

Experiment 3. Effect of irradiance level on early growth

The quadratic model indicated a unimodal response of early growth to irradiance, and the maximum predicted thallus length occurred at 95.3 µmol photons m^{-2} s^{-1} (Fig. 5). Furthermore, there was little difference in length between 10–75 µmol photons m^{-2} s^{-1} but a steep decrease in growth at higher irradiance

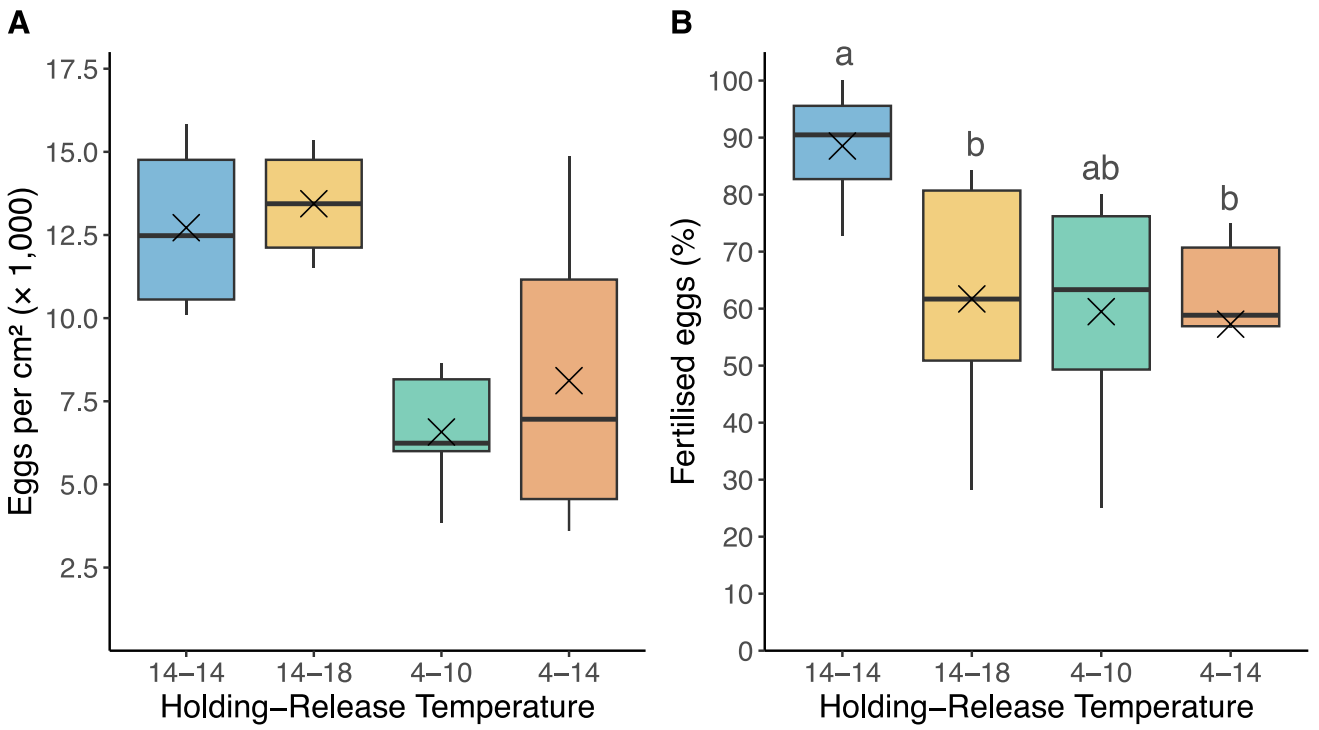

Fig. 3 Experiment 2.1: The release (**A**) and percentage fertilisation of *Durvillaea* eggs after 72 h (**B**) under four overnight holding-release temperature treatment combinations: 14–14 °C, 14–18 °C, 4–10 °C, 4–14 °C. Boxes show the interquartile range, with whiskers from the first to the third quartiles; medians are lines, means are marked with an X (n = 6). Boxes sharing a letter are not significantly different (Tukey HSD, α = 0.05)

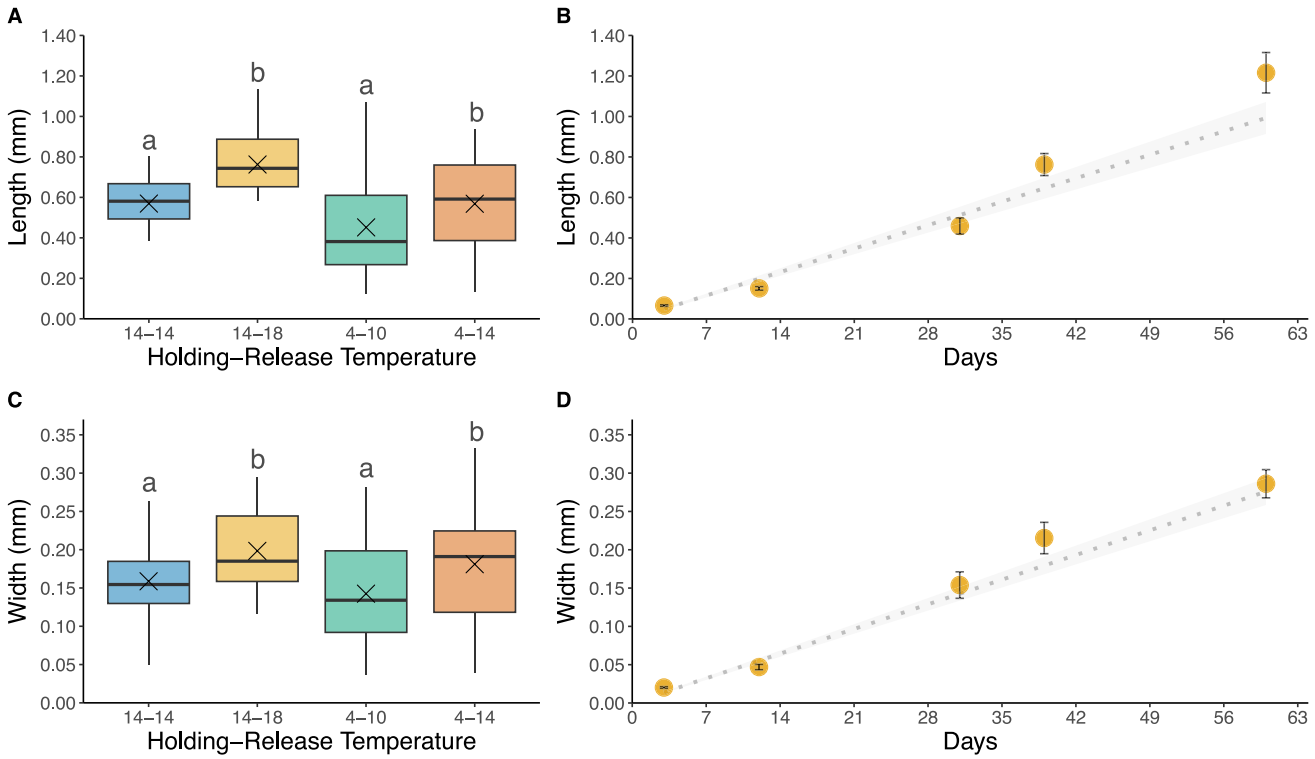

Fig. 4 Experiment 2.2: Growth (length and width) of *Durvillaea potatorum* germlings after 39 days in 12 h light:12 h dark cycle at ~ 35 µmol photons m^{-2} s^{-1} at 14 °C after four holding-release temperature treatments: 14–14 °C, 14–18 °C, 4–10 °C, 4–14 °C. Boxplots for (**A**) length and (**B**) width show the interquartile range, with whiskers from the first to the third quartiles; medians are lines, means are marked with an X (N = 6). Boxes sharing a letter are not significantly different (Tukey HSD, α = 0.05). Mean (± SE, N = 6) (**C**) length and (**D**) width at 3, 12, 31, 39, and 60 days at 14 °C for the 14–18 °C treatment (yellow); dotted lines show linear model fits with 95% confidence interval (grey shading)

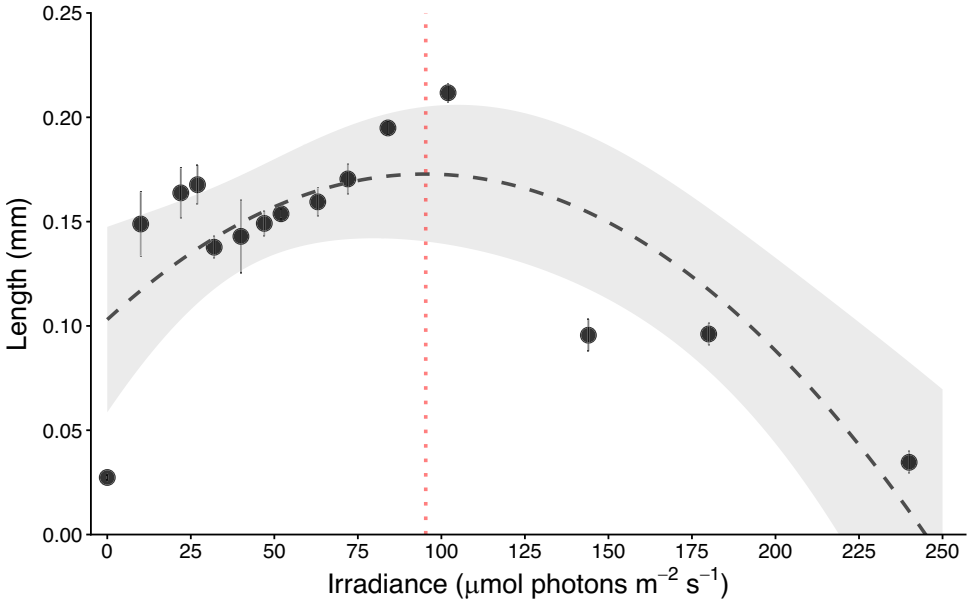

Fig. 5 Experiment 3: The effect of irradiance level (µmol photons m^{-2} s^{-1}) on *Durvillaea potatorum* germling growth after 19 days. Points are mean thallus length (mm) ± SE (n = 6). The black dashed line shows the fitted quadratic regression with 95% confidence interval (grey area) and the red dotted line indicates the irradiance corresponding to maximum predicted growth (95.3 µmol photons m^{-2} s^{-1})

levels (144–240 µmol photons m^{-2} s^{-1}). Moreover, the germlings in the highest irradiance treatment (240 µmol photons m^{-2} s^{-1}) were discoloured, which was not observed in the other irradiance treatments.

Experiment 4: Effect of temperature and nutrient medium on density and early growth

Juvenile density was not significantly affected by temperature, nutrients, or their interaction (Fig. 6A; Temperature: $F_{2,59} = 2.51$, $p = 0.090$; Nutrient: $F_{3,59} = 2.59$, $p = 0.061$; Interaction: $F_{6,59} = 0.98$, $p = 0.447$).

Juvenile length and width were significantly affected by temperature and nutrient medium (Figs. 6B and C). Example images are in Supplementary Material Fig. S1.

In terms of length, there were significant effects of temperature ($F_{2,59} = 54.10$; $p < 0.001$) and nutrient medium ($F_{3,59} = 39.09$; $p < 0.001$). However, the interaction between temperature and nutrient medium was not significant ($F_{6,59} = 1.10$; $p = 0.375$). For temperature, all pairwise comparisons were statistically significant with length at 15 °C significantly greater than at both 9 °C (mean difference = 1.49 mm, $p < 0.001$) and 12 °C (mean difference = 0.64 mm, $p < 0.001$) and length at 12 °C significantly greater than at 9 °C (mean difference = 0.85 mm, $p < 0.001$).

The F/2 medium significantly increased juvenile length compared to PES (mean difference = 1.72 mm, $p < 0.001$), the seawater only (mean difference = 1.23 mm, $p < 0.001$), and SES (mean difference = 1.22 mm, $p < 0.001$) treatments. The SES and seawater only treatments supported significantly greater length than the PES treatment (mean difference = 0.51 mm, $p = 0.017$; and mean difference = 0.50 mm, $p = 0.019$, respectively). No significant difference was found between SES and seawater only treatments (mean difference = 0.01 mm, $p = 0.998$).

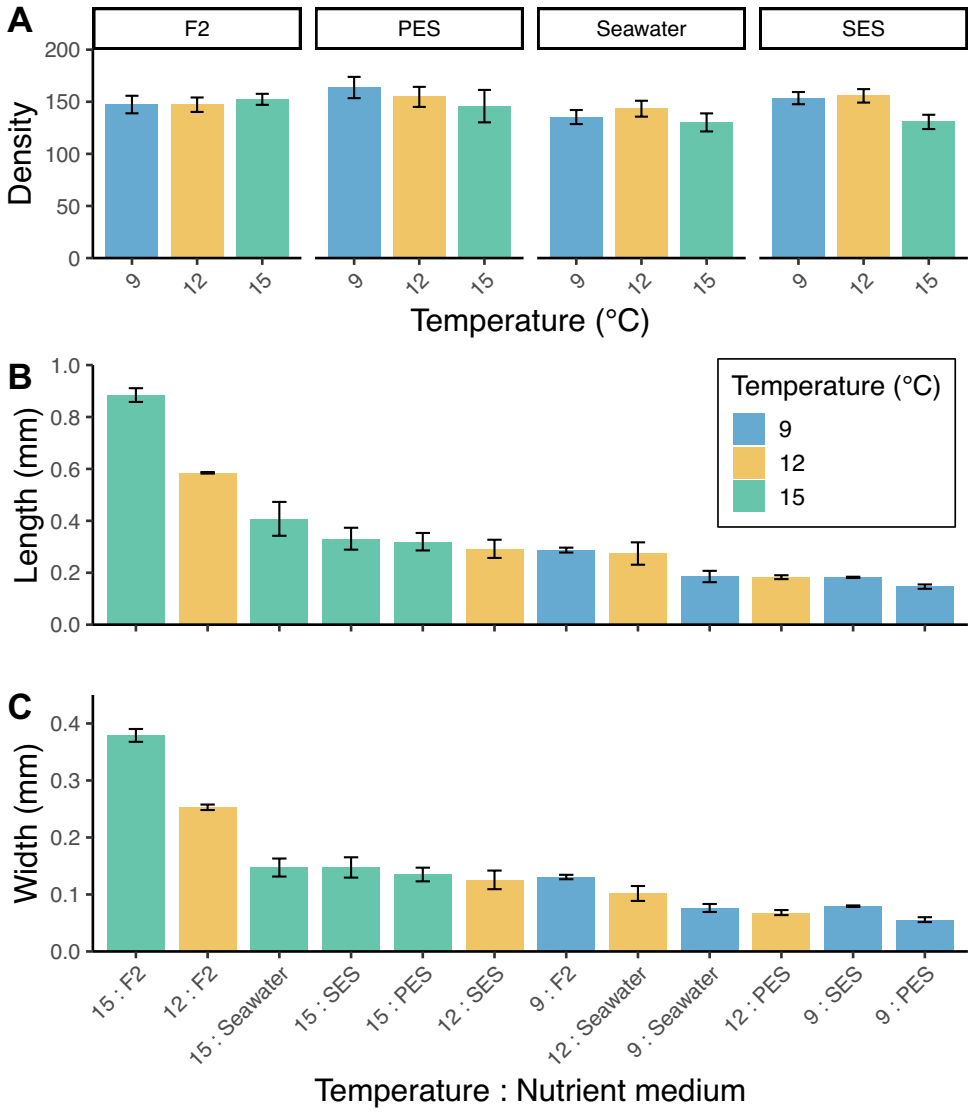

Fig. 6 Experiment 4: The effect of temperature and nutrient medium on the density and early growth of juvenile *Durvillaea* 30 days post fertilisation. (**A**) Juvenile density (individuals per well) across each temperature-nutrient treatment (mean ± SE). Juvenile (**B**) length and (**C**) width (mean ± SE, n = 6) for each treatment combination in descending order of mean-value. F/2 = Guillard's half-strength F-medium; SES = Simple Enriched Seawater (N and P only); PES = Provasoli's Enriched Seawater

Width followed a similar pattern to length (Fig. 6C). There were significant effects of temperature and nutrient medium ($F_{2,59}=62.06$; $p<0.001$ and $F_{3,59}=59.15$; $p<0.001$, respectively). The interaction between temperature and nutrient medium was not significantly different ($F_{6,59}=1.90$; $p=0.096$). Width at 15 °C was significantly greater than at both 9 °C and 12 °C (mean difference = 0.12 mm, $p<0.001$ and mean difference = 0.07 mm and $p<0.001$, respectively), and width at 12 °C was significantly greater than at 9 °C (mean difference = 0.05 mm and $p<0.001$).

The F/2 medium significantly increased width compared to PES (mean difference = 0.17 mm, $p<0.001$), the seawater only (mean difference = 0.15 mm, $p<0.001$), and SES (mean difference = 0.14 mm, $p<0.001$) treatments. Additionally, SES and seawater only treatments significantly increased juvenile width compared to PES (mean difference = 0.03 mm, $p<0.001$; and mean difference = 0.02 mm, $p=0.003$, respectively), with no significant difference between SES and seawater only treatments (mean difference = 0.01 mm, $p=0.659$).

Experiment 5: Gamete release from reproductive tissue over time

There was a significant difference in gamete release rate over time (females: $F_{9,10}=14.38$; $p<0.001$, and males: $F_{9,10}=114.47$; $p<0.001$; Fig. 7A). The majority of both male and female gametes were released within the first hour (Fig. 7B), with 91.6% of eggs and 91.1% of sperm released. Males and females continued to release some gametes up to the end of the experiment although females tended to release eggs at a relatively higher rate (~0.5% per hour) compared to the release rate of sperm by males (~0.2% per hour).

Discussion

This study presents reproducible hatchery methods for *Durvillaea potatorum*, enabling the production of hatchery-reared juveniles for subsequent at-sea cultivation. Across the early life cycle, performance was maximised by: (i) holding reproductive tissue overnight and releasing gametes at 14 °C; (ii) constraining gamete release to 10 min, which yielded the highest fertilisation rates; and (iii) cultivating juveniles at 15 °C and ~95 µmol photons m^{-2} s^{-1} in F/2 medium, which supported the best growth. These findings establish a framework for hatchery cultivation of *D. potatorum*, providing critical parameters for hatchery success in the species and a model hatchery protocol for the genus.

Temperature and duration strongly influenced both gamete release and fertilisation success. The greatest fertilisation rate was achieved by holding conceptacle-bearing tissue overnight and inducing gamete release at 14 °C for 10 min. More than 90% of sperm and eggs were released within the first hour, highlighting the importance of precise timing and short release windows to ensure synchrony of gamete release and fertilisation (Serrao et al. 1996; Pearson and Serrão 2006), characteristic for broadcast spawners relying on external fertilisation (Santelices 2002; Hatchett et al. 2022). This short release and fertilisation window in *D. potatorum* contrasts with "brooding" fucoids, such as *Sargassum* spp. or *Turbinaria ornata*, where eggs remain attached to the conceptacle until fertilised by motile sperm, allowing asynchronous gamete release between sexes without reducing fertilisation rates (Critchley et al. 1991; Uchida et al. 1991; Pang et al. 2008; Zubia et al. 2020; Liu et al. 2021). In *Sargassum heterophyllum*, fertilised eggs (i.e., zygotes) typically

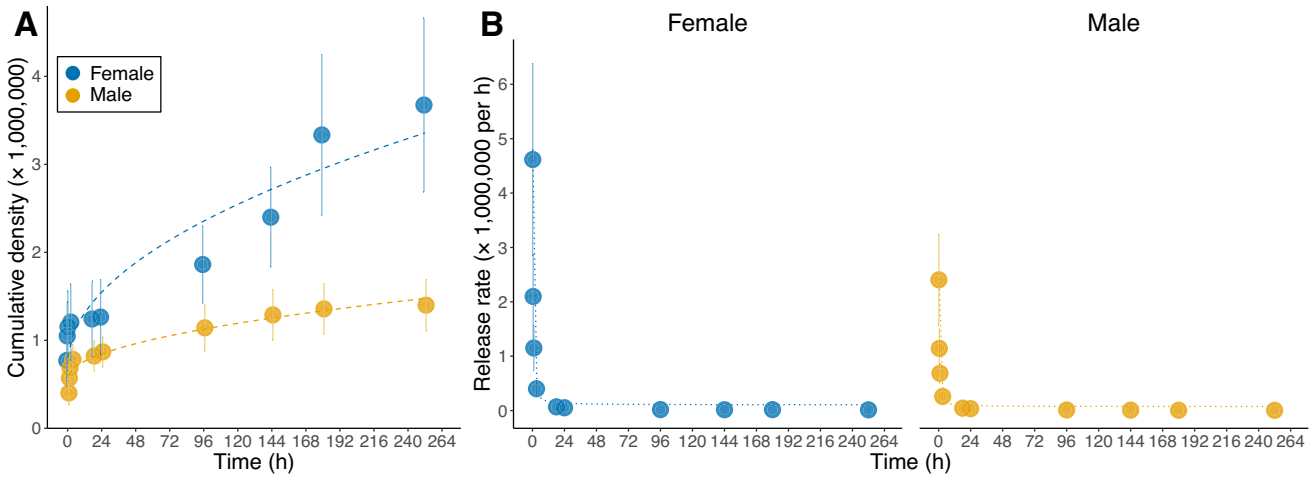

Fig. 7 Experiment 5: Gamete release from male and female *Durvillaea potatorum* over 10 days. Gamete release is shown cumulatively over time (**A**) and normalised per hour (**B**). Error bars show standard error (n = 6) and the dotted lines show the fitted values (square root model for cumulative gamete release and hyperbolic model for the gamete lease per hour)

detach once the embryos start developing rhizoids, which occurs within a few days, sink and reattach to suitable substrate (Critchley et al. 1991). Therefore, hatchery protocols for brooding species involve incubating reproductive male and female fronds for 3–7 days to allow fertilisation, zygote liberation and settlement onto cultivation substrates (Uchida et al. 1991; Le et al. 2018; Liu et al. 2021).

In contrast, *Durvillaea* spp. release negatively buoyant eggs directly into the water column, followed by the rapid release of adhesive components from vesicles present in the egg's outer cell surface (Kevekordes and Clayton 1999). After fertilisation, germlings secrete a secondary mucilaginous adhesive from newly formed vesicles, enabling strong and rapid attachment (Dimartino et al. 2016). This rapid attachment likely facilitates recruitment in the wave exposed habitat that *Durvillaea* spp. typically occurs in (Taylor et al. 2010). Hatchery protocols of *Durvillaea* spp. thus require (i) constant stirring to keep the sinking eggs in suspension during fertilisation, and (ii) seeding zygotes onto cultivation substrates (e.g. string or rope) within minutes of fertilisation to capture this brief adhesion window. Although most gametes are released within the first hour and the reproductive season lasts for several months in situ (Clayton et al. 1987), conceptacles continue to release gametes at low rates (0.2—0.5% h^{-1}) for up to 10 days under laboratory conditions, offering an extended window for hatchery seeding at low densities.

Irradiance level substantially influenced growth in *D. potatorum* germlings, with an optimal irradiance near 95 µmol photons m^{-2} s^{-1}. Interestingly, growth was relatively similar at low to medium irradiance levels (10–75 µmol photons m^{-2} s^{-1}) but declined at higher irradiances. At 240 µmol photons m^{-2} s^{-1}, germlings appeared discoloured, suggesting stress likely associated with photoinhibition and pigment degradation (e.g., Endo et al. 2017). These findings have practical implications for hatchery protocols: during the initial weeks, low irradiance levels appear sufficient for germling growth and may also help limit the proliferation of fouling organisms (Su et al. 2017). As germlings increase in size, irradiance can be gradually raised to match their higher photosynthetic capacity, a strategy commonly employed in *Sargassum* and kelp hatcheries (Su et al. 2017; Liu et al. 2021).

Thermal requirements for gamete release in fucoids typically reflect the ambient seawater temperatures experienced during their natural reproductive season, and this principle is often applied in hatchery settings (Chu et al. 2011; Kerrison and Le 2016; Liu et al. 2021). For instance, hatchery production of *Sargassum thunbergii* induce and synchronise gamete release by increasing ambient temperature by 3–4 °C (Liu et al. 2021), reflecting its in situ reproductive strategy (Stiger-Pouvreau et al. 2023). Similarly, for *Durvillaea* in southeastern Tasmania, sea surface temperatures (SST) during the reproductive period range between 12–15 °C, which aligns closely with the 14–15 °C optimum identified in this study. This correspondence highlights *Durvillaea*'s adaptation to sea surface temperatures in winter and early spring when this genus is reproductive in southern Australia (Clayton et al. 1987). However, its thermal sensitivity and vulnerability to ocean warming negatively affect northern range-edge populations, leading to increased inbreeding, reduced genetic diversity, and limited adaptive capacity in these regions (Nimbs et al. 2025). These constraints have implications for sourcing and selecting seedstock from range-edge populations for future cultivation in warming regions, such as Tasmania. Thus, the 14–15 °C optimum for *D. potatorum* in Tasmanian waters is therefore consistent with fucoid physiology in temperate climates and provides a practical target during hatchery operations.

The composition and type of nutrients can strongly influence hatchery outcomes. For *D. potatorum*, we found significantly higher growth in F/2-enriched media compared to Provasoli Enriched Seawater (PES) or when solely enriched with macro-nutrients (NO_3^-, NH_4^+, and PO_4^{3-}) at similar concentrations to PES. Ambient macro- and micronutrient levels in seawater (into which culture media are added) vary seasonally and spatially, but in Tasmanian coastal waters they are typically low, with NO_3^- and NH_4^+ rarely exceeding 5 µM, even in winter (Hurd et al. 2023). Consequently, the contribution of ambient nutrients was minimal relative to F/2 or PES in supporting improved growth. Interestingly, zygote density remained unaffected by the nutrient type, indicating no toxic effect on fertilisation. Media that are commonly used to supply nutrients in hatchery settings, such as F/2 or PES (Andersen 2005), tend to support fertilisation, zygote development and early growth in fucoid and laminarian kelps (Steen and Rueness 2004; Pang et al. 2008; Liu et al. 2021; Visch et al. 2024). Despite these recipes providing both macro- (N and P) and micro-nutrients (trace-elements and vitamins), most hatchery protocols consider total nitrogen and phosphorus in relation to the developmental stage of the germling, typically with increasing demand as germling size increases (Liu et al. 2021; Visch et al. 2024). For example, *S. thunbergii* germling growth is maintained at 32–161 µM NO_3^- and 4 µM PO_4^{3-}, which are significantly lower concentrations than in F/2 enriched seawater (i.e., 882.5 µM NO_3^- and 36.2 µM PO_4^{3-}), but at a similar N:P molar ratio of ~ 20:1 (Liu et al. 2021). This contrasts with *Sargassum fusiformis* germlings, that are typically maintained in hatchery conditions at a higher N:P-ratio (160:1), primarily driven by a lower phosphate concentration (118 µM NO_3^- and 0.7 µM PO_4^{3-}; Pang et al. 2008), or in PES medium enriched with iron at a N:P-ratio of ~ 31:1 (Hwang et al. 1997). This contrasts with our finding that *D. potatorum* had poor growth in both the PES and SES media.

It is possible that the poor growth of *D. potatorum* germlings in PES and SES media may be due to the toxic effect of a relatively high concentration of ammonium (187 µM NH_4^+), which is absent in F/2 (Guillard and Ryther 1962; Guillard 1975). Very few studies have directly tested ammonium effects on fucoid zygotes in isolation, and most data come from effluent studies that contain elevated NH_4^+ concentrations in addition to other potentially toxic compounds, with the early life stages appearing sensitive to high NH_4^+ concentrations (Ogawa 1984; Doblin and Clayton 1995; Kevekordes 2001; Bergström et al. 2003). Early life stages of *D. potatorum* that are exposed to sewage effluent show a large decline in zygote germination, embryo growth, and survival, with negligible effects only at low NH_4^+ concentrations (Doblin and Clayton 1995), indicating threshold-type toxicity rather than simple dilution effects. Similarly, in the fucoid *Hormosira banksii,* ammonium does not affect fertilisation but is damaging for germination and cell divisions in early embryos (Kevekordes 2001). Finally, the adverse effects of high ammonium concentrations likely differ across life stages in *Durvillaea*, with an increase in growth and NH_4^+-uptake in adult *D. potatorum* (author's unpublished data) and the fucoid *Phyllospora comosa* (Smart et al. 2022). Together, these results imply that early fucoid stages are especially sensitive to high NH_4^+ -concentrations, and that nitrate-based or low NH_4^+ concentration media are preferred during zygote-to-germling transitions. These findings also highlight the importance of tailoring culture media to different life-cycle stages and species-specific physiology, rather than relying on a one-size-fits-all approach.

Durvillaea potatorum germlings grew successfully in the lab, reaching > 1 mm in length after a 30-day cultivation period in 15 °C and F/2-medium. While growth rates were relatively low compared to those of laminarian kelps (Bartsch et al. 2008), they were comparable to several cultivated fucoids (Liu et al. 2021). Specifically, our results align with slower-growing fucoids such as *S. thunbergia* and *S. muticum*, that reach 1.5–2 mm over 5–8 weeks (Zhao et al. 2009; Le et al. 2018), and *P. comosa* which reaches 0.8–0.9 mm over 8–9 weeks (Cumming et al. 2020). In contrast, faster-growing species like *Sargassum vachellianum*, *S. fulvellum*, and some *S. muticum* populations can reach 3–5 mm within one month (Hales and Fletcher 1989; Hwang et al. 2006; Chai et al. 2014). Early life stage performance in fucoids is shaped by light level and temperature. In the Mediterranean fucoid *Ericaria amentacea*, relatively low light and moderate temperatures improved survival, accelerated morphogenesis, and reduced biofouling, whereas higher light and temperature caused sharp declines (Falace et al. 2018). Growth of *S. muticum* and *S. thunbergii* germlings is optimal at 25 °C and 44 µmol photons m^{-2} s^{-1}, which reflects the summer temperatures when these species are reproductive (Hales and Fletcher 1989; Zhao et al. 2009). Importantly, *D. potatorum* reached the size that is recommended (1.5–2 mm) for at-sea deployment of juvenile *Sargassum* spp. (1.5–2 mm; Xie et al. 2013) within 1–2 months, suggesting the applicability of the hatchery protocol to subsequent ocean-based cultivation.

Collectively, these results constitute a substantive advance for *Durvillaea* aquaculture. Further gains may be made through systematic optimisation of temperature, light, nutrient form and supply, and seeding density and substrate, as has been achieved for established kelp species such as *Saccharina latissima* and *Undaria pinnatifida* (e.g., Sohn 1993; Gao et al. 2017; Sæther et al. 2024). While our findings are laboratory based, they provide a foundation for scaling *Durvillaea* cultivation and for targeted refinement of protocols to enhance yields and reliability from hatchery to ocean-based farm.

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Author contribution W.V. wrote the main manuscript text. W.V. and G.F. were involved in the experimental laboratory and field work. T.A., C.H., P.S., L.W., and J.W. contributed to funding acquisition. All authors reviewed and approved the final manuscript.

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Data availability All data will be made available upon request.

Declarations

Competing interest Seasol International (SI) is the manufacturer of seaweed extract in Australia. T.A. is an employee of SI and an Adjunct Associate Professor at Deakin University. The authors declare that this research was conducted in the absence of any financial relationships that could be construed as a potential conflict of interest.

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