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The mitochondrial and chloroplast genomes of the kelp, *Ecklonia radiata*

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ABSTRACT

Ecklonia radiata is a dominant kelp across much of the southern hemisphere supporting vast economic, social and ecological values. It is also of emerging interest for aquaculture industries and in blue carbon sequestration. Despite its importance, genomic resources of this key species are scant, yet could provide important knowledge to better manage, cultivate and conserve this species in our changing oceans. In this study we report the complete mitochondrial and draft chloroplast genome for *E. radiata*. The mitochondrial genome is 37,696 bp in length and contains 66 annotated genes. Two alternative scaffold arrangements were recovered for the chloroplast genome, both of 130,955 bp and differing only in the orientation of a single ~ 43 kbp contig. Annotation of the plastid scaffolds identified 175 genes and two large inverted repeats that are typical of brown algal chloroplast genomes. Comparisons to other kelp genomes indicate that the gene sets reported here are likely complete. The recovery of two chloroplast scaffold assembly arrangements hints at the possibility of heteroplasmy in *E. radiata* though this requires further investigation. The genomic information reported here will aid in understanding functional response of *E. radiata* in changing oceans, enhance the development of *E. radiata* as an aquaculture resource and support efforts to conserve this ecologically important marine species.

1. Introduction

Ecklonia radiata is the dominant laminarian kelp throughout Australasia and eastern South Africa, underpinning vast ecological and economic values (Wernberg et al., 2019). Climatic and anthropogenic change has driven population loss of *E. radiata* throughout its range (Valentine and Johnson, 2003; Vergés et al., 2016; Wernberg et al., 2016; Carnell and Keough, 2020; Coleman et al., 2020b) prompting calls for proactive interventions to boost resilience to future stress (Coleman et al., 2020b). At the same time, there is increasing interest in developing aquaculture industries for kelp to sequester carbon, boost coastal economies and food security (Filbee-Dexter et al., 2022). Both climate interventions and aquaculture ventures require genomic knowledge to design adaptive management and selective breeding strategies (Coleman and Goold, 2019; Coleman et al., 2020a), however such knowledge is currently lacking for this key southern hemisphere species.

Mitochondrial and chloroplast genomes code for many proteins that are vital for photosynthesis and metabolism, thus knowledge of their structure can reveal evolutionary relationships among taxa, be engineered to enhance certain traits, and understand tolerance (Daniell et al., 2016; Vranken et al., 2021). With the advent of high throughput sequencing technology these genomes can now be readily sequenced to provide the genomic knowledge required to achieve such goals. Their small size relative to nuclear genomes means they are more easily and comprehensively annotated, even for non-model species such as algae and may provide critical genomic resources that can be utilised prior to full genomes being available. There are, however, currently few annotated mitochondrial genomes for laminarian kelps, especially non-harvested species, and even fewer chloroplast genomes.

Of the chloroplast algal genomes that have been sequenced, several have revealed the potential for heteroplasmy (Sauvage et al., 2019; Rana et al., 2019) and it is also thought that this occurrs in the mitochondrial genome of several brown algal taxa (Coyer et al., 2004; Tellier et al., 2011). Indeed, the chloroplast genomes of many plants and algae contain a pair of long inverted repeats that separate the Large Single Copy (LSC) and Small Single Copy (SSC) regions. The inverted repeats are thought to act as recombination hotspots as inversions involving the SSC are regularly observed. Two forms of chloroplast SSC inversions have been reported. The first involves SSC inversion rearrangement differences within closely related species or even accessions of the same

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Abbreviations: NCBI, National Center for Biotechnology Information; SSC, Small Single Copy; LSC, Large Single Copy.

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species (Liu et al., 2013; Walker et al., 2014). The second form is stable heteroplasmies involving equimolar inversion isomers within the one individual (Bourne et al., 1992; Linne von Berg and Kowallik, 1992; Cattolico et al., 2008; Wang and Lanfear, 2019). The relatively large size (> 5 kbp) and low complexity of the inverted repeat regions that border the SSC represent a technical challenge to traditional PCR methods for orientating sequenced contigs, as well *de novo* assemblers using short read (< 200 bp) high throughput sequencing data. These technical limitations have led to some debate on whether reports of unique chloroplast SSC inversions actually represent cryptic heteroplasmy (Walker et al., 2015; Wang and Lanfear, 2019). Support for this latter hypothesis has come from recent studies in flowering plants that have utilised long read sequencing (reads > 10 kb) to show that heteroplasmy has been widely underreported (Wang and Lanfear, 2019). Along with characterising the first annotated chloroplast and mitochondrial genomes of *E. radiata*, we also examine the possibility for heteroplasmy in this species. This new genomic information represents an important resource for emerging aquaculture and conservation initiatives for this key kelp species.

2. Materials and methods

2.1. Genomic DNA extraction and sequencing

Cultures of *Ecklonia radiata* gametophytes derived from a single adult sporophyte were used in the genomic DNA (gDNA) extraction. Gametophytes (1:1 male:female ratio) from an isolated sporophyte (H140) collected in Hamelin Bay, Western Australia, were vegetatively grown by fragmentation in a controlled environment with a set temperature (16 °C), light intensity (25 µmol), wavelength (red light, 660 nm) and photoperiod (13:11 h light:dark cycle). Growth medium was sterilised filtered sea water enriched with 10 ml/L of the Provasoli's enriched solution and 2 ml/L of germanium dioxide. Seawater was replaced weekly to enhance growth. For each gDNA extraction, approximately 0.1 g of fresh semi-dry gametophyte material was homogenised by freezing in liquid nitrogen and ground into fine powder with pestle and mortar. The extraction of high molecular weight gDNA required CTAB extracted DNA (method adapted from Shan and Pang, 2009) to be further purified using DNA columns (DNeasy plant kit, Qiagen). The final purified gDNA was visualised on an agarose gel to ensure it was not degraded and the purity was assessed using a fluorometer (Qubit 3.0, Life Technologies), a spectrophotometer (NanoDrop ND-1000, ThermoFisher) and the LabChip® GX Touch™ nucleic acid analyser (PerkinElmer). The gDNA was used to construct a TruSeq DNA library and sequenced on an Illumina HiSeqX machine (carried out by Macrogen Inc.). The quality of the resulting 151 paired end read data was assessed using FastQC (Andrews et al., 2012).

2.2. Mitochondrial and chloroplast genome assembly using NOVOPlasty

Mitochondrial and chloroplast assemblies were carried out using the NOVOPlasty version 4.2 (Dierckxsens et al., 2017). Adaptor sequences were trimmed using bbduk (Bushnell, 2016) with the following parameters: ktrim = r k = 23 mink = 11 hdist = 1 tpe tbo. Assembly seed sequences used for the mitochondria and chloroplast were the *E. radiata nad5* (NCBI accession number 148262.1) and *rbcL* (NCBI accession number DQ372560.1) genes, respectively. The mitochondria assembly parameters were: PE mode, read length = 151, insert size auto=yes, genome and k-mer = 33, genome range = 30,000–50,000 and type = mito_plant. The same configuration options were used for the chloroplast assembly, except genome range = 100,000–150,000, and type =chloro. Assemblies was also carried out using GetOrganelle version 1.7.1 (Jin et al., 2018), with the mitochondria parameters -R 15 -k 21, 45,85,115,145 and -F embplant_mt. For the chloroplast the GetOrganelle parameters were -R 15 -k 21,45,85,115,145 and -F other_pt. The sequenced reads were mapped to assembled scaffolds using BWA version 0.7.12-r1039 (Li and Durbin, 2009) and visualised using the Integrated Genome Viewer version 2.4.10 (Robinson et al., 2011). Annotations and circos plots were generated using GeSeq and OGDRAW, respectively, accessed from the chlorobox website (Tillich et al., 2017; https://chlorobox.mpimp-golm.mpg.de/geseq.html accessed Nov 2021) with the *Saccharina japonica* mitochondrial and chloroplast genbank annotations (accession numbers: JQ405663, AP011493) used as reference sets for annotation of identified genes. Each GeSeq prediction was manually validated by alignment to orthologues genes in the in the NR database at National Center for Biotechnology Information (NCBI) and where required the annotation coordinates were edited to correct for reading frame errors and/or missing start and stop codons. Whole mitochondrial and chloroplast genome alignments were performed using mVista with the shuffle-LAGAN algorithm, window size 100 bp, minimum conservation width 100%, consensus identity 70%, and minimum displayed conservation 50% (Frazer et al., 2004). The accession numbers of mitochondria used for comparative purposes were *Laminaria solidungula* (NC_056140), *S. japonica* (AP011493), and *Undaria pinnatifida* (KF319031). The accession numbers for the chloroplast genomes used were *L. solidungula* (NC_044690), *S. japonica* (JQ405663), and *U. pinnatifida* (MH784528), *Ectocarpus siliculosus* (FP102296) and *Fucus vesiculosus* (FM957154).

2.3. Phylogenetic analyses

Conceptual translations from mitochondrial and plastid protein coding genes were extracted from the GenBank data available at NCBI (accession numbers provided in the Fig. 2 legend). A list of 35, and 104, protein coding genes shared across the six taxa were used in the mitochondrial and plastid phylogenetic analyses, respectively (Table S1). Protein sequences encoded by each gene were aligned using Muscle (version 3.8.3; Edgar, 2004) with the default settings. Finally, a concatenated protein alignment was produced for each organelle that consisted of 9278 characters for the mitochondria and 27,807 characters for plastid. The concatenated nexus alignment files used in these analyses are available from: https://dpidave@bitbucket.org/dpi_data_analytics/kelp_phylogenetics.git. The Bayesian phylogenetic analyses was performed using MrBayes (version 3.2.7a; Ronquist and Huelsenbeck, 2003), with the alignment partitioned by gene and model parameters estimated separately for each partition. The MyBayes implementation of the GTR amino acid model with an inverse gamma rate distribution approximated using four categories was used. Each analysis consisted of two parallel runs with four chains over 1,000,000 generations with 25% of the samples discarded as the burnin.

3. Results

3.1. Illumina sequencing and E. radiata mitochondrial genome assembly

Using the Illumina HiSeqX platform we obtained ~ 382 million paired end *Ecklonia radiata* genomic DNA sequencing reads. The sequencing data was high quality, with 96.5% of bases having > = Q20. NOVOPlasty was used to assemble a single *E. radiata* mitochondrial scaffold of 37,696 bp from 166,852 reads (722X organelle coverage) with a GC content of 32.4% (Fig. 1). An assembly with GetOrganelle also resulted in a single scaffold that had 100% identity to the NOVOPlasty assembly (results not shown). The size and GC content of the mitochondrial genome was similar to that of other kelp species, such as *Saccharina japonica* (37,657 bp; GC% = 35.3) and *Laminaria solidungula* (37,862 bp; GC% = 34.9). Annotation of the scaffold identified 66 predicted intronless genes including 25 tRNA's and 3 rRNA's (Tables 1 and S2). The lack of introns is a common feature of brown algae mitochondria genomes. Based on the annotations gene content is highly conserved between the *E. radiata* and *S. japonica* mitochondria (Table 1), including both taxa sharing duplicate copies of the tRNA genes *trnI*, *trnM* and *trnS*, as well as triplicate copies of *trnL*. The standard ATG initiation

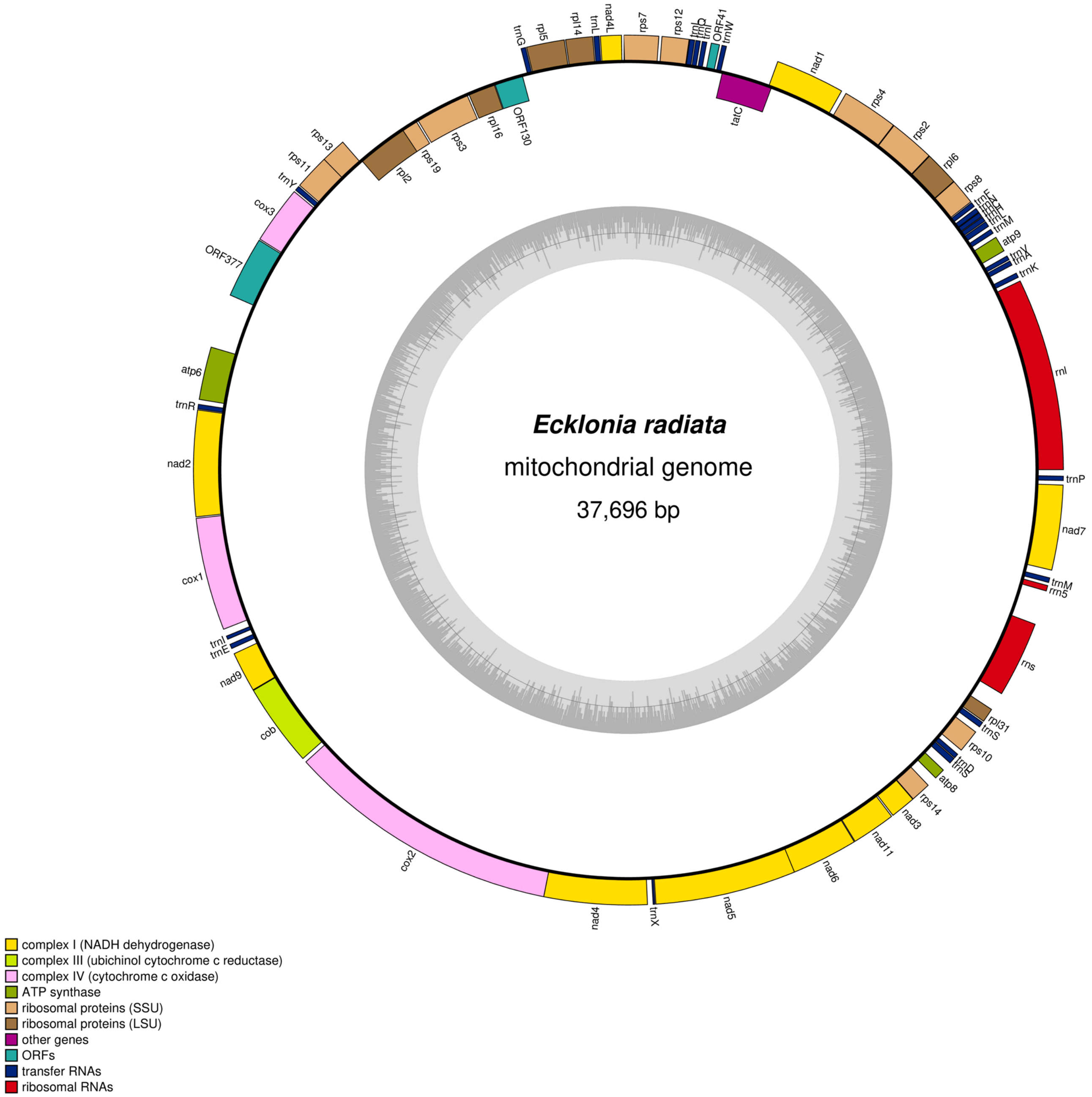

Fig. 1. Circos plot of the *Ecklonia radiata* mitochondrial assembly. Genes are coloured by annotation category as shown in the key. Genes drawn on the inside of the circle are transcribed clockwise, whilst genes on the outside of the circle counter clockwise. The bar graph in the center circle denotes GC content, with the light grey line representing 50% GC. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1
Numbers of gene types annotated by GeSeq for the *Ecklonia radiata* and *Saccharina japonica* mitochondria and chloroplasts.

Annotation	*E. radiata*	*S. japonica*
Mitochondrial genome		
CDS	38	38
tRNA	25	25
rRNA	3	3
Total genes	66	66
Chloroplast genome		
CDS	140	140
tRNA	29	29
rRNA	6	6
Total genes	175	175

codon is used in all 38 protein coding genes, with the stop codon most commonly TAA (73.6%), followed by TAG (15.8%) and TGA (10.5%). A Bayesian phylogenetic analysis derived from a concatenated alignment of 35 shared mitochondrial protein coding genes across 6 brown algal taxa recovered the expected evolutionary relationship of *E. radiata* within the Laminariales clade with high confidence (Fig. 2A). These results show that this *E. radiata* mitochondrial genome assembly is likely to contain a complete gene set.

Whole genome mVista alignments of brown algae mitochondria from *L. solidungula* , *S. japonica*, and *Undaria pinnatifida*, with that of *E. radiata* reveals high levels of sequence conservation in the genic regions. A ~ 500 bp region of high diversity between 16,500 bp and 17,000 in the *E. radiata* mitochondria genome (Fig. S1) could be useful as a high-resolution population genetic marker.

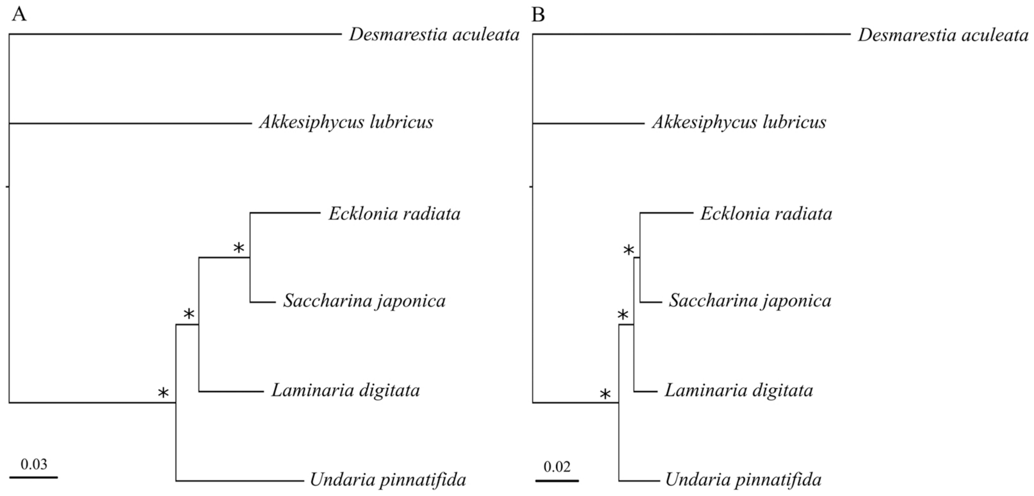

Fig. 2. Bayesian phylogenetic trees derived from proteins encoded by mitochondrial (A) and chloroplast (B) genes shared by six brown algal species. Branching arrangements with 100% posterior probability support are indicated with an asterisk. The NCBI accession numbers of the mitochondrial genomes used to obtain these sequences are: *Saccharina japonica* (AP011493), *L aminaria digitata* (AJ344328), *Undaria pinnatifida* (KF319031), *Akkesiphycus lubricus* (MZ156045), and *Desmarestia aculeata* (MZ156052). The accession numbers of the chloroplast genomes: *S. japonica* (JQ405663), *L. digitata* (MH784527), *U. pinnatifida* (KP298002), *A. lubricus* (MZ156027), and *D. aculeata* (MZ156041). The complete gene lists used to generate the concatenated protein alignments is shown in Table S1.

3.2. The draft *E. radiata* chloroplast genome

Two assembly arrangements of 130,955 bp were recovered for the *E. radatia* chloroplast from 564,146 reads (699X organelle coverage). The inability of the NOVOPlasty assembler to conclusively order contigs at the breakpoint between the two arrangements also occurs when a second assembler (GetOrgnaelle) is used (results not shown). Comparison of the two NOVOPlasty alternative assembly arrangements with BLASTN revealed that a region of 42,998 bp at the 3′ end of the scaffolds is found in opposite orientations in each arrangement (Fig. S2A). This inversion involves the entire Small Single Copy (SSC) region which is bordered by Large inverted repeats that could explain why the assembler was unable to unambiguously orientate the contig in this region. Mapping of the original short read data back to the assembled scaffolds generates BWA mapping quality scores of 0 (indicates ambiguous read positioning) at the breakpoint between the two arrangements (Fig. S2B). These observations suggest that a tangled De Bruijn assembly graph is generated in these ~ 5 kb regions of low complexity due to the relatively short reads used in this study (Fig. S2C). When comparing both *E. radiata* scaffold arrangements with four other species from the Laminariales (Fig. 3), only the scaffold shown in Fig. 4 is supported by synteny and thus this arrangement will be described in the results that follow. However, it should be noted that both scaffold arrangements share the same set of gene annotations as they differ only in the orientation of the SSC region.

The 31.0% GC content of the *E. radiata* chloroplast is similar to that observed in the kelps *S. japonica* (GC% = 31.1; 130,584 bp) and *Laminaria digitata* (GC% = 31.0; 130,376 bp). Annotation of the *E. radiata* chloroplast scaffold using the *S. japonica* chloroplast (accession JQ405663) as a reference identified a total of 175 genes, with 29 annotated as tRNA’s, and 6 as rRNA’s (Tables 1 and S4). As has been observed for other brown algae, the *E. radiata* chloroplast contains conserved gene fragments, these involve *psbI*, *ycf37*, *rpl21*, and *psaI*. BLASTN searchers of the *S. japonica* chloroplast genome also identified fragments originating from the same set of genes, indicating that the duplication occurred when these two taxa shared a common ancestor. Full length copies of all fragmented genes were found in the annotated gene set suggesting that the gene fragments are derived from deletions following duplication events (Table S4). As shown in Table 1 the *E. radiata* and *S. japonica* chloroplast annotations overlap in terms of gene categories. The list of tRNA and rRNA genes for both species is identical, including duplicate copies of the rRNA genes *rnl*, *rns* and *rrn5*. (Table S4). Bayesian phylogenetic analysis using a concatenated protein alignment from 104 protein coding genes shared across 6 brown algal species showed the same branching pattern as the mitochondrial tree (Fig. 2B) and once again supported the expected relationships of Laminariales taxa (Starko et al., 2019).

The standard ATG initiation codon is used in all protein coding genes, except for *psbF* and *rps8*, which use GTG. The GTG initiation codon in *E. radiata psbF* and *rps8* genes appears to be highly conserved, as it is also observed in orthologs from *Fucus vesiculosus*, *Ectocarpus siliculosus*, *S. japonica*, *Undaria pinnatifida*, and *Costaria costata* (Zhang et al., 2015). The termination codon TAA is predominantly used (80.7%) in *E. radiata* plastid protein coding genes, followed by TAG (17.9%) and a single TGA for the gene *ycf24*. The TGA termination codon in *E. radiata ycf24* is also conserved in orthologs of the other Laminariales taxa *S. japonica* and *U. pinnatifida* (Zhang et al., 2015). These results suggest the gene annotations reported here are likely to be an accurate and complete representation of the *E. radiata* chloroplast gene set.

The *E. radiata* chloroplast contains large inverted repeat (IR) regions at positions 1–5429 (IRA) and 82479–87907 (IRB; Fig. 4). The size of this repeat (5429 bp) is very similar to IR regions found in other kelp chloroplasts (Rana et al., 2019). The boundary genes for these repeat regions follows the conserved pattern of *ycf17*, *rpl21*-fragment, IRA, *ycf37*, *psaM*, with *rnl*, *trnA*, *trnI* and *rns* found within the repetitive region (Rana et al., 2019). The boundary for the second repeat also follows the conserved pattern of *rpl32*, *trnL*, *ycf37*-fragment, IRB, *rpl21*, and *rpl3*. The genes *rns*, *trnI*, *trnA*, *rnl* and *rrn5* are contained within the IRB repetitive region. Fragmented copies of *rpl21* and *ycf37* found at the IRA and IRB repeat boundaries, respectively, are likely pseudogenes based on the lack of conserved C- and N-terminal regions in the conceptual translation. For comparative purposes we applied the same annotation toolset to chloroplast genomes of the previously published kelp species *L. solidungula*, *S. japonica*, and *U. pinnatifida*, and the non-kelp brown algae *E. siliculosus* and *F. vesiculosus*. These annotations revealed that the fragmented versions of *rpl21* and *ycf37* at the IRA and IRB boundaries in *L. solidungula* , *S. japonica*, and *U. pinnatifida*, but not in *E. siliculosus* or *F. vesiculosus*, suggesting the arrangement is specific to kelp species. Previously, it was reported that a complete copy of *ycf37* was missing in the chloroplast genome of *L. solidungula,* potentially an adaption to the low light conditions experienced by this artic species (Rana et al., 2019). However, our GeSeq annotations contain a full-length copy of *ycf37* between 5087 and 5626 bp in the *L. solidungula* genome sequence (accession # MH784528). The conceptual translation of this putative *ycf37* locus has 100% overlap with the *ycf37* orthologue in the closely related *L. digitata* (Fig. S3). Therefore, although expression data is lacking, it is likely that the *L. solidungula* chloroplast contains a functional *ycf37* gene. As with many other brown algae species the

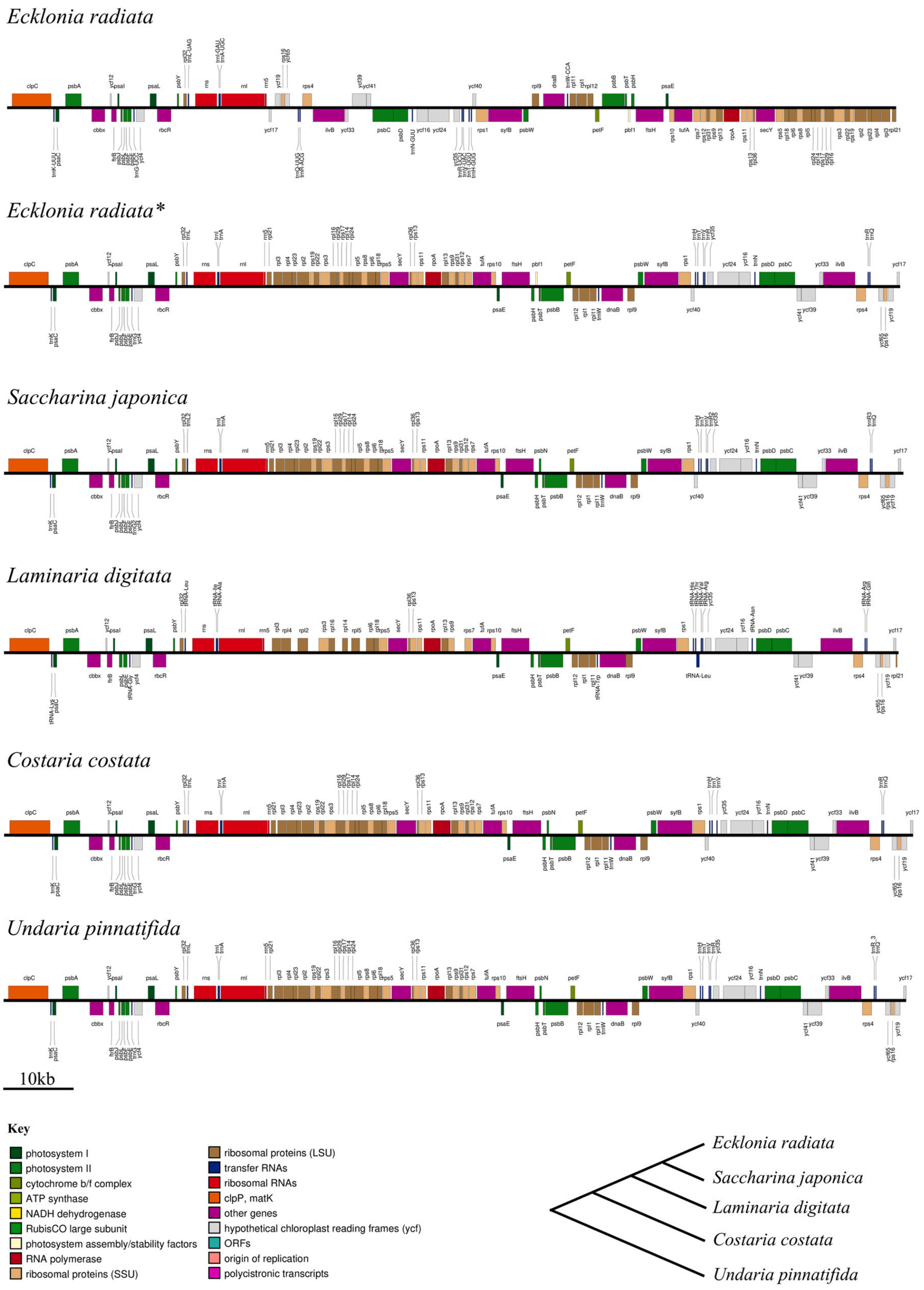

Fig. 3. Graphical maps of chloroplast gene annotations from five taxa in the order Laminariales showing the region of difference between the two *E. radiata* assembled scaffolds arrangements recovered in this study. The *Ecklonia radiata* map with the asterisk corresponds to the arrangement shown in the Fig. 4 circos plot. The scale bar represents 10 kbp and the key contains information on the gene annotation categories as well as a diagram showing the taxonomic relationships between the taxa in the Figure (branching order taken from Starko et al., 2019). The accession numbers for the published chloroplast genomes are *Saccharina japonica* (JQ405663), *Laminaria digitata* (MH784527), *Costaria costata* (KR336545), and *Undaria pinnatifida* (KP298002).

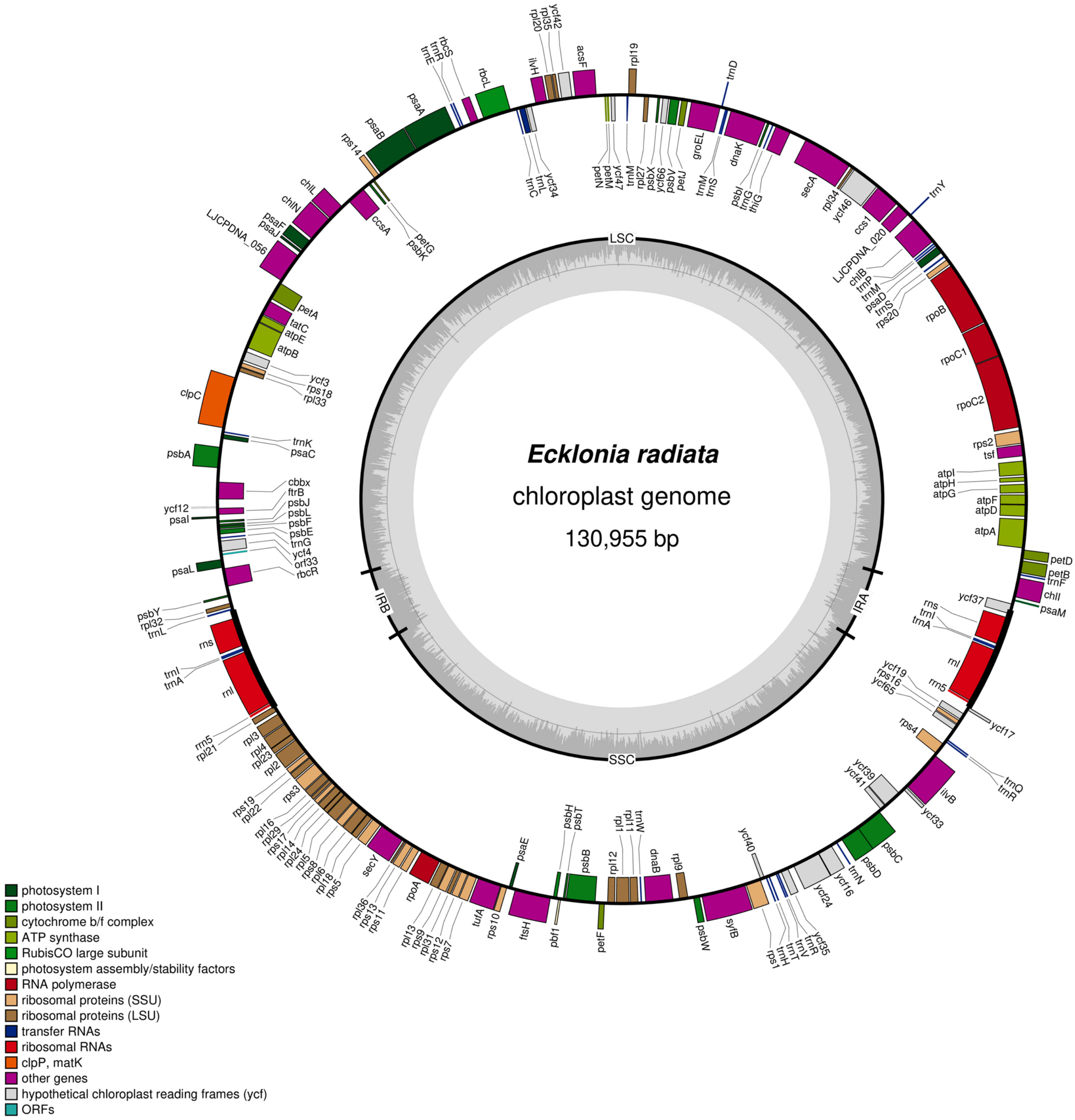

Fig. 4. Circos plot of the *Ecklonia radiata* chloroplast assembly (see Fig. 1 legend for further details). The inverted repeats (IRA and IRB) and large (LSC) and small (SSC) single-copy regions are labelled on the inner circle.

chloroplast genes of *E. radiata* lack introns.

Whole genome mVista alignments of brown algae chloroplasts from *L. solidungula*, *S. japonica*, and *U. pinnatifida*, with that of *E. radiata* reveals high levels of sequence conservation, especially in the genic regions. The only notable exception to this pattern is for the plastid-RNA polymerase complex gene *rpoA,* which shows increased levels of divergence in *E. radiata* versus the other kelp species (Fig. S4). BLASTX search using the *E. radiata rpoA* coding sequence reveals the low level of homology uncovered by the mVista alignments is due to a 78 bp in frame deletion in the region encoding the C-terminal region of the protein (results not shown). This is unexpected as being part of the plastid-encoded plastid RNA polymerase (PEP) complex *rpoA* would be required for photosynthesis, however, alignments to other *rpoA* proteins using BLASTP indicate that the core conserved domains are retained in the *E. radiata* gene suggesting that it is likely still functional. Previously it has been reported in *Chlamydomonas reinhardtii* that *rpoA* gene structure is poorly conserved and this appears to be reflected by our results also (Maul et al., 2002).

4. Discussion

The kelp *Ecklonia radiata* plays a critically important role in supporting the diverse marine ecosystems of Australasia and southern Africa. This work provides the first description of the *E. radiata* mitochondrial and chloroplast genomes and reports the full gene sets of these organelles based on comparisons to other brown algal species. Global warming represents a significant risk to the viability of these important species, yet we know little about the molecular mechanisms that explain differences in kelp population responses to ocean temperature. As organelles are early indicators of temperature stress (de Vries et al., 2020), the genes they encode could also be used as molecular markers to identify kelp communities at greatest ecological risk. Organelle encoded genes would also be important targets for direct intervention based on newer genetic and synthetic biology approaches (Coleman and Goold, 2019; Coleman et al., 2020a).

While the *E. radiata* mitochondria assembled into a single scaffold, two scaffold arrangements were recovered for the chloroplast. The De Bruijn assembly graph shows that two long inverted repeats create uncertainty in orientation of the chloroplast SSC region. In the future we are planning on using long read PacBio sequencing to bridge these repeat regions and conclusively determine the *E. radiata* chloroplast structure. At this stage, however, we cannot rule out that the two assembly arrangements represent an example of heteroplasmy in *E. radiata*. MinIon Long read sequencing has uncovered heteroplasmic chloroplast genomes in the green alga *Caulerpa ashmeadii* (Sauvage et al., 2019) and there is also some evidence based on the incongruence of SNP conservation with the phylogenetic tree arrangements in 5 kelp species, hinting at the occurrence of incomplete lineage sorting through recombination between chloroplast haplotypes (Rana et al., 2019). Mitochondrial heteroplasmy has previously been observed in the brown algae *Fucus serratus* and *Lessonia nigrescens*, with both species displaying geographically restricted haplotype distributions that could be useful markers in population genetics studies (Coyer et al., 2004; Tellier et al., 2011).

The chloroplast SSC region has also been described as a hotspot for inversion based on the observation of inversion isomers in several flowering plants and algae (Liu et al., 2013). Walker et al. (2015) criticised this idea, instead arguing that heteroplasmy was a more likely explanation for the observation of widespread variation in the orientation of the SSC (Bourne et al., 1992; Linne von Berg and Kowallik, 1992; Cattolico et al., 2008). Recent studies using long read PacBio data support this idea by showing evidence for widespread examples of plastid heteroplasmy in flowering plants (Wang and Lanfear, 2019; Lee et al., 2020). Ultimately, the frequency of chloroplast heteroplasmy awaits the wider uptake of long read technology that can bridge the long inverted repeats that often border the SSC.

4.1. *Conclusion*

Here we have reported the mitochondrial and chloroplast genomes of the laminarian kelp *E. radiata* using short read Illumina data. The similarity to other kelp species in gene content in both number and category (rRNA, tRNA) strongly suggests that the full gene list has been presented here. The two assembly arrangements for the chloroplast genome may represent a case of heteroplasmy and long sequence reads will be important to establish if this is the case. We also identify a new mitochondrial marker for species delineation of *E. radiata* that may be developed for barcoding and phylogenetic studies. This new genomic tool represents a valuable genetic resource for future conservation efforts and the emerging aquaculture industry for the dominant kelp throughout Australasia and eastern South Africa.

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Author contributions

DW carried out the bioinformatics analyses. AM carried out the wet lab work. DW, AM, TW, and MC designed the study and wrote the paper.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Thomas Wernberg reports financial support was provided by Australian Research Council. Melinda Coleman and Thomas Wernberg are on the editorial board for Aquatic Botany and Editor-in-Chief of Aquatic Botany, respectively. However, they did not, at any stage of the peer review process, have influence on the process or access to this manuscript, as is the standard practice when handling manuscripts submitted by an editor to this Journal.

Data Availability

The genomic assemblies generated as part of this study can be found at the NCBI database under reference numbers OK136178 and OK216140. The *Ecklonia. radiata* raw short read sequence data is deposited under NCBI BioProject PRJNA790643.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.aquabot.2021.103485.

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