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Synchrony of frond dynamics among patches of the clonal seaweed *Mazzaella parksii* (Rhodophyta) at local spatial scale

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This study investigated the synchrony of frond dynamics among patches of the intertidal seaweed *Mazzaella parksii* (=*M. cornucopiae*; Rhodophyta: Gigartinales) at local spatial scale. At Prasiola Point (Pacific coast of Canada), the mean synchrony of the seasonal changes in frond density among seven permanent, 100-cm^2 quadrats was significant (mean Pearson's r=0.73, with 0.65–0.81 as 95% confidence limits) between 1993 and 1995. This indicates that predicting seasonal trends for non-monitored patches at local spatial scale can be done relatively well based on observations on a limited number of quadrats. The identification of the spatial scales at which seaweed populations covary synchronously will permit minimizing sampling effort while retaining the ability to make valid predictions for non-monitored sites.

INTRODUCTION

One of the central aims of population ecology is to predict population dynamics. For any species, population dynamics vary across space (Bullock et al., 2002; Freckleton & Watkinson, 2002). Thus, given that most field studies can only monitor a limited number of sites in a given area, making predictions for non-monitored sites in the area is usually challenging. The ability to generate valid predictions for non-monitored sites depends greatly on the population synchrony among sites, that is, on how similarly sites covary in terms of abundance over time in the area of interest (Bjørnstad et al., 1999; Buonaccorsi et al., 2001). Predicting population dynamics for non-monitored sites might be done simply by considering the mean temporal trend and the associated variability observed for the monitored sites, information that is measured in most field studies. However, determining synchrony provides additional information that may improve predictions. For example, for the same degree of variability in abundance (Figure 1), synchrony among sites could be high (all populations varying similarly over time) or low (little covariation among populations). Predictions for non-monitored sites are, then, more accurate when synchrony is high. In environmental monitoring, for example, high synchrony among sites means that fewer reference populations have to be monitored to assess the status of an entire area (Burrows et al., 2002).

Most empirical studies on population synchrony have been done for animals (Bjørnstad et al., 1999; Koenig, 2002; Bellamy et al., 2003), so they constitute the main data source on which theory is being built. In comparison, plant population synchrony has been less investigated. Seaweeds have been even less studied in this respect. At local spatial scale (up to tens of metres), information about population synchrony exists for kelps (Dayton et al., 1992), Ascophyllum (Åberg & Pavia, 1997), *Ulva*, coralline seaweeds, *Sargassum* (Underwood & Chapman, 1998), *Fucus* (Driskell et al., 2001), and a few other species (Coleman, 2002). However, only the *Fucus* study (Driskell et al., 2001) actually quantified synchrony among the sampled areas. Thus, there is a need for studies that specifically measure local-scale synchrony in order to develop theory for seaweeds. The present study investigates local-scale patterns of seasonal synchrony for *Mazzaella parksii* (=*M. cornucopiae*; Rhodophyta: Gigartinales), which is a common species in the north-eastern Pacific coast (Hughey et al., 2001).

The main factors that affect population synchrony are the environmental correlation among sites (Moran effect), the degree of dispersal among populations, and the spatial correlation of interacting species such as predators (Bjørnstad et al., 1999; Hudson & Cattadori, 1999; Koenig, 2002). For *Mazzaella parksii*, abiotic conditions were apparently relatively homogeneous across the studied area, therefore potentially favouring high synchrony among the monitored patches. Spore recruitment is low for this species on an annual basis (Scrosati, 1998a), so spore dispersal should not be a significant synchronizing factor. Relevant interacting species, such as fucoid seaweeds (competitors; Kim, 2002) and littorinid snails (herbivores; Kim & DeWreede, 1996; Heaven & Scrosati, 2004), were present in the entire study area, theoretically also favouring high synchrony. Therefore, the monitored patches of *M. parksii* were predicted to vary relatively synchronously on a seasonal basis.

MATERIALS AND METHODS

The study area was Prasiola Point (48°49′N 125°10′W), located on southern Barkley Sound, Vancouver Island, British Columbia, Canada. This cold-temperate, rocky area was described in detail in Scrosati (1998b). The thallus of *Mazzaella parksii* consists of a crustose holdfast and several foliose fronds (Figure 2). It is a clonal seaweed, since its fronds function as ramets (Scrosati & DeWreede, 1997). In 1993, the position of seven 100 cm^2

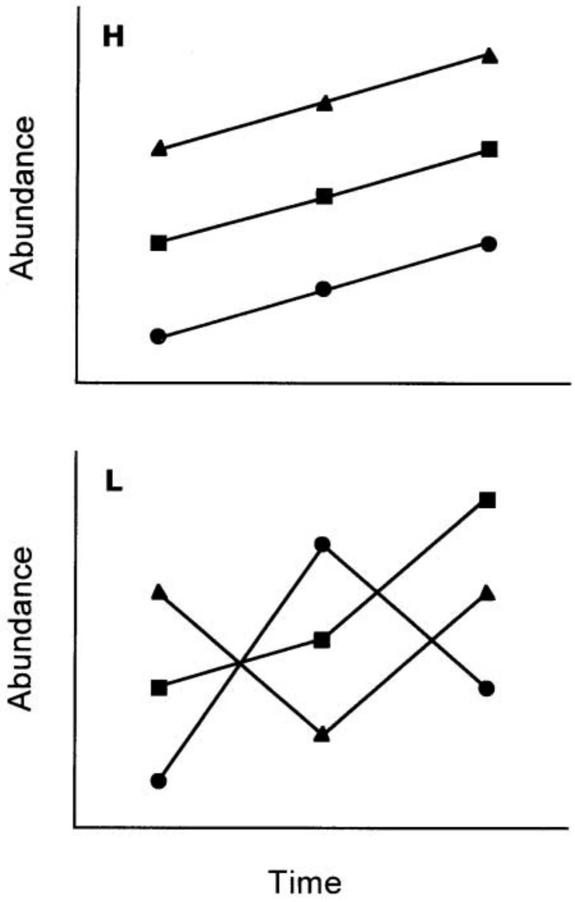

Figure 1. Example showing how population synchrony can be high (H) or low (L) with the same temporal change of the variability in abundance at three sites.

quadrats was determined randomly along a 40 m long transect parallel to the shoreline in the *M. parksii* belt, which is between 3–4 m above the lowest normal tide (Canadian chart datum). Frond density was measured for each quadrat on a seasonal basis for two years. Sampling dates were 17–19 August 1993, 10–12 December 1993, 26–28 April 1994, 19–21 August 1994, 2–4 December 1994, 30 March 1995, and 11–13 July 1995. The seven monitored patches of *M. parksii* were physically separated from one another, each one containing many fronds.

Synchrony was determined for each possible pair of quadrats as the Pearson correlation coefficient between their respective time series. Spurious correlation might have arisen had raw density data been used, because of the autocorrelative nature of the raw time series. To avoid this, first-differenced time series of the natural logarithm of density were used instead, therefore focusing on synchrony of population change (Bjørnstad et al., 1999). Then, a growth rate (Z_t) was calculated for each date as:

$$Z_t = \ln(N_t) - \ln(N_{t-1}),$$

where N was frond density and t was the date. As successive growth rates were serially dependent, the significance of the correlation coefficients based on growth rates was assessed with randomization tests (Koenig, 1999), using Resampling Stats 5.0 for Macintosh (Bruce et al., 1999) and doing 1000 random permutations per test. Perfect synchrony would result in $r=1$, while complete asynchrony would result in $r=0$. Mean sitewise synchrony was calculated as the arithmetic mean of all of the correlation coefficients (N=21). A 95% confidence interval for mean synchrony was calculated through a bootstrap analysis

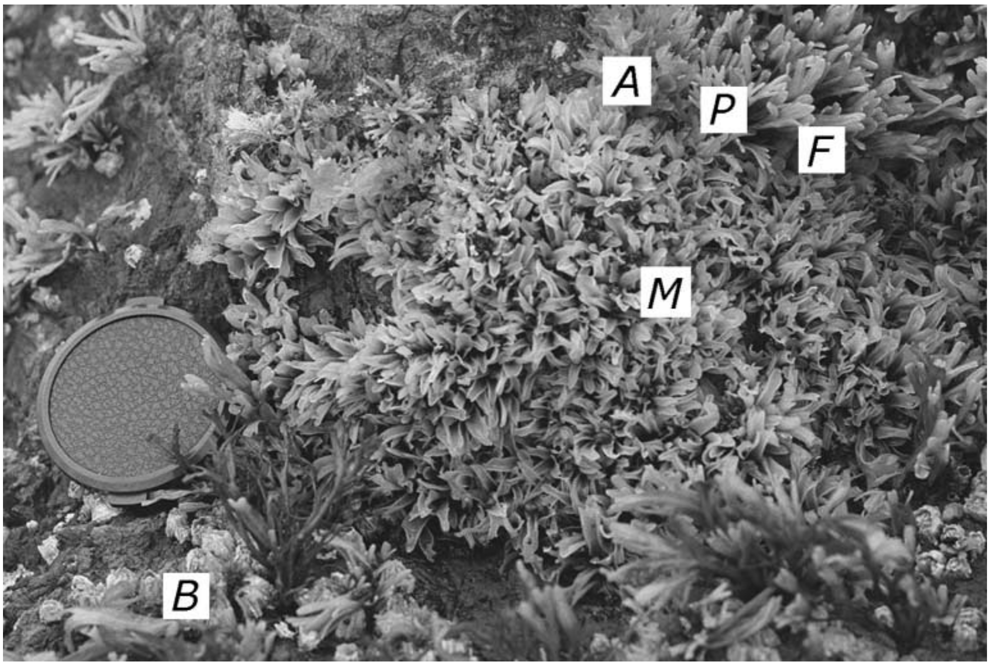

Figure 2. Patch of *Mazzaella parksii* (*M*) among specimens of the seaweeds *Mastocarpus papillatus* (*A*), *Pelvetiopsis limitata* (*P*), and *Fucus gardneri* (*F*), and of the barnacle *Balanus glandula* (*B*). Lens cap is 5 cm in diameter. Photograph taken by R. Scrosati in August 1994.

Table 1. *Synchrony of the changes in* Mazzaella parksii *frond density among seven permanent quadrats at Prasiola Point between 1993 and 1995. Results are expressed as Pearson correlation coefficients (*r*), with probability values (*P*) in parentheses. Significant correlations at the 95% confidence level are highlighted in bold.*

	1	2	3	4	5	6
2	**0.878** **(0.021)**					
3	**0.847** **(0.033)**	**0.870** **(0.024)**				
4	0.524 (0.286)	0.767 (0.075)	0.505 (0.307)			
5	**0.906** **(0.013)**	**0.958** **(0.003)**	**0.856** **(0.030)**	0.592 (0.216)		
6	0.504 (0.308)	0.728 (0.101)	**0.850** **(0.032)**	0.394 (0.439)	0.693 (0.127)	
7	0.610 (0.198)	**0.890** **(0.017)**	0.689 (0.130)	**0.947** **(0.004)**	0.749 (0.087)	0.657 (0.156)

(using Resampling Stats 5.0 and generating 1000 resamples with replacement), since the 21 correlation coefficients were not independent from one another (Bjørnstad et al., 1999; Koenig, 1999).

To characterize the variability of frond density among the quadrats during the study period, the coefficient of variation (CV) for density was calculated for each sampling date (N=7 quadrats) and then averaged among all of the dates (N=7 dates). A 95% confidence interval was calculated for this average through a bootstrap analysis, using Resampling Stats 5.0 and generating 1000 resamples with replacement.

RESULTS AND DISCUSSION

The density of *Mazzaella parksii* fronds varied seasonally between 1993 and 1995 at Prasiola Point, being generally higher in spring and summer than in autumn and winter (Figure 3). Several pairs of quadrats varied synchronously during this period. Nine of the 21 correlation coefficients were statistically significant at the 95% confidence level. Although not significant (at the 0.05 level), the rest of the coefficients were still associated to low P values (Table 1). The mean sitewise synchrony was r=0.73 (N=21 correlation coefficients), with 95% confidence limits of 0.650.81, indicating statistical significance. Frond density was variable among the quadrats on each sampling date (Figure 3). For the study period, the mean variability (mean CV) of frond density among the quadrats was 0.47 (N=7 dates), with 95% confidence limits of 0.410.54.

For any species, the accuracy in predicting population dynamics for non-monitored sites in a given area depends greatly on the degree of synchrony among sites. For *Mazzaella parksii*, the seasonal changes in frond density were relatively synchronous among quadrats. Therefore, synchrony estimates are potentially valuable tools to predict seasonal population trends at local spatial scale for this species based on a few monitored quadrats. Microscale (that is, quadrat-specific) abiotic and biotic information is lacking for the study site. However, the considerable level of synchrony found in this study suggests that abiotic conditions and interacting species (competitors and herbivores) were relatively spatially homogeneous, according to current theory on factors that affect population synchrony (Bjørnstad et al., 1999; Buonaccorsi et al., 2001; Koenig, 2002).

How does this study compare with local-scale studies on other seaweeds? Are there any common patterns for seaweeds in general? Information on local-scale

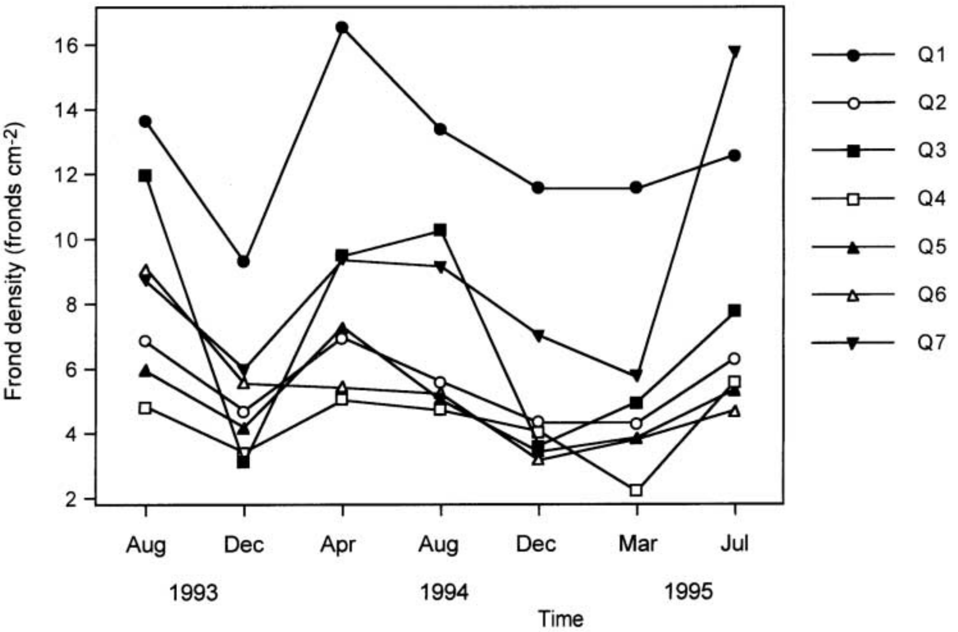

Figure 3. Temporal variation of *Mazzaella parksii* frond density (fronds cm^{-2}) in seven permanent quadrats from Prasiola Point; see text for sampling dates.

population synchrony is available for a number of macroalgae. For example, a study was done at a scale of tens of metres for subtidal kelps from California (Dayton et al., 1992); cross-correlations between sites were not given, but the published figures suggest that synchrony was quite variable and site dependent. At a similar spatial scale, *Ectocarpus* and *Colpomenia* (Phaeophyceae) from south-eastern Australia also showed variable synchrony patterns (Coleman, 2002), although cross-correlations between sites were not given either. Underwood & Chapman (1998) determined the population dynamics of *Ulva*, coralline seaweeds, and *Sargassum* from south-eastern Australia for several quadrats at a scale of a few metres, although synchrony among quadrats was not measured either. At a scale between 30 m and 100 m, sites (represented by the average of a number of quadrats) showed a varying degree of synchrony, depending on their geographic location (Underwood & Chapman, 1998). For *Fucus* from southern Alaska, Driskell et al. (2001) did measure synchrony, finding a low average value among pristine (undisturbed by oil) quadrats at a scale of tens of metres on an annual basis (that is, one annual estimation of abundance per quadrat) during six years.

Clear patterns of local-scale population synchrony are, therefore, not evident for seaweeds as a group as yet. More systematic studies are needed to advance this research line. The identification of patterns might be achieved by focusing future studies on the effects that the abiotic correlation among sites, the spatial correlation of interacting species, and algal dispersal capabilities have on the degree of population synchrony for a variety of seaweeds.

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