RESEARCH

Novel pink-spot disease in North American kelp nurseries

Siobhan Schenk[1] · Andrea Sarah Jackman[1] · Jennifer Samantha Clark[2] · Laura Wegener Parfrey[1,3]

Abstract

Cultivation of kelp and other macroalgae is a growing industry in North America. In the well established macroalgal growing regions in Asia and Africa, macroalgal disease cause crop losses, placing a significant economic burden on growers. As kelp cultivation intensifies in North America, disease prevalence is expected to increase in tandem. Here, we describe the prevalence and bacterial community associated with a novel disease of kelp in the land based nursery stage that is characterized by bright pink spots, termed pink-spot disease. With input from the kelp-growing community through an online survey, we show that pink-spot disease has been widely observed in Canada and the United States on nursery cultivation spools of the kelps *Saccharina latissima*, *Alaria marginata*, *Nereocystis luetkeana*, and *Macrocystis tenuifolia*. We conducted 16S rRNA amplicon sequencing in 2021 and 2022 to investigate the causative agent of pink-spot disease and associated bacterial community changes on infected *S. latissima* (sugar kelp) spools in one nursery. Our data in both years showed that a member of the genus *Algicola* is enriched on visibly diseased spool regions compared to asymptomatic spool regions and may be the causative agent of pink-spot disease. Visible disease is associated with an altered bacterial community, but community change is not consistent acorss years. As macroalgal cultivation continues to intensify in North America monitoring the emergence and distribution of diseases will play an important role in managing disease and mitigating the associated economic burden.

Keywords Kelp · Disease · Bacteria · Microbiome · Aquaculture · Cultivated seaweeds

Introduction

Macroalgal cultivation is a growing global industry worth 14.7 billion US$ in 2019 (Cai et al. 2021). However, macroalgal cultivation operations (Coleman et al. 2022) and wild macroalgal populations are threatened by direct and indirect effects of climate change (Bindoff et al. 2019; Smith et al. 2024). As macroalgal cultivation increases and climate change continues to intensify,

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the frequency macroalgal disease are likely to increase due to a stressed host (Egan et al. 2013). This pattern has been observed in Africa, where cases of macroalgal disease have increased in prevalence and frequency (Msuya et al. 2022), particularly for macroalgae with low genetic diversity in industrial culture (strain exhaustion), as seen with ice-ice disease of *Kappaphycus* (Ward et al. 2022). Macroalgal disease research has mainly taken place in Asia, where disease costs growers 15 to 30% of their total crop yields, leading to significant economic losses (Ward et al. 2020). Macroalgal disease appears rare in North America, but this is likely because the industry is comparatively small (1.36% of global production, 0.19 billion US$; Cai et al. 2021). The existing large-scale negative impacts of disease on macroalgal crops globally, paired with the lack of research into macroalgal disease, poses a risk to the viability and sustainability of the global macroalgal aquaculture industry (Campbell et al. 2019, 2020).

Disease-causing organisms are part of a broad category of host-associated microorganisms known as the microbiota, which includes microeukaryotes, viruses, archaea, and bacteria. Macroalgae-associated bacteria have a strong impact on host development (Provasoli and Pintner 1980; Marshall et al. 2006), host stress-resistance (Dittami et al. 2016), and

host-health (see bacterial infections in Ward et al. (2020)). Due to the strong influence of bacteria on host physiology, researchers have characterized the bacterial community of commercially cultivated macroalgal species, including kelps. This research spans both wild (*Saccharina latissima* (Lemay et al. 2018; King et al. 2022; Park et al. 2025), *Nereocystis luetkeana* (Weigel and Pfister 2019), *Alaria marginata* (Lemay et al. 2018), and *Macrocystis* sp. (Florez et al. 2017; Lin et al. 2018; Weigel and Pfister 2019)) and cultivated kelps (*S. latissima* (Davis et al. 2023) and *Alaria* sp. (Davis et al. 2023; Inguanez et al. 2024)). However, research on the microbiota of cultivated kelps is limited (Marzinelli et al. 2024). Understanding the composition of the typical, presumably healthy, microbiota of kelps in cultivation provides a necessary comparison for the microbiota observed in disease and will enable identification of disease-causing organisms.

Within the seaweed aquaculture sector, growers take great care to reduce the growth of unwanted organisms (which they sometimes collectively call culture contaminants), including pathogens (e.g., fungus-like oomycetes) and biofouling organisms (e.g. diatoms; Redmond et al. 2014). Both pathogens and biofouling organisms have the potential to cause significant economic impacts to growers. Some are well described and have relatively effective mitigation techniques, including the addition of germanium dioxide to inhibit biofouling diatom growth and treating *Chondrus* spp. (red macroalgae) cultures infected with oomycetes with sodium dodecyl sulfate (Redmond et al. 2014). However, many unwanted organisms in macroalgal culture are poorly understood and do not have an established preventative or curative protocol (Ward et al. 2020; Spagnuolo and Genovese 2024). For diseases, one of the main challenges is the difficulty of determining the causative agent of disease.

Traditionally, a microbe's capacity to cause disease is validated with Koch's postulates, which requires isolating the disease agent from a diseased organism and infecting a healthy individual with the isolated disease agent, among other requirements (Koch 1890). Although Koch's postulates remain relevant today, they are sometimes too stringent (Antonelli and Cutler 2016) and do not always provide a complete picture of the disease process in marine systems, because marine diseases can occur through multiple mechanisms (Egan and Gardiner 2016). For example, some diseases are caused by a consortium of microbes (polymicrobial infection; Egan and Gardiner (2016), see coral black band disease; Sato et al. (2016)) and host-associated microbes can switch from an apparently mutualistic or neutral interaction to one that only benefits one of the partners, as seen in the *Phaeobacter gallaeciensis* and *Emiliania huxleyi* system (Seyedsayamdost et al. 2011; Egan and Gardiner 2016). In addition, visible symptoms may only occur after a preliminary infection or disruption of the microbial community

has already taken place (Egan and Gardiner 2016). In this case, characterizing the microbes associated with visibly diseased regions may describe a community of opportunistic colonizers, and the disease agent may no longer be present (Egan and Gardiner 2016). A lack of clear symptoms early in the disease process is particularly important in the kelp cultivation context, where growers do not have the capacity to thoroughly examine most of their crops closely (e.g. by microscope) due to the scale of biomass production required.

Kelp cultivation can be divided into two main phases, production of 'kelp seed' in the land-based nursery stage and growth of kelp sporophytes to harvest size in the ocean stage (Fig. 1A) (Redmond et al. 2014). Kelp seed is a term used by industry to refer to the production of juvenile kelp fronds, or 'plants', that can be outplanted to ocean farm sites, although kelp are brown algae and reproduce through spores rather than seeds. The process is started by the collection of wild reproductive sporophytes, followed by release of spores and settling spores onto spools (twine wrapped around PVC pipe); these spools are the 'kelp seed' (Fig. 1A). Over approximately six weeks, the kelp develop from spores to juvenile sporophytes (~ 2 mm), at which point, the kelp seed are outplanted on the ocean farm. The kelp sporophytes grow in the ocean stage for 4 to 6 months, during which the sporophytes grow in size (to ~ 1 m in length) before being harvested (Fig. 1A).

The nursery stage is a cost-intensive and challenging stage in the kelp cultivation process (Coleman et al. 2022). One of the main risks during the nursery stage is biofouling (e.g., diatom blooms) or the development of disease (many reviewed in Ward et al. (2020) and in Spagnuolo and Genovese (2024)). Although there are recent studies examining the bacterial community of diseased kelps (for example, Yan et al. (2023) *S. japonica* malformation disease), many kelp diseases remain either undescribed or were described before the advent of modern sequencing tools (Ward et al. 2020; Spagnuolo and Genovese 2024). For this reason, studying the microbial community of kelps at the nursery stage in partnership with growers should be prioritized to establish a better understanding of the healthy nursery microbial community and detect emerging diseases. Doing so may help to safeguard the growing North American macroalgal industry.

Following informal talks with growers, we learned that multiple nurseries in North America have observed bright pink spots develop on their kelp spools (referred to herein as pink-spot disease). Pink-spot disease is visually similar to red-spot disease previously reported on the kelp *S. japonica* in Japan (Ezura et al. 1988; Yumoto et al. 1989; Sawabe et al. 1998). See Figs. 1 and 7 of Ezura et al. (1988) for images of red-spot disease. In red-spot disease, the infection spreads outwards from the origin site along the spool surface as rings, dislodging kelps from spools (Yumoto et al. 1989). Growers observe the same pattern in pink-spot disease. We
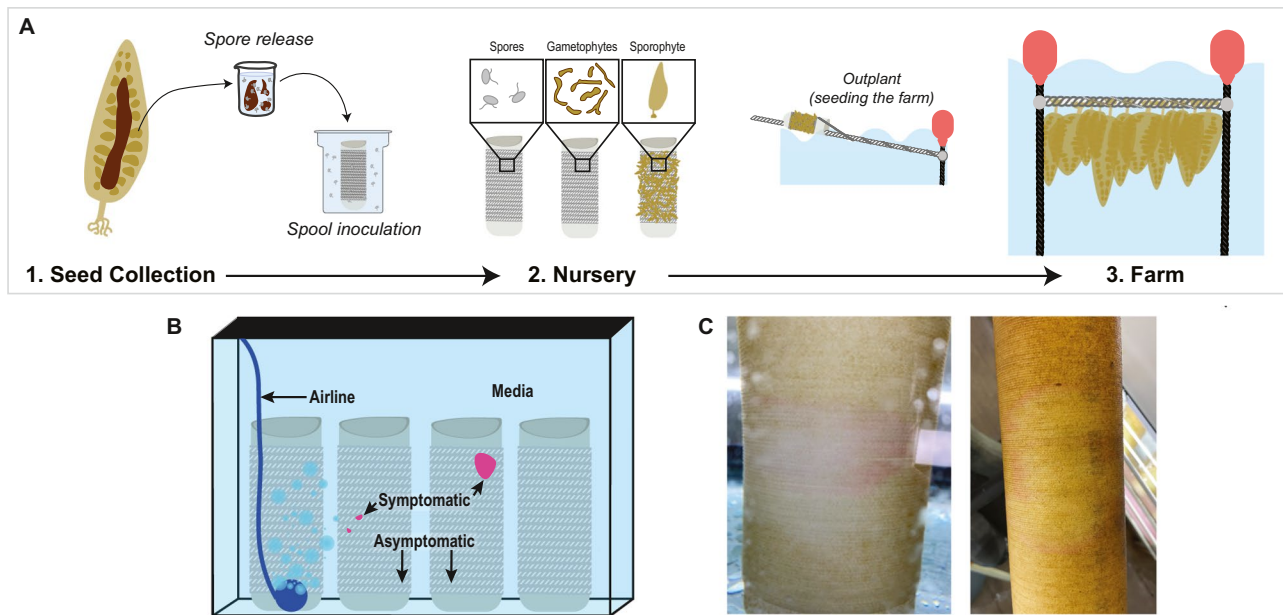
Fig. 1 **A)** *Saccharina latissima* lifecycle contextualized within kelp cultivation steps. (1) Wild reproductive sporophytes are collected, and spores are released from the cleaned sori patch. Spores are inoculated onto the spool (twine wrapped around PVC pipes) and maintained in (2) the nursery for approximately six weeks. These kelp spools are the "kelp seed". (3) The kelp seed is outplanted onto the ocean farm where the sporophytes grow for four to six months before harvest. **B)** Sample types collected for this study. The symptomatic samples were from visibly pink regions on the spool, while asymptomatic samples were from non visibly pink regions. Asymptomatic samples were taken as far away as possible from visibly pink spots. Media and airline (substrate) samples were also taken to assess the background bacterial community in the aquaria. **C)** Two representative examples of the presentation of pink-spot disease on *S. latissima* spools in the nursery. The pink spots are less visible in earlier stages of disease and when the spool has a higher density of sporophytes. Schematics (panel **A** and **B**) were designed in Adobe Illustrator and photos (panel **C**) are original photos by the authors

are not aware of red-spot disease affecting adult kelp sporophytes or non-Laminariales (kelp) algae. These similarities between red-spot and pink-spot disease led us to hypothesize that they are caused by similar disease agents. Both red-spot and pink-spot disease are a concern for growers because crop loss due to disease causes economic losses. In the case of red-spot and pink-spot diseases, the economic loss is due to visibly diseased spool areas becoming bare as the infection progresses. Bare spool regions will not produce harvestable kelp. The prevalence and impact of pink-spot disease is unknown, and to our knowledge, pink-spot disease has not been documented elsewhere in the literature.

We conducted an online survey of kelp growers across North America to 1) assess the prevalence of pink-spot disease, 2) assess the level of concern regarding kelp diseases in general, and 3) start gathering information about disease mitigation strategies already in use by growers. Additionally, we describe the results of an opportunistic sampling of the bacterial community on *S. latissima* spools affected with pink-spot disease. Symptomatic and asymptomatic regions of *S. latissima* spools were sampled from one nursery across two growing seasons. With these data, we aimed to 1) identify a putative pathogen and 2) assess the bacterial community changes associated with pink-spot disease.

Methods

Stakeholder survey

We designed a semi-structured survey to quantify the occurrence of pink-spot disease in kelp nurseries and understand the perspective of growers regarding kelp diseases (Table S1). The survey included 17 questions about: disease occurrence, nursery conditions, disease concern, and open-ended questions for participants to describe other evidence of disease, suggest why disease may occur, and provide additional information they felt was important (Table S1). The survey was divided into four sections: (1) contact information (Q1-Q3), (2) disease occurrence and nursery conditions (Q4-Q11), (3) details of the disease (only to be completed if disease was observed in the past year; Q12-Q16), (4) final comments (Q17). Any of the questions could be left blank by the respondent. The survey was distributed to known kelp growers through email, within kelp grower networks, and posted online on the GreenWave community forum. Links to the survey are provided in the data availability section.

Of 16 respondent organizations, 8 are based in Canada, 7 in the United States of America, 1 in the United Kingdom,

and 1 did not specify. Of these organizations, four focus on kelp restoration, four on research, and six farm kelp commercially. Four of the respondents did not work in an industrial setting.

Bacterial sample collection and DNA extraction

We collected bacterial samples from a kelp nursery in British Columbia when the nursery team noticed pink-spot disease on *S. latissima* spools in 2021 and 2022. For each aquarium where pink-spot disease was found, we swabbed the symptomatic region (pink; Fig. 1B) and the asymptomatic region (not pink; Fig. 1B). The asymptomatic swab was taken as far away as possible from visibly symptomatic regions. We specifically refer to pink and non-pink spool regions as "symptomatic" and "asymptomatic" respectively in our study because with the available data, it is not possible to determine if the asymptomatic regions are healthy regions (uninfected), or if they represent an early, visually asymptomatic, stage of pink-spot disease.

Swabs of small pink spots (below 5 cm^2) included the entire surface area of the symptomatic area. For larger symptomatic regions, we focused our swabbing effort on the leading edge of the pink spots, except for early samples in 2021, where we swabbed the entire symptomatic area (2 samples). Because the pink spots spread outwards, the leading edge of the pink spot should have a bacterial community that is more representative of earlier infection stage than the middle of the pink spots, which represent a later infection stage. The two whole symptomatic region samples do not appear to be significantly different from the samples where only the leading edge was swabbed, so we included them in our analysis.

We also collected surface swabs of the airline feeding the bubbler (abiotic substrate, Fig. 1), and media samples (F/2 + Germanium dioxide at 8.95×10^{-3} g L^{-1}; Fig. 1). Surfaces were gently rinsed with filtered seawater prior to swabbing vigorously for 10 s. Media samples were collected by passing a total volume of 50 mL through a 0.2 µM filter (Millipore Sigma, SVGP010) with a pre-rinsed syringe.

In 2021, all samples were taken from a single farm (Farm 1), while in 2022, samples were taken from three farms (Farm 2, Farm 3, and Farm 4). In this context, one farm represents one cycle of spore release from wild-collected sori that will be outplanted in the ocean within 50 km of where the wild sori were collected. The kelp for all farms are reared in the same nursery for 6 weeks before outplanting, meaning the aquaria have the same water source for all farms in the nursery stage. Water does not freely flow between aquaria, so the spools in different aquaria were physically separated. Aquaria are reused between farms but are manually scrubbed with 1% bleach and rinsed multiple times with fresh water. Spools from different farms are never combined in the same aquarium.

Bacterial samples were stored at −65 °C until transport back to the University of British Columbia on ice, where they were stored at −70 °C until DNA extraction with the DNeasy PowerSoil Pro Kit 96-well plate (QIAGEN 47017) in 2021 and the ZymoBIOMICS MagBead DNA/RNA extraction kit (Zymo R2136 and lysis racks S6002-96–3) in 2022. We included one extraction blank per DNA extraction plate.

PCR

The bacterial community samples were profiled using 16S rRNA amplicon sequencing. PCR reactions contained 3 µL of DNA, 15 µL of Phusion Flash High-Fidelity PCR Master Mix (F548L, ThermoFisher), 0.6 µL DMSO, and 2.4 µL of forward (515 F, 5'-GTGYCAGCMGCCGCGGTAA-3') and reverse (806R, 5'-GGACTACNVGGGTWTCTAAT-3') dual-indexed primers from a 2.5 µM stock, and water to a 30 µL final reaction volume. All PCR reactions consisted of an initial denaturation (30 s at 98 °C), 25 cycles of amplification (30 s at 98 °C, 30 s at 55 °C, and 20 s at 72 °C), and a final elongation step (10 min at 72 °C). Samples that failed with 25 cycles twice were conducted with 35 cycles, indicated in the metadata associated with this study. We included one PCR blank per plate.

PCR reactions were quantified with the Quan-IT Pico-Green assay kit (Thermo Fisher, P7589), pooled to equal DNA concentration, cleaned with the Invitrogen PureLink Quick PCR purification kit (K310001), and sent to the University of British Columbia Sequencing and Bioinfomatics Consortium for Bioanalyzer quality analysis and Illumina Next Generation Sequencing (MS-1023003 kit; MiSeq v3, 2 × 300).

Illumina data processing

Raw, demultiplexed reads were imported into R (v4.4.1; R Core Team 2022) and processed with the dada2 pipeline (v1.32.0; Callahan et al. 2016). Briefly, forwards and reverse reads were trimmed to 200 bp and primers were removed with the filterandtrim function. Then, amplicon sequence variants (ASVs) were merged into a single sequence table with the mergeSequenceTable function before assigning taxonomy with Silva v138 (McLaren 2020) formatted for dada2 (McLaren & Callahan 2021). We removed taxa assigned as chloroplasts, mitochondria, eukaryotes, or unassigned at the phylum level. Then, samples with less than 1000 reads, ASVs representing less than 0.001% of the dataset, or found in less than 3 samples were removed. Then, occurrence counts of 3 or less were converted to 0 for non-rarefied data only. Our filtering retained 1,137,331/1,403,759 paired-end reads, 767/1,535 ASVs, with a per-sample mean read depth of 27,079.31.

We rarefied our data with coverage-based rarefaction (Chao and Chiu 2016) with the iNEXT package (v3.0.0; Hsieh et al. 2022) and the metagMisc package (v0.0.4; Mikryukov 2022) with the coverage set to 0.8 and the rarefaction was iterated 1000 times.

One of our libraries in 2022 included the addition of chloroplast blockers in the PCR reactions (at 1.6 μM) because some samples had a very high number of reads assigned to chloroplasts (blocker information included in associated metadata) in the initial library. Adding the chloroplast blockers decreased the number of chloroplast sequences in the reads by roughly 25% for the samples that included kelp, but did not affect the number of chloroplast sequences in the airline and media samples. We used the general chloroplast blocker 5′-GGCTCAACC CTGGACAG-3′ from (Lundberg et al. 2013) and designed a custom *S. latissima* chloroplast blocker 5′-KKAAATGT AATAGAAACTAC-3′, both from PNA Bio.

To assess consistency in sequencing for the same swab, we performed duplicate PCR reactions for 6 samples (4 symptomatic and 2 asymptomatic) in 2022. The bacterial composition of the reads was extremely similar for duplicate samples (validated visually with a taxaplot and NMDS), so we randomly removed one of the two duplicate samples for data analysis.

Attempts to isolate a causative agent

Our attempts to isolate a causative agent were unsuccessful, but we outline the protocols we used in our attempts here. We tested three different types of agar plate: 100% DIFCO marine agar, 100% agar, and 100% agar + approximately 80 g L^{-1} (wet weight) of ground-up *S. latissima* thallus. The ground-up *S. latissima* was added to the 100% agar before autoclaving.

We attempted to isolate the causative agent from three sources. First, swabs of the leading edge of the symptomatic region which we then rubbed onto the plate to transfer the collected bacteria to the plate. Second, we pipetted 100 μL of liquid media from aquaria with symptomatic spools onto the plate. Third, we cut pieces of symptomatic twine and placed them on the plates both without liquid and with 100 μL of liquid from symptomatic aquaria. All plate types and combinations of bacterial sources had ample bacterial growth. We serially selected bacterial clones to isolate single strains. We sequenced these isolates, but none of the pure isolates were the putative pathogen.

Illumina data analysis

To identify differentially enriched sequences between the symptomatic and asymptomatic regions, we ran a DESeq analysis with the package DESeq2 (v1.44.0; Love et al. 2014) on unrarefied data at the ASV level to retain the highest possible community-level resolution. We used the Wald method with a parametric type fit and set our alpha value to 0.01. Taxa that met the alpha cutoff also had to be 3 or more spool samples (total of symptomatic + asymptomatic) to be considered for further analysis. We analyzed both sampling years together because a causative agent should be present across all symptomatic samples. Airline and media samples were excluded from this analysis to allow ASVs that are less substrate-specific to be detected by DESeq.

To test for community-wide changes between asymptomatic and asymptomatic spool communities, we ran a PERMANOVA followed by a betadispersion test with the R package vegan (v2.6–8; Oksanen et al. 2022). We also used the package vegan to calculate the Shannon-Weiner diversity index (diversity function). We compared symptomatic and asymptomatic spool sample diversity with an ANOVA. Assumptions of equal sample size and normality were assessed visually with plots, while equal variance was tested with the LeveneTest function in the car package (v3.1–2; Fox and Weisberg 2019). We ran the PERMANOVA, diversity, and dissimilarity analyses within the same year because different extraction kits were used between years (QIAGEN in 2021, Zymo in 2022), which could influence community composition.

Tree construction

We used the EukRef pipeline (del Campo et al. 2018) to pull closely related ASVs into our tree with a modification for vsearch. First we pulled *Pseudoaltermonas* sequences from Silva v138 (McLaren 2020) with seqkit (Shen et al. 2016, 2024) and standardized them by converting all uracil (U) bases to thymine (T). We separated the *Algicola* sequences from our ASVs from the rest of the data to prevent clustering and added them back in after the outgroup sequences. We used vsearch to remove sequences less than 500 bp long to improve alignments (Rognes et al. 2016). We manually selected outgroup sequences from a sister clade and added sequences from taxa associated with kelp diseases from Silva v138. All sequences were aligned with mafft (Katoh and Standley 2013) and trimAl (Capella-Gutiérrez et al. 2009) was used to trim the tree. We removed the following sequences due to exceptionally long branch lengths: AB536964.1.1284, HF912441.1.1438, GU056801.1.1446, and KR054340.1.1206. We generated the backbone tree with RAxML (Stamatakis 2014) using the GRCAT model with 25 rate categories and 100 bootstrap replicates. We then aligned our ASVs using mothur (Schloss et al. 2009) and placed them in the tree with EPA-ng (Barbera et al. 2019). The final tree was converted to newick format with gappa

(Czech et al. 2020) and visualized in figtree (http://tree.bio.ed.ac.uk/software/figtree/).

Analysis of existing datasets

To assess the prevalence and relative abundance of the putative pathogen across available kelp microbe datasets, we analyzed 5 other kelp datasets. One of these datasets is of cultivated kelp (Davis et al. 2023), while the others are of wild kelp in British Columbia (Lemay et al. 2018; Park et al. 2025; Schenk et al. 2025) and in the United Kingdom (King et al. 2022). All datasets were processed with the dada2 pipeline as described above. We did not filter these data to maximize the chance of detecting our ASVs of interest.

Results and discussion

Visual description of the pink spots

The pink spots first appeared as small patches. The pink was flush along the twine surface and was very difficult to remove fully from the spool. As the pink spots grew, they expanded outwards along the spool surface (Fig. 1C). As the infection spread outwards, the older infection sites became bare of visible kelp (gametophytes or sporophytes). Because we observed pink-spot disease in an active kelp nursery, symptomatic spools were immediately removed from the aquaria and treated with ethanol or bleach (described below) in accordance with the nursery's disease containment protocol. Thus, the typical growth rate of the pink spots and the rate of spread to other spools was not studied. However, we noted that asymptomatic spools were present alongside symptomatic spools in the same aquaria when pink-spot disease was detected early (small spots) these asymptomatic spools did not develop pink spots. Removing the symptomatic spools from the aquaria appeared to mitigate the spread to other spools to some extent, although we did not quantify this. The majority of aquaria in the nursery remained asymptomatic throughout both the 2021 and 2022 production seasons.

Prevalence

Out of the 16 respondents who grow kelp, 10 (62%) observed pink spots on spools at some point in their nursery. The affected nurseries were on both the west and east coasts of North America. Some of the affected nurseries grew multiple kelp species, so we report the number of affected nurseries that observed pink spots on a kelp species at any time (numerator) over the total number of affected nurseries who grow that kelp species (denominator): 9/9 *S. latissima*, 3/3 *Nereocystis luetkeana*, 3/4 *Alaria marginata*, and 1/1 *Macrocystis tenuifolia*. These results showed that pink-spot disease affected multiple kelp species. Growers reported that pink spots on all species were generally small, usually not exceeding ~5 cm^2 in area before detection and treatment. The causative agent(s) of disease may or may not be the same between kelp species.

Treatment and prevention

Surveyed growers have a consistent practice of removing the infected spools immediately from nursery aquaria. In less severe cases, spools are immediately spot treated with 1% bleach or 70% ethanol and moved to a quarantine aquarium. The infected spools were maintained in the nursery in quarantine to assess the efficacy of treatments. The results were mixed, potentially due to variation in the penetrance of the sterilization agent and the size of the pink spot treated. In severe cases (pink spots larger than ~5 cm^2 and/or very numerous), spools were immediately removed from the nursery, soaked in 10% bleach, and disposed of. These methods were similar to sterilization methods reported in the historical literature to mitigate red-spot disease (Ezura et al. 1990). In this series of experiments, the authors tested the capacity of various chemicals to 1) treat red-spot disease and to 2) remove a bacterial inoculum thought to cause red-spot disease from experimentally infected sori. Treatment with stabilized chlorine dioxide was best for infected spools while hydrogen peroxide was best to clean sori in terms of infection treatment and kelp survival (Ezura et al. 1990).

Survey respondents identified equipment sterilization between cultivation cycles, regular water changes, water circulation, and appropriate crop density as important measures to prevent disease. All growers who encountered disease stated that rapid intervention to remove infected spools is an important measure to reduce disease severity and prevent spread to other spools. This is in line with best practices reported in other published literature (Redmond et al. 2014; Ward et al. 2020).

Most growers who responded to the survey were interested in further collaboration with researchers in general and to learn more about pink-spot disease specifically. Therefore, we encourage other researchers to collaborate with local kelp growers to effectively target region-specific concerns.

Stakeholders' perspective on disease

We asked survey respondents to report their general level of concern about kelp diseases. We also asked about their concern regarding diatom fouling to gauge their general level of concern about crop health. In general, there was very little apparent relationship between industry stakeholder concern regarding diatom biofouling and kelp disease. Additionally, there was no apparent relationship between observation of pink-spot disease and disease concern, suggesting that individual perspectives in the industry vary greatly and may be

due to factors not captured in our survey. However, 11/16 growers surveyed had at least a moderate level of concern regarding kelp diseases, indicating that disease is a concern for growers in Canada and the United States.

Is there a putative disease agent?

We assayed the bacterial community of symptomatic and asymptomatic regions to identify changes in the community composition associated with disease and gain insight into the underlying causes of disease. As pink-spot disease is visually similar to red-spot disease of *S. japonica*, we hypothesized that pink-spot disease may be caused by a similar bacterial pathogen. If pink-spot disease was caused by a single bacterial pathogen, we expected a high and consistent enrichment of a single ASV in symptomatic spool samples across years and farms. Alternatively, if pink-spot disease was caused by a polymicrobial infection or disruption of the normal microbiome due to other stressors, we did not expect to see a consistent enrichment of a single bacterium across symptomatic samples.

To statistically test for differential abundance of taxa by spool health status, we ran a DESeq analysis comparing the symptomatic and asymptomatic spool samples (both years together). DESeq2 identified 16/767 ASVs (2%) that were differentially enriched by spool health (Fig. 2, Table S2). Only 1 ASV (*Algicola* ASV80) is present and enriched in all symptomatic samples. ASV80

has the greatest absolute log2 fold-change value (8.199) of all differentially enriched ASVs, corresponding to a 16-fold increase in symptomatic samples compared to asymptomatic samples. This pattern of enrichment points to *Algicola* ASV80 being strongly associated with pink-spot disease and may be the causative agent of pink-spot disease (Fig. 2). Red-spot disease has been associated with several bacteria, including *Algicola bacteriolytica* (Ezura et al. 1988; Sawabe et al. 1998), *Pseudoalteromonas distincta* (Sawabe et al. 2000), or *Alteromonas* sp. (Yumoto et al. 1989; Sawabe et al. 2000). However, the strongest evidence supports that *A. bacteriolytica* is the causative agent of red-spot disease on *S. japonica* (Ezura et al. 1988; Sawabe et al. 1998).

Other taxa show differential enrichment in symptomatic and asymptomatic swab samples; however, these changes are less consistent between years (Fig. 2). This suggests that other changes are occuring in the bacterial community when pink-spots are present in the aquaria, highlighting the importance a need to investigate the microbial communities typically associated with kelp in the nursery.

Distribution of *Algicola* in other datasets

We investigated the prevalence of the genus *Algicola* in existing wild and cultivated kelps datasets (Table 1) to assess how commonly *Algicola* is associated with kelp. Pink-spot disease was not observed in any of these samples. We found
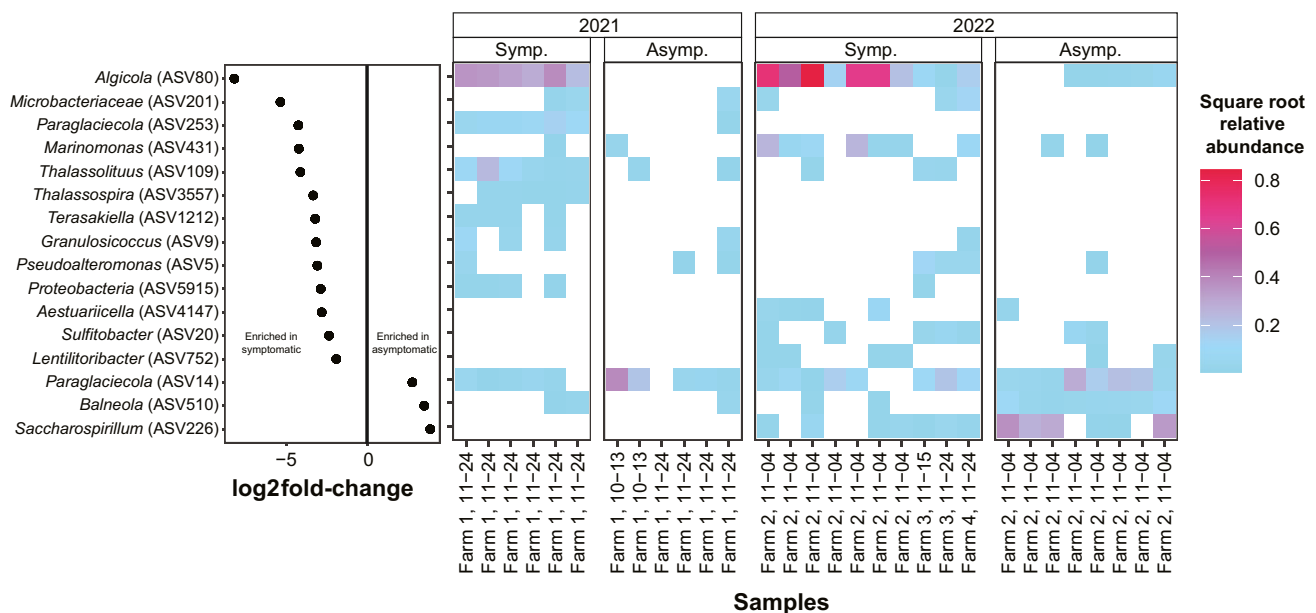

Fig. 2 Output of DESeq analysis comparing symptomatic and asymptomatic spools. The left panel y-axis indicates the genus and ASV number that corresponds to the log2 fold-change (x-axis). The right panel shows a heat map the square root of the per-sample rela-

tive abundance of the differentially enriched ASVs. Heat map facets divided by symptomatic or asymptomatic and year (years differ in DNA extraction kit). The x-axis shows the sampling date and farm. Full DESeq output is available in Table S2

Table 1 Table showing other datasets where we investigated the prevalence of target ASVs. The study with the ENA accession number used to download the reads is listed in the first column along with the study locale. The next column indicated the sample types and numbers for each study. The following columns show the total number of samples that contained the sequences listed in the column header. The number in the parentheses indicates the mean relative abundance of the ASV in the samples that contained the ASV. Note, we include *Pseudoalteromonas* ASVs in this table as a reference because 1) *Pseudoalteromonas* is closely related to *Algicola* (Fig. 3) and 2) *Pseudoalteromonas* are very fast growing and common in samples, so they contrast the comparatively rare *Algicola*

Study (ENA accession)	Sample number	*Algicola*					*Pseudoalteromonas*	
		NR_036838.1 (*A. bacteriolytica* type strain)	ASV80 (pink-spot)	ASV2876	ASV28106	ASV29305	ASV5	ASV353
Schenk et al. (2025) PRJEB60884 British Columbia	kelp (311)	0	0	0	0	0	186 (0.0151)	61 (0.0006)
	water (118)	0	0	0	0	2 (< 0.0001)	89 (0.0236)	68 (0.0035)
	substrate (106)	0	0	0	0	0	76 (0.0175)	31 (0.0017)
Park et al. (2025) PRJEB64485 British Columbia	kelp (93)	0	0	0	1 (< 0.0001)	0	40 (0.0024)	22 (0.0007)
	water (5)	0	0	0	0	0	4 (0.0054)	0
	substrate (24)	0	0	0	0	0	11 (0.0032)	3 (< 0.0001)
Davis et al. (2023) PRJEB52544 British Columbia and Washington	kelp (87)	0	0	0	0	0	33 (0.0041)	33 (< 0.0001)
	water (23)	0	0	0	0	0	6 (0.0008)	1 (< 0.0001)
	substrate (30)	0	0	0	0	0	12 (0.0028)	2 (0.0001)
King et al. (2022) PRJEB50679 United Kingdom	kelp (59)	0	0	0	0	0	55 (0.0012)	0
Lemay et al. (2018) PRJEB15100 British Columbia	kelp (31)	0	0	0	0	0	24 (0.0004)	0
	water (14)	0	0	0	0	0	10 (0.0004)	0
	substrate (20)	0	0	0	0	0	14 (0.0012)	0

that the *Algicola bacteriolytica* type strain (NR_036838.1) and ASV80 (enriched in pink-spot disease) were not present in any of the unfiltered datasets, showing that these taxa are not ubiquitously associated with kelps.

Next, we expanded our search to include other *Algicola* ASVs present in the pink-spot disease data and the other datasets (Table 1). Here, we identified two water samples from Schenk et al. (2025) and one water sample from Park et al. (2025)—all from the same sampling site on different days—that contained trace levels of different *Algicola* ASVs (Table 1). These results suggest that different *Algicola* ASVs were present at low levels in coastal waters where kelp was present, even when the kelps themselves did not show visible signs of disease.

Finally, we probed online databases for records of *A. bacteriolytica*. We searched the Encyclopedia of Life (*Algicola bacteriolytica*—EOL, 2024) and the Ocean Biodiversity Information System (*Algicola bacteriolytica*—OBIS, 2024), both of which contained records of *A. bacteriolytica*. These results confirm that *Algicola* is globally distributed in coastal waters. In addition, the OBIS database contained records of *A. bacteriolytica* associated with the kelp *Ecklonia radiata* in Australia, suggesting that *Algicola* can be detected on wild kelps that appeared healthy at the time of sampling.

Algicola phylogeny

Algicola bacteriolytica (NR_036838.1) is the proposed causative agent of red-spot disease on *S. japonica* (Ezura et al. 1988; Sawabe et al. 1998), which had a very similar phenotype to pink-spot disease. The main visual difference between these two diseases was the color. A "prodigiosin-like" (red) color in red-spot disease (Ezura et al. 1988; Sawabe et al. 1998) and a pink color in pink-spot disease.

To assess the relatedness of the proposed causative agents of red-spot and pink-spot disease, we constructed a phylogeny of *Pseudoalteromonadaceae* with sequences available on NCBI. *Pseudo*alteromonas is polyphyletic, and *Algicola* forms a monophyletic clade within *Psuedoalteromonas* (Fig. 3).
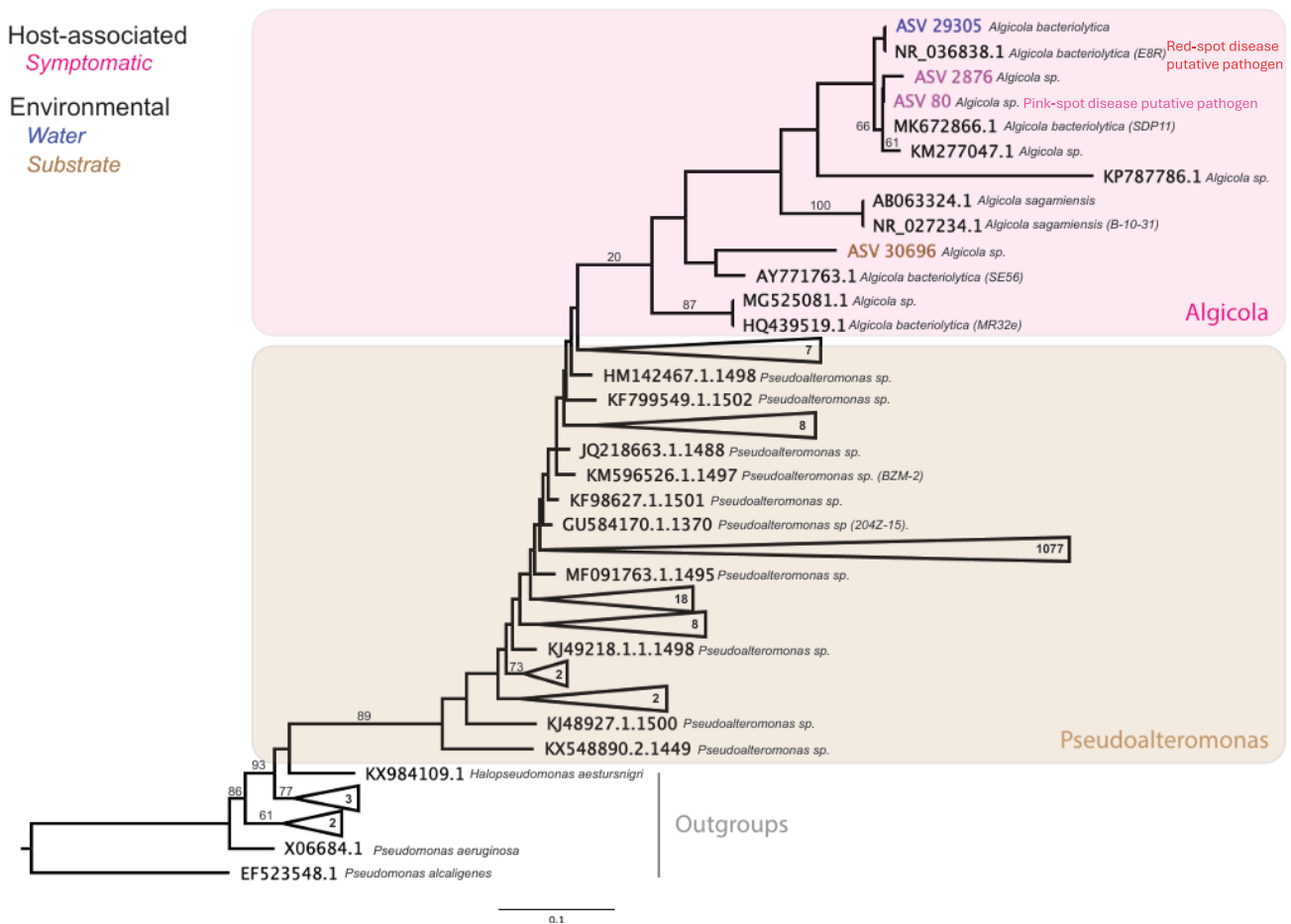
Fig. 3 Maximum likelihood (ML) phylogenetic tree of *Pseudoalteromonadaceae* showing the placement of the genus *Algicola* within the *Pseudoalteromonas* genus. Sequences from SILVA are labeled with their accession number, while ASVs from this study and other unpub-lished studies are labeled with their ASV number corresponding to the taxonomy table and are colored by the sample type they were found in

ASV80 and *A. bacteriolytica* (NR_036838.1) fall within distinct clades within the *Algicola* clade, suggesting that ASV80 and NR_036838.1 are distinct taxa. This points to 1) pink-spot disease and red-spot disease being caused by two distinct members of the genus *Algicola* and 2) a capacity of multiple members of the genus *Algicola* to cause diseases during the kelp nursery stage.

Is the bacterial community different between asymptomatic and symptomatic spools?

To investigate if the entire community differed by disease status, we ran a PERMANOVA for each sampling year (Fig. 4). We ran this analysis both including and excluding all sequences assigned to the *Algicola* genus. We found that the bacterial community associated with symptomatic pink-spot disease was distinct from asymptomatic regions of the kelp spool even after removing *Algicola*, showing that community-wide changes in bacterial composition extended beyond *Algicola* presence and absence (Fig. 4), aligning with the DESeq output that showed polymicrobial shifts in the community by disease status (Fig. 2).

Kelp spools from multiple kelp farms developed pink-spot disease in 2022. Each farm corresponds to a distinct locale from where sori (parent material) were collected to seed the farm; different parent material sources likely affected the bacterial community of the spools. When restricting to only samples from farm 2, which had samples from asymptomatic and symptomatic spool regions, the significant difference between asymptomatic and symptomatic regions persisted (Farm 2; $F_{1,14} = 2.514$, $R^2 = 0.162$, $p = 0.023$). This aligns with previous work that by Marzinelli et al. (2015) that showed that disease status (bleaching) of the kelp *Ecklonia radiata* was more important than spatial proximity (analogous to
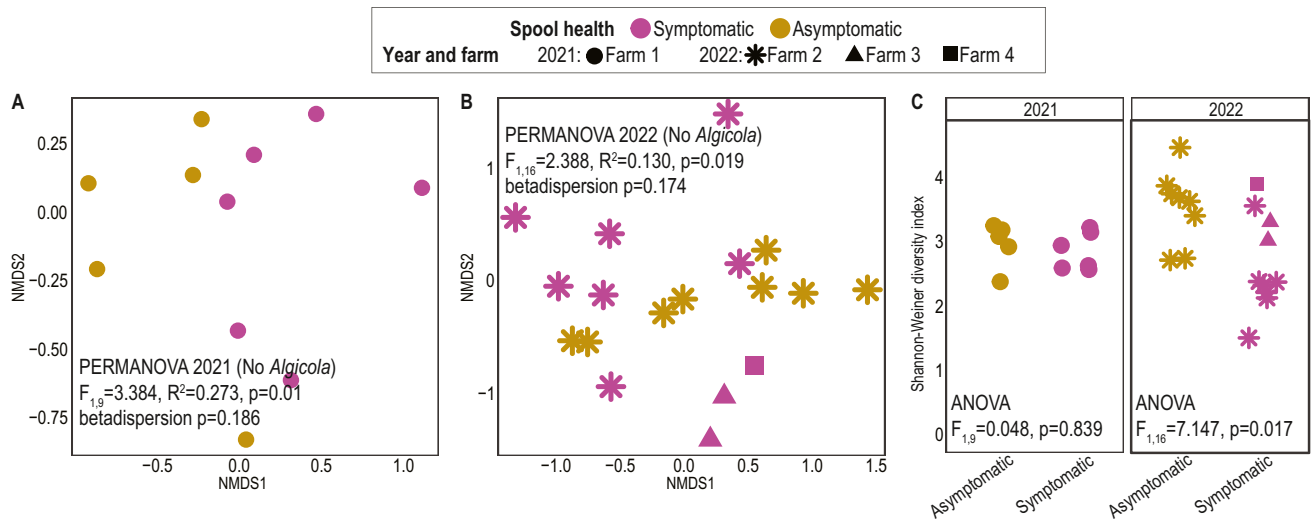
Fig. 4 NMDS plot showing spool samples by healthy status with *Algicola* removed from the dataset in **A**) 2021 and **B**) 2022. PER-MANOVA results are indicated in the corresponding facets along with the *p*-value of the corresponding betadispersion test. **C**) The diversity of asymptomatic and symptomatic samples by year (which were processed with different DNA extraction kits)

different farms in our data) in explaining variation in the bacterial community. We also tested for differences in alpha-diversity between symptomatic and asymptomatic spool samples (Fig. 4C). In 2022 only, we observed a significant decrease in diversity in the symptomatic samples compared to the asymptomatic samples. Further studies that track the progression of disease over time and comparison to spools in disease-free aquaria are needed to clarify the relationship between microbial community changes and disease.
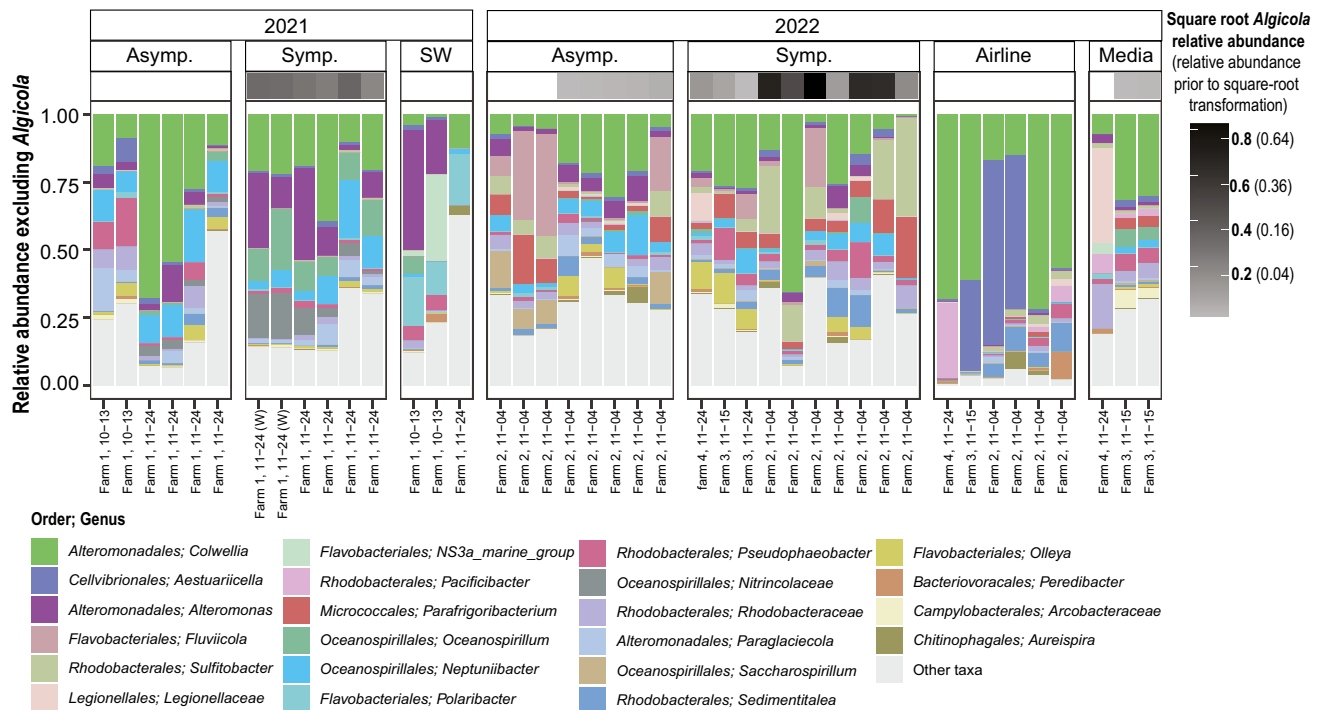
Fig. 5 Plot of the 10 most abundant genera by sample type and spool health status, excluding the genus *Algicola*. The square root of the relative abundance of *Algicola* is shown in the heatmap bar on top, with white squares showing true 0 relative abundance. The x-axis shows the date the sample was taken, along with the farm. The facets divide the samples by year (different DNA extraction kits), sample type, and spool health. Note, for the symptomatic swabs, we indicate the two samples where the whole pink area was swabbed (W) in 2021, rather than only the leading edge

To assess changes in higher taxonomic levels in the bacterial community of the spools, we calculated the ten most abundant genera in all four sample types, excluding *Algicola* (Fig. 5). We observe consistency in the most abundant taxa (*Colwellia*) by spool health and sampling years, but also some differences between years (*Alteromonas* is much more abundant in 2021 and *Sulfitobacter* is much more abundant in 2022). Overall, all genera were found in both the asymptomatic and symptomatic samples, showing low turnover at the genus level associated with spool health.

Conclusions

Pink-spot disease is a novel disease found in kelp nurseries and is currently present in multiple kelp nurseries across North America. Kelp diseases in the region should be monitored and studied. Growers employ many practices to prevent and mitigate disease in the nursery, including sori cleaning with iodine or weak bleach, water filtration, water UV irradiation, and sterilization of culturing equipment in-between uses. Growers also ubiquitously monitor their spools for disease and separate diseased spools from asymptomatic spools to limit the spread of disease.

Our data suggested that pink-spot is a novel disease, likely caused by a member of the genus *Algicola*. *Algicola* ASV80 was strongly enriched in symptomatic samples and present in all symptomatic samples compared to asymptomatic samples. Pink-spot disease was also accompanied by broader, non-specific changes in the bacterial community, but we cannot determine whether these were a cause or a consequence of the disease. ASV80 is closely related but distinct from the causative agent of red-spot disease identified by Sawabe et al. (1998), *A. bacteriolytica*. Isolating ASV80 and testing Koch's postulates (Koch 1890) are important next steps to test if ASV80 is the causative agent of pink-spot disease. These efforts should be paired with broader efforts characterizing the nursery microbiota to gain a baseline understanding of what a healthy microbial community in kelp nurseries looks like.

Declarations

References

Algicola bacteriolytica—EOL (2024) Encyclopedia of life. https://eol.org/pages/972497

Algicola bacteriolytica—OBIS (2024) Ocean biodiversity information system. https://obis.org/taxon/570326

Antonelli G, Cutler S (2016) Evolution of the Koch postulates: towards a 21st-century understanding of microbial infection. Clin Microbiol Infect 22:583–584

Barbera P, Kozlov AM, Czech L, Morel B, Darriba D, Flouri T, Stamatakis A (2019) EPA-ng: massively parallel evolutionary placement of genetic sequences. Syst Biol 68:365–369

Bindoff NL, Cheung WWL, Kairo JG, Arístegui J, Guinder VA, Hallberg R, Hilmi N, Jiao N, Karim MS, Levin L, O'Donoghue S, Purca Cuicapusa SR, Rinkevich B, Suga T, Tagliabue A, Williamson P (2019) Changing ocean, marine ecosystems, and dependent communities. In: Pörtner H-O, Roberts DC, Masson-Delmotte V, Zhai P, Tignor M, Poloczanska E, Mintenbeck K, Alegría A, Nicolai M, Okem A, Petzold J, Rama B, Weyer NM (eds) IPCC special report on the ocean and cryosphere in a changing climate. Cambridge University Press, Cambridge, pp 447–587

Callahan BJ, McMurdie PJ, Rosen MJ, Han AW, Johnson AJA, Holmes SP (2016) DADA2: high-resolution sample inference from Illumina amplicon data. Nat Meth 13:581–583

Campbell I, Kambey CSB, Mateo JP, Rusekwa SB, Hurtado AQ, Msuya FE, Stentiford GD, Cottier-Cook EJ (2020) Biosecurity policy and legislation for the global seaweed aquaculture industry. J Appl Phycol 32:2133–2146

Campbell I, Macleod A, Sahlmann C, Neves L, Funderud J, Øverland M, Hughes AD, Stanley M (2019) The environmental risks associated with the development of seaweed farming

in Europe—prioritizing key knowledge gaps. Front Mar Sci 6:107

Capella-Gutiérrez S, Silla-Martínez JM, Gabaldón T (2009) trimAl: a tool for automated alignment trimming in large-scale phylogenetic analyses. Bioinformatics 25:1972–1973

Chao A, Chiu C-H (2016) Species richness: estimation and comparison. In: Wiley StatsRef: statistics reference online. John Wiley & Sons, Ltd, pp 1–26

Coleman S, Gelais AT, St. Fredriksson DW, Dewhurst T, Brady DC (2022) Identifying scaling pathways and research priorities for kelp aquaculture nurseries using a techno-economic modeling approach. Front Mar Sci 9:894461

Czech L, Barbera P, Stamatakis A (2020) Genesis and Gappa: processing, analyzing and visualizing phylogenetic (placement) data. Bioinformatics 36:3263–3265

Davis KM, Zeinert L, Byrne A, Davis J, Roemer C, Wright M, Parfrey LW (2023) Successional dynamics of the cultivated kelp microbiome. J Phycol 59:538–551

del Campo J, Kolisko M, Boscaro V, Santoferrara LF, Nenarokov S, Massana R, Guillou L, Simpson A, Berney C, de Vargas C, Brown MW, Keeling PJ, Parfrey LW (2018) EukRef: phylogenetic curation of ribosomal RNA to enhance understanding of eukaryotic diversity and distribution. PLoS Biol 16:e2005849

Dittami SM, Duboscq-Bidot L, Perennou M, Gobet A, Corre E, Boyen C, Tonon T (2016) Host–microbe interactions as a driver of acclimation to salinity gradients in brown algal cultures. ISME J 10:51–63

Egan S, Gardiner M (2016) Microbial dysbiosis: rethinking disease in marine ecosystems. Front Microbiol 7:00991

Egan S, Daniel NF, Kumar V, Gardiner M, Thomas T (2013) Bacterial pathogens, virulence mechanism and host defence in marine macroalgae. Env Microbiol 16:925–938

Ezura Y, Hara Y, Kimura T (1990) A control method for the red-spots injury occurring on seed twines for the cultivation of makonbu (*Laminaria japonica*). Nippon Suisan Gakkaishi 56:2045–2051

Ezura Y, Yamamoto H, Kimura T (1988) Isolation of a marine bacterium that produces red-spots on the culture bed of makonbu *Laminaria japonica* cultivation. Nippon Suisan Gakkaishi 54:665–672

Cai J, Lovatelli A, Aguilar-Manjarrez J, Cornish L, Dabbadie L, Desrochers A, Diffey S, Garrido Gamarro E, Geehan J, Hurtado A, Lucente D, Mair G, Miao W, Potin P, Przybyla C, Reantaso M, Roubach R, Tauati M, Yuan X (2021) Seaweeds and microalgae: an overview for unlocking their potential in global aquaculture development. FAO Fisheries and Aquaculture Circular No. 1229. FAO, Rome

Florez JZ, Camus C, Hengst MB, Buschmann AH (2017) A functional perspective analysis of macroalgae and epiphytic bacterial community interaction. Front Microbiol 8:2561

Fox J, Weisberg S (2019) An R companion to applied regression, 3d edn. Sage Publications. https://socialsciences.mcmaster.ca/jfox/Books/Companion/

Hsieh TC, Ma KH, Chao A (2022) iNEXT: interpolation and extrapolation for species diversity, version 3.0.0. http://chao.stat.nthu.edu.tw/wordpress/software-download/

Inguanez L, Zhu X, Patange A, de Oliveira Mallia J, Tiwari BK, Valdramidis VP, Kakagianni M (2024) Microbial characterization of raw biomasses of Alaria esculenta. Chlorella vulgaris. The Microbe 2:100053

Katoh K, Standley DM (2013) MAFFT multiple sequence alignment software version 7: improvements in performance and usability. Mol Biol Evol 30:772–780

King NG, Moore PJ, Thorpe JM, Smale DA (2022) Consistency and variation in the kelp microbiota: patternsof bacterial community structure across spatial scales. Microbial Ecol 85:1265–1275

Koch R (1890) Über bakteriologische Forschung. Verhandlung des X Internationalen Medicinischen Congresses, Berlin. August Hirschwald Verlag, Berlin, pp 650–660

Lemay MA, Martone PT, Keeling PJ, Burt JM, Krumhansl KA, Sanders RD, Wegener Parfrey L (2018) Sympatric kelp species share a large portion of their surface bacterial communities: kelp-associated bacterial diversity. Environ Microbiol 20:658–670

Lin JD, Lemay MA, Parfrey LW (2018) Diverse bacteria utilize alginate within the microbiome of the giant kelp *Macrocystis pyrifera*. Front Microbiol 9:1914

Love MI, Huber W, Anders S (2014) Moderated estimation of fold change and dispersion for RNA-seq data with DESeq2. Genome Biol 15:550

Lundberg DS, Yourstone S, Mieczkowski P, Jones CD, Dangl JL (2013) Practical innovations for high-throughput amplicon sequencing. Nat Methods 10:999–1002

Marshall K, Joint I, Callow ME, Callow JA (2006) Effect of marine bacterial isolates on the growth and morphology of axenic plantlets of the green alga *Ulva linza*. Microb Ecol 52:302–310

Marzinelli EM, Campbell AH, Zozaya Valdes E, Vergés A, Nielsen S, Wernberg T, de Bettignies T, Bennett S, Caporaso JG, Thomas T, Steinberg PD (2015) Continental-scale variation in seaweed host-associated bacterial communities is a function of host condition, not geography. Environ Microbiol 17:4078–4088

Marzinelli EM, Thomas T, Vadillo Gonzalez S, Egan S, Steinberg PD (2024) Seaweeds as holobionts: current state, challenges, and potential applications. J Phycol 60:785–796

McLaren MR (2020) Silva SSU taxonomic training data formatted for DADA2 (Silva version 138*)* [Dataset]. Zenodo

McLaren MR, Callahan BJ (2021) Silva 138.1 prokaryotic SSU taxonomic training data formatted for DADA2 . Zenodo. https://doi.org/10.5281/zenodo.4587955

Mikryukov V (2022) *metagMisc:* miscellaneous functions for metagenomic analysis, version 0.0.4

Msuya FE, Bolton J, Pascal F, Narrain K, Nyonje B, Cottier-Cook EJ (2022) Seaweed farming in Africa: current status and future potential. J Appl Phycol 34:985–1005

Oksanen J, Simpson GL, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Solymos P, Stevens MHH, Szoecs E, Wagner H et al. (2022) vegan: comm ecol package. https://CRAN.R-project.org/package=vegan

Park J, Kohn E, Schenk S, Davis K, Clark J, Parfrey LW (2023) Exploring the impact of microbial manipulation on the early development of kelp (*Saccharina latissima*) using an ecological core microbiome framework. Appl Environ Microbiol

Provasoli L, Pintner IJ (1980) Bacteria induced polymorphism in an axenic laboratory strain of *Ulva Lactuca* (Chlorophyceae). J Phycol 16:196–201

R Core Team (2022) R: a language and environment for statistical computing. R Foundation for Statistical Computing. https://www.R-project.org/

Redmond S, Green L, Yarish C, Kim J, Neefus C (2014) New England seaweed culture handbook. *Seaweed Cultivation*. 1. https://digitalcommons.lib.uconn.edu/seagrant_weedcult/1

Rognes T, Flouri T, Nichols B, Quince C, Mahé F (2016) VSEARCH: A versatile open source tool for metagenomics. PeerJ 4:e2584

Sato Y, Civiello M, Bell SC, Willis BL, Bourne DG (2016) Integrated approach to understanding the onset and pathogenesis of black band disease in corals. Environ Microbiol 18:752–765

Sawabe T, Makino H, Tatsumi M, Nakano K, Tajima K, Iqbal MM, Yumoto I, Ezura Y, Christen R (1998) *Pseudoalteromonas bacteriolytica* sp. nov., a marine bacterium that is the causative agent of red spot disease of *Laminaria japonica*. Int J Syst Bacteriol 48:769–774

Sawabe T, Tanaka R, Iqbal MM, Tajima K, Ezura Y, Ivanova EP, Christen R (2000) Assignment of *Alteromonas elyakovii* KMM 162T and five strains isolated from spot-wounded fronds of *Laminaria japonica* to *Pseudoalteromonas elyakovii* comb. nov. and the extended description of the species. Int J Syst Evol Microbiol 50:265–271

Schenk S, Wardrop CG, Parfrey LW (2025) Abiotic stress destabilizes the bacterial community of sugar kelp, Saccharina latissima (Phaeophyceae). J Phycol 1–18

Schloss PD, Westcott SL, Ryabin T, Hall JR, Hartmann M, Hollister EB, Lesniewski RA, Oakley BB, Parks DH, Robinson CJ, Sahl JW, Stres B, Thallinger GG, Van Horn DJ, Weber CF (2009) Introducing mothur: open-source, platform-independent, community-supported software for describing and comparing microbial communities. Appl Environ Microbiol 75:7537–7541

Seyedsayamdost MR, Case RJ, Kolter R, Clardy J (2011) The Jekyll-and-Hyde chemistry of *Phaeobacter gallaeciensis*. Nat Chem 3:331–335

Shen W, Le S, Li Y, Hu F (2016) SeqKit: a cross-platform and ultrafast toolkit for FASTA/Q file manipulation. PLoS ONE 11:e0163962

Shen W, Sipos B, Zhao L (2024) SeqKit2: a swiss army knife for sequence and alignment processing. PLoS ONE 11:e0163962

Smith KE, Aubin M, Burrows MT, Filbee-Dexter K, Hobday AJ, Holbrook NJ, King NG, Moore PJ, Sen Gupta A, Thomsen M, Wernberg T, Wilson E, Smale DA (2024) Global impacts of marine heatwaves on coastal foundation species. Nat Commun 15:5052

Spagnuolo D, Genovese G (2024) Macroalgal diseases: exploring biology, pathogenesis, and management strategies. Phycology 4:450–464

Stamatakis A (2014) RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics 30:1312–1313

Ward GM, Faisan JP, Cottier-Cook EJ, Gachon C, Hurtado AQ, Lim PE, Matoju I, Msuya FE, Bass D, Brodie J (2020) A review of reported seaweed diseases and pests in aquaculture in Asia. J World Aquaculture Soc 51:815–828

Ward GM, Kambey CSB, Faisan JP Jr, Tan P-L, Daumich CC, Matoju I, Stentiford GD, Bass D, Lim P-E, Brodie J, Poong S-W (2022) Ice-Ice disease: an environmentally and microbiologically driven syndrome in tropical seaweed aquaculture. Rev Aquac 14:414–439

Weigel BL, Pfister CA (2019) Successional dynamics and seascape-level patterns of microbial communities on the canopy-forming kelps *Nereocystis luetkeana* and *Macrocystis pyrifera*. Front Microbiol 10:346

Yan Y, Wang S, Liu K, Mo Z, Yang H, Rong X, Li J (2023) Divergence of epibacterial community assemblage correlates with malformation disease severity in *Saccharina japonica* seedlings. Front Mar Sci 10:1089349

Yumoto I, Ezura Y, Kimura T (1989) Distribution of the A*lteromonas* sp., the causative agent of red-spots on the culture bed of makonbu *Laminaria japonica*, in the coastal area of Funka Bay. Nippon Suisan Gakkaishi 55:453–462