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Clump structure, population structure and non-destructive biomass estimation of the New Zealand carrageenophyte *Sarcothalia lanceata* (Gigartinaceae, Rhodophyta)

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Abstract: *Sarcothalia lanceata* is a New Zealand carrageenophyte with tetrasporophytic thalli that produce carrageenan very close to the idealised structure of lambda-carrageenan. As such there is interest in its potential for commercial utilisation. There is no information on the biology and ecology of natural populations of this species, but this knowledge is critical for determining whether a species is a suitable candidate for sustainable wild harvest or for aquaculture. Population studies were conducted at two sites in New Zealand's South Island in order to provide fundamental information on this species. The structure (abundance and composition of male, female, tetrasporophytic and non-reproductive clumps) of the two populations was assessed monthly over a year, and population biomass estimated using regression methods. Seasonal variation was not evident in most of the parameters measured, but differences between sites were found in total population density, the density of different life-history phases, and clump size and structure. The turnover in biomass occurs more frequently at the blade

level than at the clump level and the presence of a basal crust in this species promotes population stability.

Keywords: carrageenophyte; New Zealand; population structure; *Sarcothalia lanceata*.

Introduction

Members of the Gigartinaceae contain variants of the polysaccharide carrageenan, which is widely used as a thickener and gelling agent. The commercial value of carrageenans means that many gigartinacean species have been the subject of ecological investigations (e.g. Hansen and Doyle 1976, Hansen 1977, Dyck et al. 1985, Levitt et al. 1995, Avila et al. 1996, Otaiza et al. 2001, Scrosati 2001). Information on the biology and ecology of natural populations is critical for determining whether a species is a suitable candidate for sustainable wild harvest, and also whether or not the species has potential as a candidate for aquaculture. It is particularly important to document the relative abundance and stability over time of the various life-history phases within those species where the gametophytes and tetrasporophytes produce different carrageenans.

Phase dominance in species of the Gigartinaceae varies, ranging from gametophytic dominance of populations (e.g. Dyck et al. 1985, May 1986, Zamorano and Westermeier 1996, Scrosati 1998a, Pacheco-Ruiz and Zertuche-Gonzalez 1999, Westermeier et al. 1999, McLachlan et al. 2011), tetrasporophytic dominance of populations (e.g. Hansen and Doyle 1976, Hansen 1977, Craigie and Pringle 1978, Bhattacharya 1985, Dyck et al. 1985, Lazo et al. 1989) and alternation between the two over time (e.g. De Wreede and Green 1990, Bolton and Joska 1993, Dyck and De Wreede 1995, Avila et al. 1996, Piriz 1996, Avila et al. 1999, Otaiza et al. 2001). Different patterns in phase dominance can also occur within the same genus (e.g. De Wreede and Green 1990), and among populations of the same species (Mathieson and Burns 1975, Dyck et al. 1985, Mudge and Scrosati 2003, Thornber and Gaines 2003, Guidone and

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Grace 2010, Garbary et al. 2011). Differentiation between male gametophytes and female gametophytes in the field is not common among the Gigartinaceae (Thornber 2006), but has been reported for *Chondrus verrucosus* (Mikami 1965) (Bellgrove and Aoki 2008).

The maintenance of phase dominance or the occurrence of phase alternation has been attributed to ecological differences between phases (Scrosati and De Wreede 1999), and may be driven by demographic and reproductive mechanisms (May 1986). These ecological patterns include differences among life-history phases in terms of: growth; density; spatial and temporal distribution; perennation; biomechanical properties; salinity; desiccation tolerance; fertilisation success; spore production, germination and survival; and susceptibility to grazing (Craigie and Pringle 1978, Hannach and Santelices 1985, May 1986, Luxoro and Santelices 1989, De Wreede and Green 1990, Dyck and De Wreede 1995, Avila et al. 1996, Lindgren and Åberg 1996, Carrington et al. 2001, Fierst et al. 2005, Guidone and Grace 2010, McLachlan et al. 2011). However, Scrosati and De Wreede (1999) stressed the need for a combination of modelling and fieldwork to understand the G:T ratio within populations.

Sarcothalia lanceata (J. Agardh) Hommersand (Gigartinaceae, Rhodophyta) is a red seaweed endemic to New Zealand. It occurs between 41.5° and 51° S on the South Island as well as on the Chatham Islands, Stewart Island, and a number of sub-Antarctic islands (Chapman 1979, Adams 1994 as *Gigartina lanceata*, Nelson 2013). *Sarcothalia lanceata* inhabits the lower intertidal and upper subtidal zones of exposed rocky shores and has a triphasic life history with an isomorphic alternation of generations. This species is a carrageenophyte, with gametophytes and tetrasporophytes containing kappa- and lambda-type carrageenans, respectively (Pickmere et al. 1975). The structure of the carrageenan from the tetrasporophytic life stage of *S. lanceata* is close to the idealised structure of lambda-carrageenan (Falshaw and Furneaux 1998), and has commercial potential as a thickener and stabiliser in food uses. The market for carrageenan-producing seaweeds continues to grow (Bixler and Porse 2011), but opportunities for the commercial use of wild seaweed stocks remain largely unexplored in New Zealand and collection is still managed under a permit system (see Hurd et al. 2004).

The lamina or blades of *S. lanceata* are predominantly lanceolate (strap-like) and a large number of blades (ramets) arise from a basal crust on short stipes forming a “clump” (= genet) (Figure 1). Blades are sometimes covered with surface or marginal proliferations (Adams 1994) but blades with sterile margins (up to 5 mm wide) are also found (Chapman 1979). Each clump contains a mixture

of fertile and vegetative (non-reproductive) blades. Fertile female blades are easily recognisable by their large, raised cystocarps (Figure 1A). In contrast, male blades are pale and thin (Figure 1A) while tetrasporophytic blades are robust (Figure 1B) and have tetrasporangia scattered over the blades in rounded sori (only visible at high magnification in this image) (Nelson 2013). Mature male thalli of *S. lanceata* are easily distinguishable from female gametophytes and tetrasporophytes in the field; male blades are

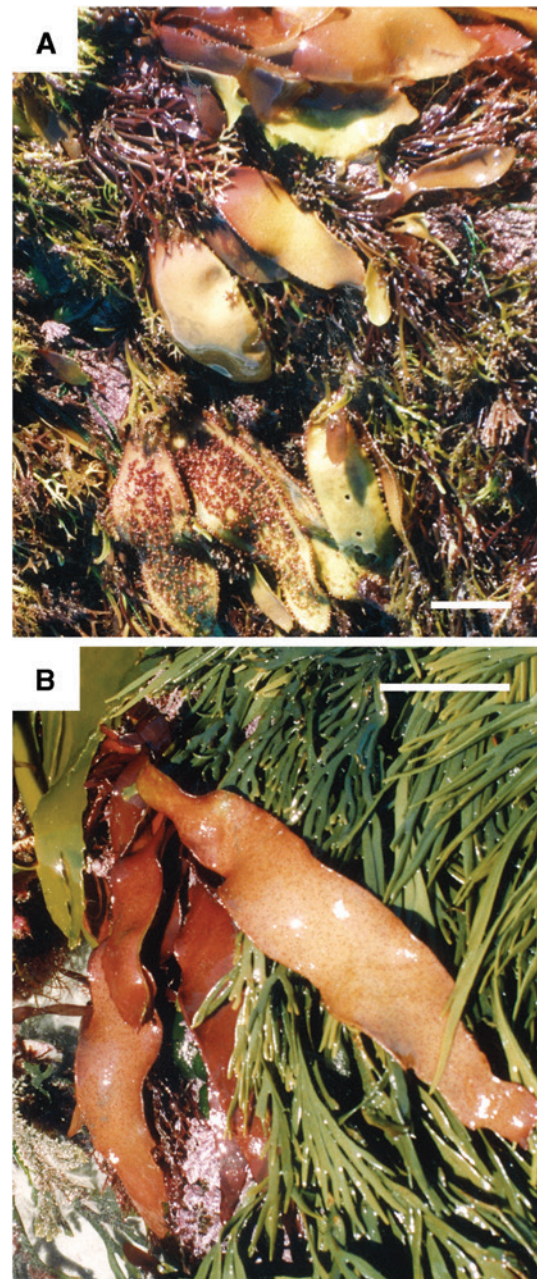


Figure 1: *Sarcothalia lanceata*: (A) Male gametophytes are thin and pale and are shown above, with female gametophytes bearing large cystocarps below. (B) Tetrasporophytes. Scale bars = 10 cm.

wider, of thinner texture and have no visible reproductive structures.

This paper describes a fundamental assessment of two populations of *S. lanceata* from Otago, South Island, New Zealand. The aim of this work was to identify and quantify any differences in population structure between the two sites, with a view to potential utilisation. The characteristics of population structure assessed were clump size and structure, clump densities and the ratio of gametophytes to sporophytes. The following questions were addressed: (i) were temporal changes evident in population structure; (ii) were there differences between the two populations; and (iii) could *S. lanceata* biomass be estimated using non-destructive methods? Factors affecting or regulating populations are discussed, along with differences between populations.

Materials and methods

Study sites

Two *Sarcothalia lanceata* populations on the Otago coastline were selected for this study (Figure 2): Murdering Beach (45.759978° S, 170.674067° E) and Purakaunui (45.739555° S, 170.629692° E). Both were situated in small crescent shaped bays on rocky headlands at the eastern ends of the sandy surf beaches. The intertidal region in each site was gently sloping, consisting of jumbled boulders and cobbles interspersed with areas of shell gravel and sand. At Murdering Beach, the boulders were predominantly phonolite (a fine-grained volcanic igneous rock), while, at Purakaunui, the beach was dominated by scoriaceous and vesicular basalt boulders interspersed with phonolite boulders. At Purakaunui, the large “bull kelp” *Durvillaea antarctica* (Chamisso) Hariot was notably more common than at the Murdering Beach site, which is indicative of greater wave exposure.

Clump structure

Throughout this paper, the growth form of *Sarcothalia lanceata* (crust and blades combined) is referred to as a clump and was the individual sampled in order to determine the proportions of different life-phases within a population. To be considered genets, the individuals sampled should be spatially separated from each other (Scrosati 1998a) and have developed from one original zygote or spore (Scrosati 2002). In this study, clumps



Figure 2: *Sarcothalia lanceata* study sites: map showing location of sampling sites Murdering Beach ($45^{\circ}46'S$, $170^{\circ}40'E$) and Purakaunui ($45^{\circ}45'S$, $170^{\circ}37'E$). Both sites are situated north of Dunedin on the Otago coastline of the South Island, New Zealand.

were considered to be separate genets where their basal crusts were separated by at least 2 cm. Two to three small (< 50 mm) non-reproductive blades were collected from each of 32 *S. lanceata* clumps (16 female and 16 tetrasporophytic), and were tested with the resorcinol reagent (Garbary and De Wreede 1988) to investigate their ploidy levels and to determine if clumps contained more than one life phase.

Random paired co-ordinates were generated using a restricted randomisation method and were used to select eight points below the upper edge of the intertidal zone. At each point, the nearest female, male and tetrasporophytic clumps were located and tagged with electrical ties giving a total of 24 tagged clumps in each study area. Individual clumps were identified by fitting different combinations of coloured plastic tubing over each electrical tie. Any lost tagged clumps or blades were continually replaced with other nearby clumps to maintain the required numbers of replicates.

Each month, clump sizes were measured by counting the numbers of blades present in each of nine 50-mm size classes (i.e. 0–50 mm, 51–100 mm ... > 400 mm). The numbers of blades in each size class were averaged across

clumps to provide a mean ($n=6-8$, \pm SE) for each life-history phase.

Population structure

The density and composition of each population were assessed between November 1999 and October 2000. Sampling events were undertaken during low-water tides at approximately 28-day intervals. Sampling was carried out at Murdering Beach from November 1999 to October 2000 (13 sampling events), and at Purakaunui from January 2000 to October 2000 (11 sampling events). Two sampling events fell within August 2000 and these are referred to as August 1 (A1) and August 2 (A2).

At both sites, a 60-m transect was established along the upper edge of the intertidal zone. For each sampling event, 21 sets of co-ordinates were randomly generated using a restricted randomisation method and used to place and sample 21 quadrats (0.5 m^2 , approximately $0.71 \times 0.71 \text{ m}$) within the area 3 m below the transect (giving a study area of approximately 180 m^2). The numbers of gametophytic (females and males), tetrasporophytic, and non-reproductive clumps were counted within each quadrat.

Biomass estimation

Biomass was estimated monthly by establishing a relationship between blade length (mm) and wet weight (g) to avoid the necessity of regular destructive harvests. A single destructive harvest was carried out in March 2000 in the area immediately adjacent to the Purakaunui sample site. Numerous clumps of each of the three life-history stages (female, male and tetrasporophytic) were haphazardly collected, placed in three large plastic bags and transferred to the laboratory (1 h away) in a plastic cooler. In the laboratory, each blade was washed with clean seawater, dabbed dry with a paper towel, picked or scraped clean of obvious epibionts, weighed and the length measured to the nearest millimetre. A total of 550 female, 501 male and 590 tetrasporophytic blades were weighed and measured.

The data for each life-history stage were used to generate wet weight vs length regression equations. In cases where the blades were not simple, but were divided (i.e. they were “v” shaped or palmate), they were treated as consisting of primary and secondary blades, and were entered into the regression equations as two separate lengths.

Length and weight data for each life-history phase were used to obtain an average wet weight for each size class. For each clump, the number of blades in each size class was multiplied by the mean wet weight for that class, and an overall estimate of individual clump wet weight was obtained. The accuracy of this method of estimating clump wet weights was then tested. In October 2000, a further destructive harvest was carried out at Purakaunui and clumps of each life-history stage were collected and placed in individual plastic bags before being transported to the laboratory (30 min away) where the wet weight of each clump, and the lengths of all blades in that clump were measured. Lengths were then grouped by size class, and the number of blades in each size class was multiplied by the mean wet weight, minimum wet weight and first quartile (25th percentile) wet weights (derived from the previous harvest) for that class and compared with actual clump wet weights.

Statistical analysis

During the course of this research, both study sites were subject to sand inundation events. The months affected were June 2000 for Murdering Beach, and August 1, September and October 2000 for Purakaunui. Density data collected during these events were anomalous and were therefore excluded from the density analysis. However, on the assumption that those sections of the sites remaining unburied were representative of the site as a whole, data from inundation months have been included in the proportional analysis of reproductive states and life-history phases.

The number of clumps present in each 0.5-m^2 quadrat was extrapolated to clumps per m^2 in order to facilitate comparison with the published literature. For each site, clump densities were analysed using analysis of variance (ANOVA). Two-way ANOVA of square-root transformed data were used to test for the effect of season (8 to 12 levels – month) on life history phase (4 levels – female, male, tetrasporophyte and non-reproductive) and reproductive phases (2 levels – gametophytes and tetrasporophytes). Pairwise comparisons were carried out on significant results using the Holm-Sidak method. All analyses were carried out using the Systat statistics package. The square-root transformed data met the ANOVA assumptions of equal variance. Analysis of variance is sufficiently robust to deal with departures from normality, particularly where samples are balanced and of sufficient size (Underwood 1997).

Results

Clump structure

The small (<50 mm) blades tested with resorcinol indicated that the vegetative blades were of the same ploidy level as the reproductive blades from the clumps within which they were collected.

Blades in the female clumps of *Sarcothalia lanceata* at Murdering Beach occurred in every size class from 0–50 mm to >400 mm class (Figure 3A) with the longest blade measuring 612 mm in October. At Purakaunui, female blades were shorter, with the longest blades occurring in the 351–400 mm size classes (Figure 3B). This pattern was repeated in the male and tetrasporophytic clumps at both sites (Figure 3C–F). All *S. lanceata* clumps were numerically dominated by blades in the 0–50 mm size class (Figure 3A, B) and such blades comprised over 50% of the total number of blades in most months (Figure 3A–F). In the majority of the size classes of all three life-history phases, the numbers of blades did not vary significantly among months. The only exceptions occurred in the female clumps of *S. lanceata* at both sites (Figure 3A, B), where the numbers of blades in the 0–50 mm size class were significantly different among months (2-way ANOVA, $p < 0.001$ for Murdering Beach and $p = 0.018$ for Purakaunui) and were most abundant in winter and spring.

The total number of blades in clumps of *S. lanceata* did not vary significantly over time within any of the three life-history phases at either site but there were always more blades per clump at Murdering Beach than at Purakaunui ($p < 0.001$ for all; Figure 3). There were also differences among life-history phases. At Murdering Beach, female and tetrasporophytic clumps contained significantly more blades than male clumps (2-way ANOVA, $p = 0.005$), while the total number of blades in female clumps was significantly greater than either male or tetrasporophytic clumps at Purakaunui (2-way ANOVA, $p < 0.001$).

Population structure

Clump densities of the two *Sarcothalia lanceata* populations are shown in Figure 4A (Murdering Beach) and Figure 4F (Purakaunui). The sand inundation events are marked with arrows. When the sand inundation months were excluded from the analysis, there was significant seasonal variation in total population density of *S. lanceata* at Murdering Beach ($p = 0.003$), and multiple comparison

tests indicated that the differences between November and May densities at this site were significant ($p = 0.032$) (Table 1). There was no evidence of significant seasonality at Purakaunui (Table 1). There were significant differences among the densities of the life-history phases at both sites (Table 1; Figure 4B–E and Figure 4G–J). The ratio of gametophytes to tetrasporophytes (G:T ratio) at the two study sites appeared to vary over time (Figure 5) but differences between sites and months were not significant (2-way ANOVA, $p = 0.146$ and $p = 0.167$, respectively).

Estimated biomass

Results from regression analysis indicated that blade length was an effective predictor of blade weight (Figure 6). Clump weights were over-estimated by up to 25% when the average blade weight for each size class was used, and the minimum weight for each size-class led to underestimation of actual weights by up to 50%. The 1st quartile (25th percentile) of the blade weights for each class was found to give estimates of clump weight that fell within 5% of the actual clump weights (data not shown). Consequently, *Sarcothalia lanceata* clump weights of the three life-history phases were estimated from blade length size classes and 1st quartile weights for each size class (Figure 7). Female clumps were heavier than either tetrasporophytic or male clumps, and clump weights for all three life-history phases were lower throughout the year at Purakaunui than at Murdering Beach (Figure 7B). For each life-history phase, there were no significant temporal differences in estimated clump weights at either site.

Estimated biomass was also greater in all months at Murdering Beach (Figure 7C) than at Purakaunui (Figure 7D). At Murdering Beach, estimated biomass (wet weight) ranged between 44.2 and 348.9 g m⁻² for females, 39.3 and 130.8 g m⁻² for males, 88.5 and 221.6 g m⁻² for tetrasporophytes and for the total biomass 216.8 g m⁻² and 608.9 g m⁻². At Purakaunui, estimated biomass ranged between 23.4 and 99.4 g m⁻² for females, 2.5 and 33.8 g m⁻² for males, 9.8 and 77.5 g m⁻² for tetrasporophytes and total biomass varied between 35.8 and 185.3 g m⁻² (Figure 7D).

Discussion

Seasonal variation was not evident in most of the parameters measured, but differences between the sites were found in total population density, life-history phase density and clump structure. Assessment of the numerical

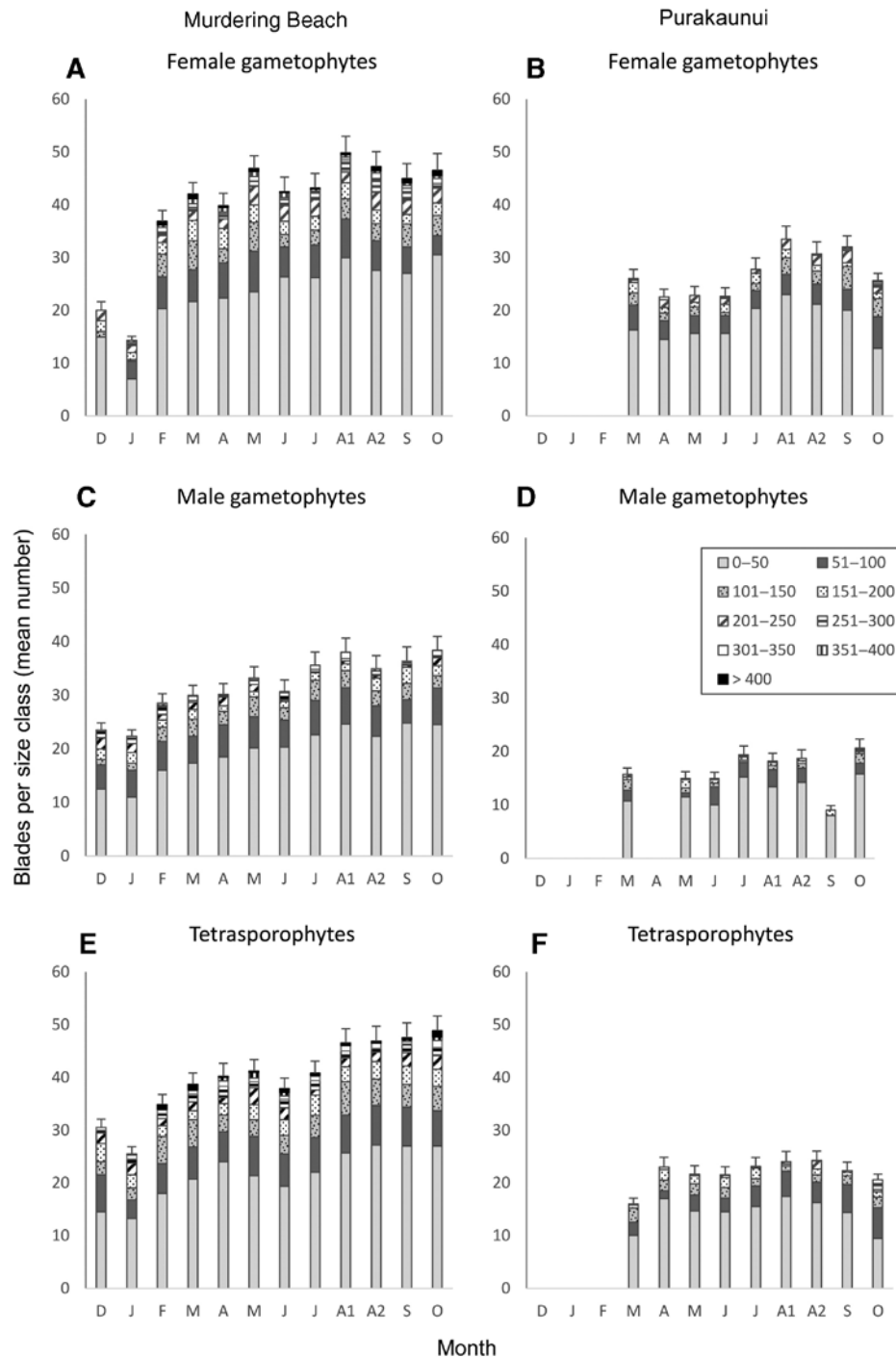


Figure 3: *Sarcothalia lanceata* clump structure: average number of blades per size class (50-mm classes) each month at Murdering Beach (A, C and E) and Purakaunui (B, D and F). Error bars are SE of the total number of blades, $n = 6-8$.

and relative abundance of life-history phases may vary according to the method of sampling. In the present study, field data were determined from the presence of reproductive structures alone and no clump was seen to contain more than one type of reproductive blade in 13 months of field observations. In addition, all non-reproductive

blades tested were of the same ploidy level as the reproductive blades from the same clump. These observations parallel those of Pickmere et al. (1975) who also tested vegetative blades taken from another large bladed New Zealand species (*Sarcothalia atropurpurea*, as *Gigartina atropurpurea*) and found they had the same ploidy levels

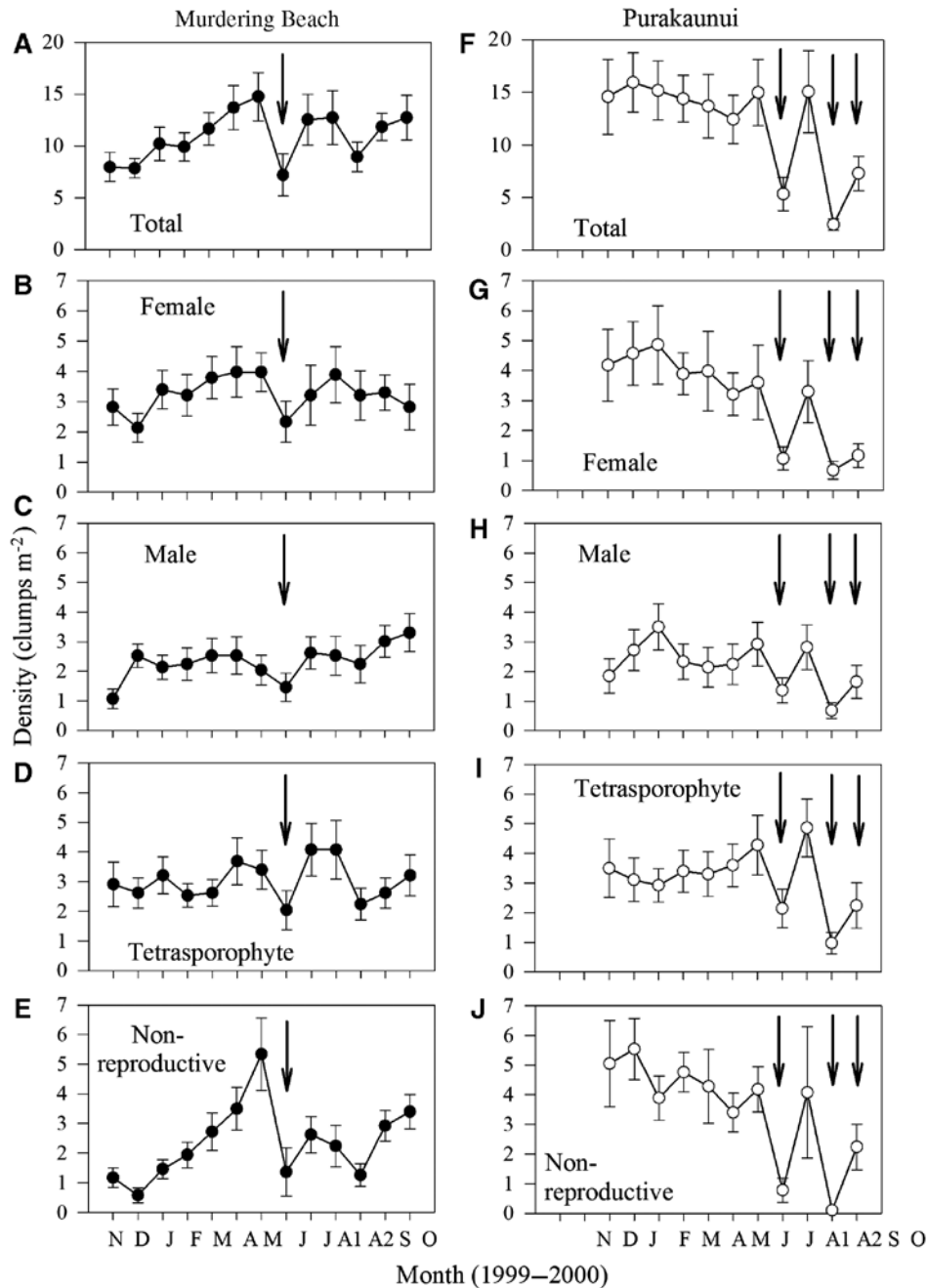


Figure 4: *Sarcothalia lanceata* clump density: clump density at Murdering Beach (A–E) and Purakaunui (F–J). Values are means ± SE, n = 21. Note the scale for panels (A) and (F) differ from the other panels. Arrows indicate sampling events affected by sand inundation.

as reproductive blades from the same individual. Although no evidence of clump coalescence was found in *Sarcothalia lanceata*, it has been reported in other members of the Gigartinales (e.g. Santelices 2004, Vera et al. 2008).

The two *S. lanceata* populations examined showed a seasonal stability in clump size, as the total number of blades within clumps did not vary significantly between months for any of the three life-history phases

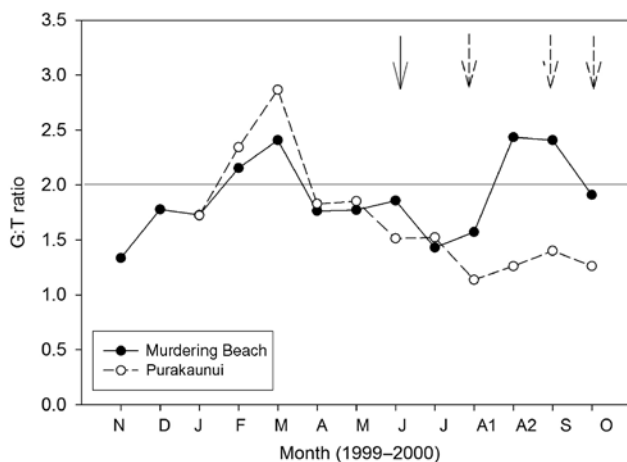
at Murdering Beach or Purakaunui. This stability may be attributable to *S. lanceata* blades eroding or tearing rather than completely detaching. A similar phenomenon has been observed in other species (Hansen and Doyle 1976, Klein 1987, Santos 1994), and may act as a dispersal mechanism in some species (Gomez and Westermeier 1991).

There was seasonal stability within most *S. lanceata* blade size classes. It is likely that new blades are initiated

Table 1: *Sarcothalia lanceata*: analysis of variance on the effects of season and life history phase on clump densities.

Source of variation	DF	SS	MS	F	p
Murdering Beach					
Month	11	30.41	2.76	2.56	0.003
Phase	3	19.09	6.36	5.90	<0.001
Month×phase	33	42.31	1.28	1.18	0.216
Residual	960	1035.56	1.07		
Total	1007	1127.38	1.12		
Purakaunui					
Month	7	12.72	1.81	1.18	0.307
Phase	3	35.59	11.86	7.75	<0.001
Month×phase	21	11.58	0.55	0.36	0.997
Residual	640	979.38	1.53		
Total	671	1039.28	1.54		
Pairwise comparisons					
Murdering Beach					
Month	May vs. Nov ^a				
Phase	Fem. vs. NR ^a and Male ^a				
	Tetra vs. NR ^a				
Purakaunui					
Phase	NR vs. Tetra ^b and Male ^b				
	Fem. vs. Tetra ^a and Male ^a				

Pairwise comparisons were carried out using the Holms-Sidak method. Bold type indicates significance at: ^a $p < 0.05$; ^b $p > 0.001$. Phases included male, female (Fem.), tetrasporic (Tetra), non-reproductive (NR). All data were square-root transformed after exclusion of sand inundation months.

**Figure 5:** *Sarcothalia lanceata*: ratio of gametophytes to tetrasporophytes (G:T ratio) at Murdering Beach (solid circles) and Purakaunui (open circles). Data from sand inundation months (arrows) are included. Solid arrow indicates inundation event at Murdering Beach, broken arrows indicate inundation events at Purakaunui.

throughout the year, and growth occurs at a constant rate, resulting in the absence of any significant seasonal variation. Seasonal variation was only evident in the 0–50 mm size class of female clumps at both sites. The

presence of papillae and large cystocarps on the surface of female blades (Figure 1A) may make them more susceptible to detachment than male or tetrasporophytic blades. However, it is unknown whether blade loss stimulates the initiation of new blades.

Sarcothalia lanceata densities were significantly reduced by sand inundation in some months of this study so comparisons between the two sites is possible only for January to May, July and August 2. Significant seasonal variation in population size (density) was evident only at Murdering Beach where a summer low occurred, followed by a peak in winter. This peak may be solely attributed to a change in density of non-reproductive blades (i.e. the development of reproductive blades), as the densities of reproductive blades showed no evidence of significant seasonality. A lack of seasonality has been reported in total population densities (e.g. Hansen and Doyle 1976) and standing crop (Santelices et al. 1989). Santelices et al. (1989) suggested that this lack of variation resulted from stability in population densities.

The presence of a basal crust is common in members of the Gigartinales and, in some species, is thought to be the primary mechanism of population maintenance (Scrosati 1999). A basal crust most likely explains the seasonal stability observed in the *S. lanceata* populations examined here. Basal crusts can act as a space saver during times of blade loss or senescence (e.g. Hansen 1977, Lazo et al. 1989, Scrosati 1999, Pratt and Johnson 2002) by preventing the establishment of other species on the substrate (e.g. Santelices et al. 1989). Basal crusts are also a survival strategy in environments where seaweeds are subjected to periodic sand inundation (Daly and Mathieson 1977, Hansen 1977, Santelices et al. 1989).

In many species, basal crusts are thought to be primarily responsible for the recruitment of new blades into populations (Lazo et al. 1989, Scrosati 1999), with recruitment from spores being more important only in times of catastrophic disturbance (Scrosati 1998b). Over a relatively short timeframe (i.e. 1 year), the stability of reproductive clump densities in the populations of *S. lanceata* studied here provide support for the role of basal crusts in population maintenance. Their longer-term role, and the role of recruitment via spore settlement, remain unknown, however.

The two populations sampled showed significant differences in both clump size and structure, and population size and structure. Clumps at Murdering Beach were larger, contained more blades, and had longer blades than clumps at Purakaunui. At both sites there were significant differences in clump density among life-history phases, and gametophytes were numerically

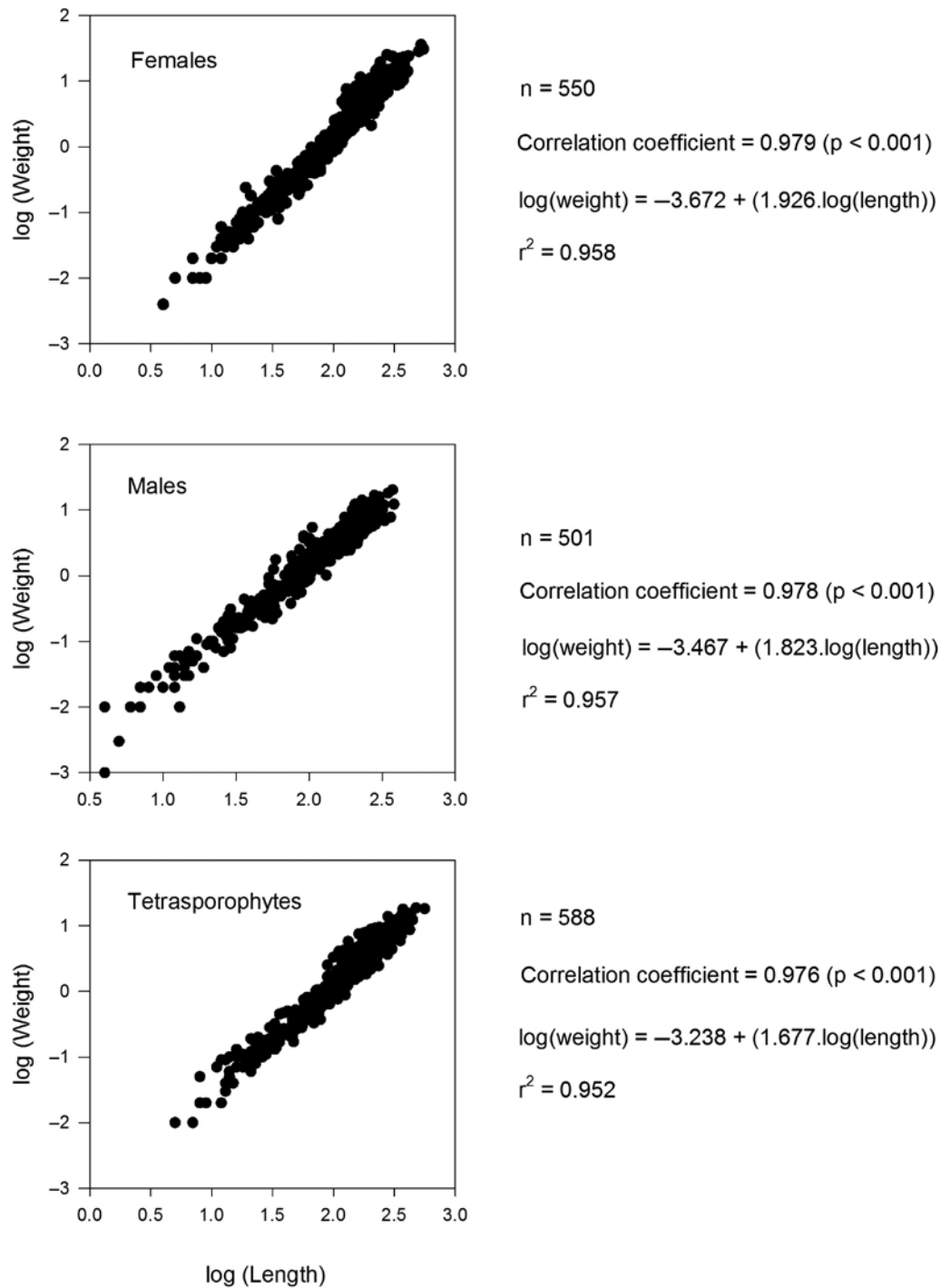


Figure 6: *Sarcothalia lanceata* biomass estimation: scatterplots showing relationship between log(blade length) and log(blade wet weight) of blades collected from Purakaunui in March 2000. Correlation coefficients and their corresponding p-values are shown, along with linear regression equations for estimating blade wet weight from blade length.

more abundant than tetrasporophytes throughout the sampling period.

Data from the months affected by sand inundation were not excluded from the analysis of life-history phase proportions on the assumption that the smaller number

of individuals counted (i.e. those unburied at the time of sampling) would still be proportionally representative of the population as a whole even though the distribution of life-history phases across the shore was not documented in this study. Differences in the vertical distribution of

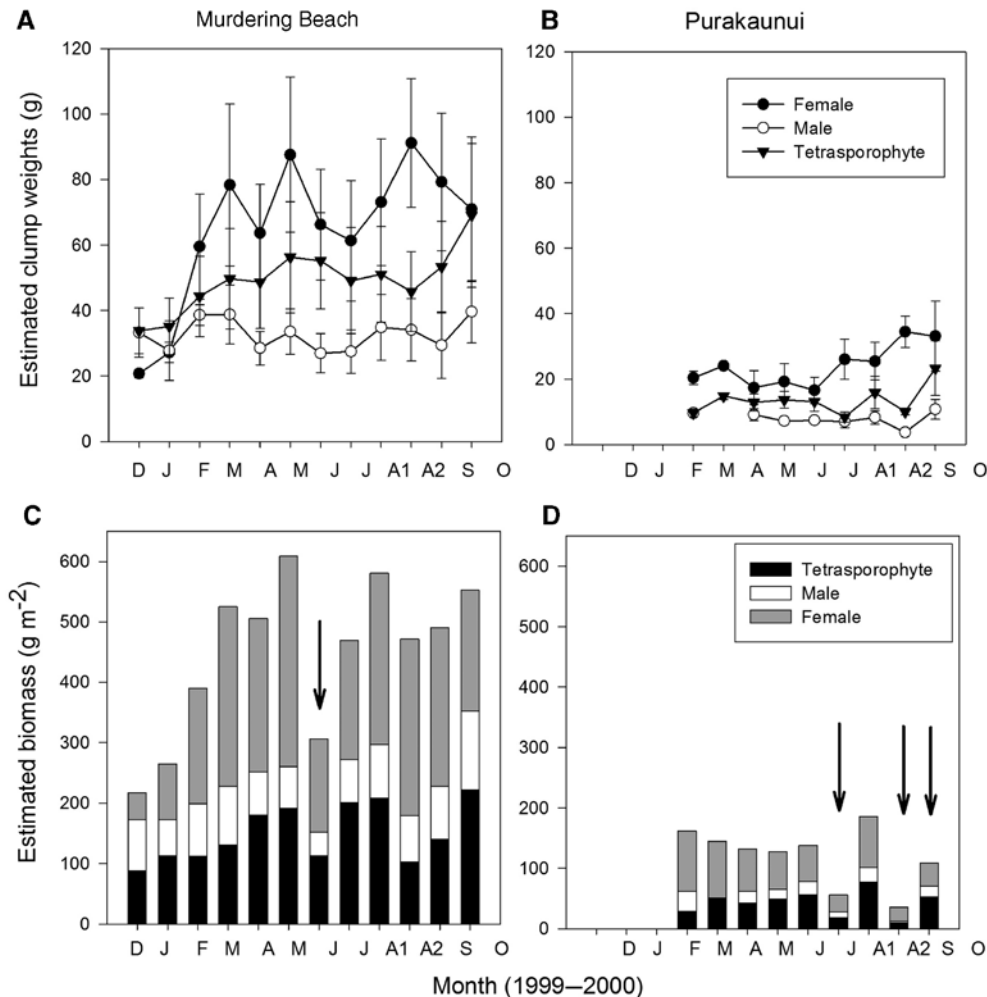


Figure 7: *Sarcothalia lanceata* biomass: estimated wet weight of clumps (A, B) and biomass (C, D). Estimates of clump wet weight were obtained by multiplying number of blades per size class by the 1st quartile weight for that class. Values in (A) and (B) are means \pm SE. Arrows mark sand inundation events at each site.

gametophytes and tetrasporophytes within populations of *Iridaea*, *Mazzaella* and *Chondrus* species have been previously observed, however, with tetrasporophyte dominance increasing with depth (e.g. Mathieson and Burns 1975, Craigie and Pringle 1978, Luxoro and Santelices 1989, Scrosati and Mudge 2004). Conversely, no evidence of differences in vertical distribution was found in a population of *Chondrus crispus* Stackhouse (Lazo et al. 1989).

The presence of a basal crust in *S. lanceata* may maintain year-round dominance of gametophytes over tetrasporophytes. For example, May (1986) studied a predominantly gametophytic population of *Mazzaella splendens* (as *Iridaea cordata*) and concluded that “blades of both phases are shed and regenerated each year without change in population structure, largely because of perennation from existing (and gametophytic) holdfasts.” A

different pattern, where phase dominance over the course of a single year is stable but changes over longer periods, has also been reported (e.g. Hansen and Doyle 1976, Hansen 1977, Dyck et al. 1985) and the structure of populations might change over even longer time periods than seasons or years (Dyck et al. 1985, De Wreede and Green 1990, Dyck and De Wreede 1995).

Dyck and De Wreede (1995) demonstrated that seasonal alternation in life-history phase dominance in a Vancouver population of *M. splendens* was a result of variation in the rates of density change among the life-history phases of this species. Gametophytes dominated the population in summer, apparently as a result of their ability to increase in density more rapidly than tetrasporophytes during spring. Gametophyte densities also decreased more rapidly in autumn resulting in a winter dominance by tetrasporophytes.

Biomass or standing stock is commonly estimated by destructive sampling but a non-destructive method of estimating biomass by counting size classes was used in this study. Similar methods have been used by Scrosati (2006) and Ko et al. (2008) across a range of species. No significant seasonal variation in biomass occurred at either site in the current study, but biomass was higher at Murdering Beach than at Purakaunui throughout the study period. This is not a surprising result given the lack of seasonality in *S. lanceata* clump densities and the differences in clump size and structure between the two sites. The lack of seasonality may also be a reflection of the method used to estimate biomass. The 1st quartile class weights used to estimate biomass for the whole year were calculated from blades collected from a single time and a single site. These weights may not be representative of weight changes throughout the year (e.g. as a result of seasonal changes in blade width or thickness or the density of reproductive structures), or weights from other sites and could potentially under- or overestimate biomass in different seasons.

This study indicates that the two populations of *S. lanceata* investigated were predominantly stable in size and composition over the period monitored. The presence of a basal crust appears to facilitate stability in this species whose populations are found on wave-exposed shores subjected to periodic sand inundation. However, strong inter-population differences were evident, which raised questions about environmental drivers affecting the two sites and also emphasised the value of considering inter-site variation. Loss of biomass appears more likely to occur via loss of blades rather than loss of clumps and, as such, may suggest a sustainable harvest method. However, further research would be required to assess the longer-term effects of harvesting.

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