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Life history bias in endophyte infection of the Antarctic rhodophyte, *Iridaea cordata*

Abstract: Endophytic organisms are known to have varied effects on their host organism in terrestrial and marine environments. In previous studies on marine algae, these symbioses range from innocuous to pathogenic depending on the host and endophyte species. The present study further assessed a pathogenic relationship between filamentous algal endophytes and a red algal host from the western Antarctic Peninsula. We analyzed endophyte presence (appearance of filamentous thalli) in the three life history stages of *Iridaea cordata* and potential impacts on fertility in the fertilized female gametophytes (carposporophytes) and tetrasporophytes. We found that endophytes proliferate throughout significantly more thallus area in tetrasporophyte and unfertilized gametophyte hosts than in carposporophyte hosts, but there was no correlation between endophyte cover and fertility in these individuals. This study also provides a demographic analysis of *I. cordata* populations surrounding Palmer Station, Antarctica, showing that these populations are haploid dominated (~78% of individuals). The differential presence of filamentous algal endophytes indicates that endophyte pathogenicity indirectly has greater effect on tetrasporophytes and unfertilized gametophytes than on the carposporophytes, which house the products of sexual recombination.

Keywords: Antarctica; endophyte; *Iridaea cordata*; life history; symbioses.

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Introduction

The shallow coastline along the western Antarctic Peninsula is often dominated by large algal communities (Wiencke and Amsler 2012). *Iridaea cordata* (Turner) Bory de Saint-Vincent is a member of the Gigartinaceae and common in shallow sub-tidal communities but can be found down to a depth of 30 m (Amsler et al. 1995, Wiencke and Clayton 2002, Wiencke and Amsler 2012). This is a dominant species in shallow basins and newly exposed substrata (Quartino et al. 2013), suggesting that it is a good colonizer. The life history of *I. cordata* is characterized by triphasic isomorphic alternation of generations and both sporophytes and gametophytes have been described, although male gametophytes may be rare (Wiencke and Clayton 2002). This species is a pseudo-perennial seasonal responder: growth initiates with lengthening photoperiod and a portion of its thallus is shed every year (Wiencke and Clayton 2002). Morphologically, the Antarctic *I. cordata* resembles *I. cordata* from South America (type locality), but there is >3% dissimilarity in *rbcL* genes, indicating that the Antarctic entity is probably a different species (Hommersand et al. 2003, 2011). However, until a formal taxonomic reappraisal is done, "*I. cordata*" is the appropriate name for the Antarctic entity.

Many of the algae in this geographic region are a host to filamentous algal endophytes (Peters 2003, Amsler et al. 2009). The prevalence of these endophytes is probably a result of intense mesograzer pressure within chemically defended macroalgal canopies (Amsler et al. 2014). The effect of these algal endophytes on their algal hosts has been investigated using various parameters of the host in nine common macroalgae from the area (Schoenrock et al. 2013, in press). Species that exhibited negative impacts of endophyte infection were differentially affected: *Pachymenia* sp. (Hommersand, personal communication) showed a decrease in thallus toughness, *Trematocarpus antarcticus* (Hariot) Fredericq & R.L. Moe and *Gymnogongrus turquetii* Hariot grew less when endophyte infection was abundant throughout the thallus, and *I. cordata* grew less with widespread endophyte presence and host photosystems had lower maximum quantum yield adjacent to endophyte presence (Schoenrock et al. 2013, in press). However, many macrophyte species were not affected, highlighting

variability in the symbioses between Antarctic algal hosts and algal endophytes. Parameters measured in previous studies were those that directly contribute to the fitness of an algal host, but actual impact on reproduction was not quantified in any species.

In *I. cordata*, endophytic species are located throughout the thallus but rarely penetrate the cortical cell layer in any life history stage. These endophytes are mostly green filamentous algae (observation), although three brown endophyte genotypes, one unique to *I. cordata*, grew in culture when removed from mesograzer pressure (Amsler et al. 2009). Pathogenicity (i.e., galls or deterioration of host) is not visually apparent in *I. cordata* as it can be in other host species (Correa et al. 1994, Gauna et al. 2009, Thomas et al. 2009), and endophyte presence does not weaken thallus toughness or change palatability to sympatric mesograzers (Schoenrock et al. in press). Despite molecular identification of brown endophytes and ongoing identification of green endophytes, it is impossible to determine which species drive pathogenicity in the host, *I. cordata*. In some species, endophyte infection can be considered an infectious disease and be extremely destructive (Fujita et al. 1972, Ishikawa and Saga 1989, Correa et al. 1994, Potin 2012), removing the host from populations (Goff and Cole 1976, Buschmann et al. 1997) as well as the pathogen (Toft and Karter 1990). Removal would ultimately decrease the fitness of a host (perhaps as well of the pathogen), but currently there are few studies that translate the effect of endophyte infections to the fitness of the host algae.

Endophyte infection has varied effects on different life history stages of the related marine rhodophyte, *Chondrus crispus* Stackhouse (Gigartinaceae). The endophyte *Achrochaete operculata* J.A. Correa & R. Nielsen infects the sporophytes of *C. crispus* profusely, causing bacterial infection and deterioration of the thallus, but does not penetrate the cortical layer of gametophytes (Correa et al. 1988, Correa and McLachlan 1991, 1992, 1994). These life history stages differ in sulphation patterns of their extracellular matrix carrageenans (Bouarab et al. 1999); λ-carrageenan oligosaccharides in sporophytes elicit a H_2O_2 response from the endophyte *A. operculata*, which triggers a molecular cascade resulting in increased pathogenicity of specific polypeptides of *A. operculata* (Bouarab et al. 1999). κ-carrageenans in gametophytes hinder carrageenolytic responses in *A. operculata* and enhance pathogen recognition by the host, which responds to the endophyte with a H_2O_2 response 10–15 times greater than that of the sporophyte (Bouarab et al. 1999). In *Iridaea laminarioides* [=*Mazaella laminarioides* (Bory de-Saint Vincent) Fredericq], another pigmented endophyte, *Endophyton* sp., causes serious degradation in both gametophytes and sporophytes equally (Correa et al. 1994). Other studies have shown that endophyte presence, especially in the reproductive structures of an alga, can decrease the fitness of specific life history stages in their host species (Muller 1996, Faugeron et al. 2000).

The goal of the present study was to elucidate endophyte impact on the fitness of *I. cordata* by evaluating endophyte coverage and fertility in all life history stages. In order to assess the impact of variation in endophyte infection between stages in *I. cordata*, it is necessary to ascertain the species demography in the study area (Thornber et al. 2006). Isomorphic life history stages thrive in stable conditions like those found in Antarctica (John 1994, Wiencke et al. 2007), but the haploid to diploid ratio within populations can impact the life history cycle of a species. Many algal populations are sporophyte dominated (De Wreede and Klinger 1988), including rhodophytes in Gracilariaceae and Ceramiaceae, but Gigartinaceae populations are often gametophyte dominated (Fierst et al. 2005).

Haploid:diploid ratios shift when spore recruitment, coalescence, fecundity, fertilization success, survival, and disease differentially impact life history stages within a species (Carrington et al. 2001, Thornber et al. 2006, Krueger-Hadfield et al. 2013). Densities of asexually reproducing organisms are known to increase towards margins of a population, in what is termed geographic parthenogenesis (Craigie and Pringle 1978, De Wreede and Klinger 1988). Populations under adverse conditions, such as the cold temperatures or high disturbance levels characterizing the western Antarctic Peninsula, are hypothesized to be sporophyte dominated (Hansen and Doyle 1976) because diploid individuals have the ability to mask mutations (increased genetic variability; Sosa and Garcia-Reina 1992) and adapt quickly to environmental variation (Bell 1982). Still, there is no pattern describing every species population (De Wreede and Green 1990). By coupling population demography with differential endophyte presence and impacts on fertility in the sexual life histories of *I. cordata*, we can infer how the known pathogenicity of these predominantly green endophytes (Schoenrock et al. 2013, Schoenrock 2014) affects the fitness of populations along the western Antarctic Peninsula.

Materials and methods

The present study was conducted within the archipelago surrounding the United States Antarctic Programs Palmer

Station, located toward the south of Anvers Island along the western Antarctic Peninsula (Figure 1). Using SCUBA, individuals were collected from six locations where *Iridaea cordata* is relatively abundant: the Bahia Paraiso shipwreck near De Laca Island (site a; 64° 46.829′S 64° 05.749′W) at a depth of 6 m; Bonaparte Point (site c; 64° 46.679′S 64° 04.013′W) at a depth of 4 m; Kristie Cove at a depth of 6 m (site b; 64° 46.912′S 64° 02.989′W); the southeast cove of Shortcut Island (site d; 64° 46.991′S 64° 02.379′W) at a depth of 4 m; Stepping Stones Island (site e; 64° 47.111′S 64° 59.691′W) at a depth of 4 m; and the northern cove at Laggard Island (site f; 64° 98.374′S 64° 00.720′W) at a depth of 5 m. A 1 m^2 quadrat was randomly placed over dense crops of *I. cordata*, and all *I. cordata* individuals within the quadrat were collected. This procedure was always done without identifying the reproductive stages to eliminate sampling bias. Sampling was done twice in 2011: March and late May, which represent autumn and early winter in the Antarctic Peninsula region.

Individuals were immediately transported to Palmer Station; 50 individuals from each site were blindly chosen from the sampling bag to be photographed on a fluorescent light table for use in image analysis. Life history stages were identified visually on the basis of the reproductive structure or lack thereof, and the image analysis program CPCe (Kohler and Gill 2006) was used to determine sporangial density and percent cover of endophyte presence in individuals. Sporangial density (sporangia cm^{-2}) was calculated by averaging the number of cystocarps or tetrasporangia within five 1 cm^2 quadrats along a transect from the stipe to the distal end of an individual. Endophyte presence was determined as a percentage of the host covered (cm^2 endophyte cm^{-2} blade).

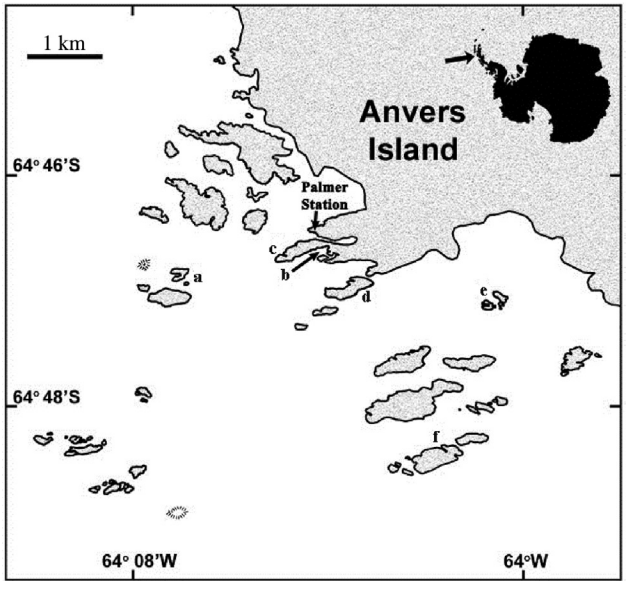

Figure 1 Map of collection sites in the archipelago surrounding Palmer Station, Antarctica: (a) the Bahia Paraiso shipwreck, (b) Kristie Cove, (c) Bonaparte Point, (d) southern cove on Shortcut Island, (e) Stepping Stones, and (f) northern cove on Laggard Island. Inset: Antarctic continent, with arrow indicating position of Anvers Island along western Antarctic Peninsula.

Life history stages

Life history stages were easily identified in lab and grouped as female gametophytes with carposporophytes (hereafter simply referred to as carposporophytes), tetrasporophytes, or "sterile" gametophytes. Sterile individuals were identified as gametophytes by characterizing carrageenan content. A total of 10 individuals of each apparent life history stage were sub-sampled from the collections, frozen at -20°C, and shipped back to the University of Alabama at Birmingham (UAB). At UAB, each blade was thawed, patted dry with lab towels, and a 1.2 cm diameter disk was excised and placed in a 10 ml test-tube. These disks were treated with resorcinol-acetal test reagent and incubated for 1 min at 80°C following the methods of Garbary and DeWreede (1988). Using this reaction, the haploid (κ-carrageenan) and diploid (λ-carrageenan) individuals were distinguishable. All sterile gametophytes and carposporophytes contained κ-carrageenan and were grouped as haploid individuals.

Given that individuals were randomly sampled from each site during the two sampling periods, they are assumed to be representative of each population. A Goodness-of-Fit test was used to determine whether populations deviated from the expected ratio of √2:1 (haploid:diploid) within each site for each season, assuming they have life history stages that have equal fitness (Destombe et al. 1989, Thornber and Gaines 2004). The haploid:diploid ratios at all sites were compared between seasons using a paired t-test (SPSS ver. 22, IBM, Foster City, CA, USA) to evaluate whether population demography shifts with season (De Wreede and Green 1990). Endophyte percent coverage data were arc-sin transformed and fertility data were square root transformed to fit the assumptions of normality for all statistical tests. To determine whether the populations at each site and time could be grouped in further analyses, the percent cover of endophyte presence was used to calculate a Bray-Curtis (BC) similarity matrix with the factor site and collection season. A CLUSTER analysis with a SIMPROF test was run using the BC matrix to show similarities between sites and sampling times using PRIMER (v6.3, UK) (Clarke and Gorley 2006).

Endophyte coverage and fertility

Because all the collection sites are similar in terms of exposure (sheltered coves) and other physical features (depth), and there was no significant structure found in site data using the CLUSTER analysis (SIMPROF; p=0.67), the populations were grouped. To determine differences in endophyte presence between life history stages (sterile gametophytes, carposporophytes, and tetrasporophytes), all sites and seasons were grouped for each collection time, and a one-way ANOVA was used to compare percent cover of endophyte (dependent variable) and life history stage (independent variable). To determine the effect of endophyte cover on fertility of the host, all sites and seasons were grouped and correlations were used to determine if sporangial density (dependent variable) varied with percent cover endophytic algae (independent variable) in both tetrasporic and carposporic life history stages.

Results

Life history stages

The goodness-of-fit test showed that most sites in all seasons had significantly more haploid individuals than expected, with the exception of Shortcut Island (autumn and winter) and the Bahia Paraiso (early winter), which had even ratios (Table 1). Only the winter population of Shortcut Island exhibited the expected haploid:diploid ratio. Overall, the population surrounding Palmer Station had a haploid to diploid ratio of ~3:1 (the populations are 78% haploid). We saw no change in most haploid:diploid ratios between autumn and early winter (paired t-test; p=0.279). However, there was a trend for a decrease in the percentage of carposporophytes between autumn and winter (large decreases at two collection sites, Kristie Cove and the Bahia Paraiso, with moderate to very small decreases at the other four sites; Figure 2). A Bray-Curtis similarity matrix and CLUSTER analysis with SIMPROF test showed that all sites exhibited extreme likeness in fertility and endophyte presence through both seasons.

Endophyte coverage and fertility

The one-way ANOVA showed significant differences in endophyte cover between life history stages (F=11.484, p<0.0005, Figure 3). A Tukey's HSD test showed significantly more endophyte coverage in the tetrasporophytes and gametophytes than in carposporophytes. There was no correlation between endophyte coverage and fertility in either tetrasporophytes or carposporophytes (Pearson correlation=0.082 and -0.037, respectively; p=0.226 and 0.626, respectively).

Discussion

Demographical information about populations of species is fundamental to understanding the species contribution to ecosystem processes, especially for the present study

Table 1 Haploid to diploid ratios and results from the goodness-of-fit test at all sites in both seasons.

Site	Season	Individuals		Ratio	G	p-Value
		Haploid	Diploid			
Bonaparte Point	Autumn	81	31	2.62:1	9.147	0.002
	Winter	66	14	4.72:1	21.076	4.41^-6
Kristie Cove	Autumn	59	8	7.38:1	28.2	1.09^-9
	Winter	67	11	6.09:1	27.589	1.5^-7
Bahia Paraiso	Autumn	82	36	2.28:1	6	0.014
	Winter	21	29	1:1.38[a]	5.552	0.018
Shortcut Island	Autumn	138	44	1:1.04[a]	23.838	1.05^-6
	Winter	108	90	1.2:1[a]	1.316	0.251[b]
Laggard Island	Autumn	61	15	4.07:1	16.183	5.7^-4
	Winter	109	8	13.63:1	72.325	1.85^-17
Stepping Stones	Autumn	94	3	31.3:1	79.068	6^-19
	Winter	57	25	2.28:1	4.186	0.041

[a]Indicates haploid:diploid ratio that is almost even.

[b]Indicates haploid:diploid ratio that is expected (Thornber and Gaines 2004); ^ indicates 10 × the given integer.

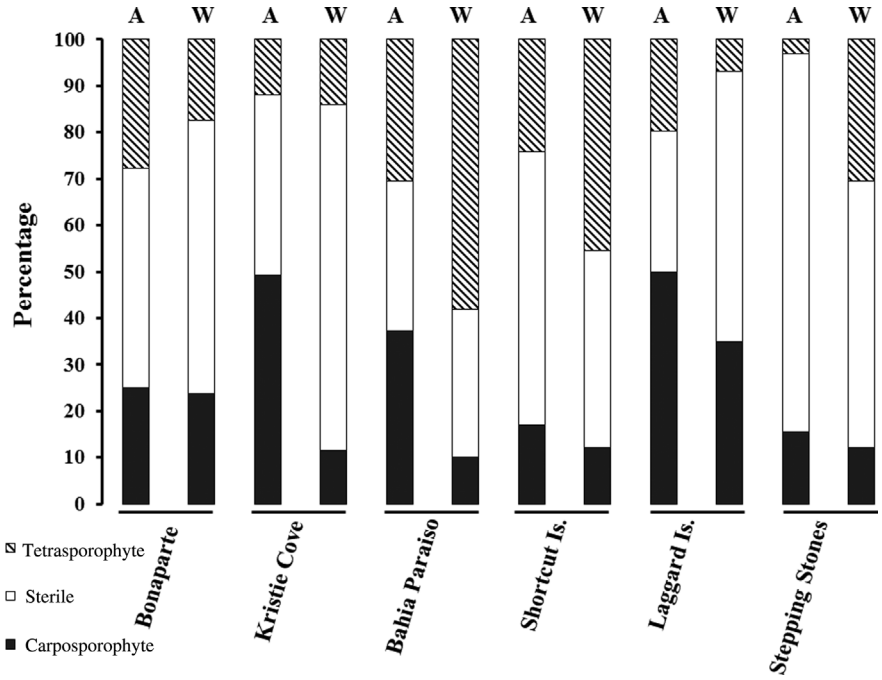

Figure 2 Percentage of *Iridaea cordata* life history stages at each site in each season. A, Autumn; W, winter.

because we investigated isomorphic life history stage response to endophytic algae. In *Iridaea cordata*, endophytes are known to be pathogenic (Schoenrock et al. 2013, in press), making any differential presence of endophytes and impacts on fitness important in the ecology of this species. Populations of *I. cordata* around Palmer Station are haploid dominated; fertilized gametophytes with cystocarps and sterile gametophytes (presumably both male and female) are more abundant than tetrasporophytes. Although variation in endophyte presence did not impact fertility in any stage, the lower incidence of endophytes in the carposporophytes is ecologically relevant as they represent individuals who amplify the products of sexual recombination (Searles 1980).

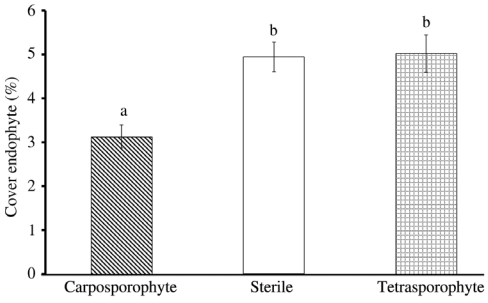

Figure 3 Endophyte coverage in different life history stages of *Iridaea cordata*. Different letters indicate significance at p=0.05 (one-way ANOVA).

The lower incidence of endophytes in the cystocarpic female gametophytes can be ecologically important in two ways: fertilization of the female gametophyte may be more successful in individuals with lower endophyte coverage or fertilization may stimulate defence against endophyte settlement and proliferation. Defences in the gametophytes of *Chondrus crispus* protect them from expansive endophyte coverage (Bouarab et al. 1999), and this may occur in the Antarctic *I. cordata* as well, although in *I. laminioides* carrageenans had no affect on the *Endophyton* sp. infections (Correa et al. 1994). To date, there are no known defences against endophyte settlement in *I. cordata,* but carrageenan content of life history stages is consistent in the Gigartinaceae (Shaughnessy and De Wreede 1991 and references therein), which indicates that known sulphation of these compounds (Foltran et al. 1996) may trigger a defence response as seen in *C. crispus* (Bouarab et al. 1999). A previous study showed that this species can produce reactive oxygen species (ROS) in response to wounding (McDowell et al. 2014), although it is uncertain whether a life history stage would produce more ROS in response to stimuli such as endophyte presence.

In the present study, fertility was not correlated with endophyte presence in any life history stage of *I. cordata*. Germination potential or fecundity of the reproductive

structures was not examined (Santelices and Martinez 1997, Faugeron et al. 2000), but endophyte structures were never seen proliferating throughout tetrasporangia or cystocarps, indicating there is no mechanical damage to reproductive structures. Indeed, endophyte filaments rarely penetrate the cortical layer of these life history stages, and both tetrasporangia and cystocarps develop in the medulla just below the cortical layer (Wiencke and Clayton 2002). This study provides a reason to investigate reproductive potential in individuals given that the presence of reproductive structures does not ensure successful spore release and germination. Potential defences against endophyte settlement and proliferation in carposporophytes should be evaluated as well. The two potential mechanisms suggested (i.e., fertilization of gametophytes with low infection or defence against infection after fertilization) can be elucidated by fertilizing female gametophytes with a range of endophyte coverage and experimental inoculation of previously fertilized individuals. Very little is known about the settlement and establishment of Antarctic algal endophytes. Therefore, we do not suggest that the endophytes die off and recolonize *I. cordata* within a growing season (Austral summer). It is very likely that they establish a presence in algal thalli early in the growing season because they grow so slowly in culture (personal observation).

Annual shifts between haploid and diploid dominance are not uncommon in algal populations (De Wreede and Klinger 1988, De Wreede and Green 1990). In the Austral autumn-winter of 2011, populations in the Palmer area were 78% haploid and 22% diploid, or consisted of 24% tetrasporophyte, 51% sterile gametophytes, and 25% carposporophytes (Figure 2). Haploid dominance may drive the observed fertilization success: ~30% of gametophytes found in the field. Because the deleterious effects of endophyte infection are less likely to occur in carposporophytes (less endophyte coverage), the fitness of this life history stage is probably amplified, which may result in diploid dominance the following season if reproductive potential is not impacted. Because both sporophyte and gametophyte dominance have been documented for the entity previously called *I. cordata* in the western USA [=*Mazzaella splendens* (Setchell & N.L. Gardner) Fredericq] (Hansen 1977, May 1986), this could be tested over multiple years using modern techniques like rapid gender testing (Huan et al. 2013). However, the observed pathogenicity of these endophytes could also select for haploid dominance in these populations because tetrasporophytes have more endophyte coverage.

We found that *I. cordata* populations along the western Antarctic Peninsula are haploid dominated in the Austral autumn-winter and the carposporophytes have significantly less endophyte presence. This difference between the life history stages of the Antarctic *I. cordata* could have ecologically significant influences on population demography. The main findings of this research should be further supported by investigating the dominant ploidy level in *I. cordata* populations over multiple years, endophyte effects on reproductive potential in gametophytes and sporophytes, and host defences against endophyte settlement and proliferation, specifically in the fertilized female gametophytes.

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