# Mechanisms of recolonization of the clonal intertidal alga *Mazzaella cornucopiae* (Rhodophyta, Gigartinaceae) after disturbances<sup>1</sup>

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**Abstract**: The recolonization of the clonal intertidal alga *Mazzaella cornucopiae* (Postels et Ruprecht) Hommersand is considered here, as part of a larger project on its population ecology. Recolonization in Barkley Sound, Pacific Canada, started a few months after completely clearing experimental 100-cm<sup>2</sup> quadrats in late spring and occurred both by vegetative growth of perennating holdfasts bordering disturbed quadrats and by recruitment from spores. In terms of percent cover, both mechanisms contributed similarly to recolonization during the first 2 years, although vegetative recolonization was highly variable among quadrats. Great spatial variability prevented the detection of a temporal pattern for recruit density on statistical grounds. However, cohort demography showed some degree of seasonality. Turnover rates of recruits were high; they lived 2.6 months on average. Recruitment was highest between fall or winter and midspring (as might be expected, given that reproductive structures appeared in fall and winter) and null in the first two summer seasons. The highest mortality was recorded in summer, when desiccation and irradiance are highest on an annual basis. Frond density was very variable on a spatial scale and did not follow a clear temporal pattern. The average number of fronds per recruit apparently increased between winter and summer, paralleling frond dynamics in mature stands. By monitoring recolonization in quadrats of the same size cleared previously by other researchers, the time of full recovery of *M. cornucopiae* was estimated to be 2.7–3.5 years.

Key words: demography, disturbance, Gigartinaceae, Mazzaella cornucopiae, mortality, recolonization, recruitment.

Résumé : L'auteur a examiné ici la recolonisation par l'espèce d'algue clonale intertidale Mazzaella cornucopiae (Postels et Ruprecht) Hommersand, dans le cadre d'un projet élargi sur l'écologie de ses populations. À Barkley Sound, sur la côte du Pacific, la recolonisation a commencé quelques mois après son élimination complète sur des quadrats expérimentaux de 100 cm<sup>2</sup>, tard au printemps, et s'est effectuée à la fois par croissance végétative à partir de pieds pérennes situés en bordure des quadrats expérimentaux et à partir de spores. En termes de pourcentage de couverture, les deux mécanismes contribuent de façon similaire à la recolonisation au cours des 2 premières années, bien que la recolonisation végétative varie beaucoup entre les quadrats. La grande variabilité spatiale empêche de perçevoir un patron temporel pour la densité des nouveaux arrivants (spores) sur une base statistique. Cependant, la démographie des cohortes montre un certain degré de saisonalité. Les taux de remplacement des nouveaux arrivants sont élevés; ils vivent en moyenne pendant 2,6 mois. Les arrivées sont plus nombreuses entre l'automne ou l'hiver et le début du printemps (comme on pourrait s'y attendre, compte tenu que les structures reproductives apparaissent à l'automne et en hiver) et sont nulles pendant les deux premiers saisons d'été. La plus forte mortalité a été enregistrée en été, lorsque la dessication et l'irradiance sont à leur plus fort sur la base annuelle. La densité de frondes était variable à l'échelle spatiale et ne suivait pas un patron temporel clair. Le nombre moyen de frondes est très variable pour chaque arrivant et augmente apparemment entre l'hiver et l'été, parallèlement à la dynamique des frondes des stations adultes. En suivant la recolonisation de quadrats de la même grandeur préalablement nettoyés par d'autres chercheurs, le temps nécessaire pour la récupération complète par le M. cornucopiae est de 2,7 à 3,5 ans.

*Mots clés* : démographie, perturbation, Gigartiniaceae, *Mazzaella cornucopiae*, mortalité, recolonisation, nouveaux arrivants.

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# Introduction

From an ecological perspective, disturbance is an event that removes biomass from a site and opens up space for recolonization. Disturbances affect the structure and the dynamics of natural communities, e.g., they pose limits to the size and growth rates of populations, and they may maintain local species richness through the existence of patches at different successional stages. The ability of organisms to recolonize a disturbed site depends on an interplay between the magnitude, timing, and frequency of disturbances, the shape of the affected area, the reproductive and regenerative strategies of the organisms, and direct and indirect interactions among the organisms themselves (Connell and Slatyer 1977; Sousa 1979, 1984; Menge and Sutherland 1987; Foster et al. 1988; Farrell 1991; Dayton et al. 1992; Sousa and Connell 1992; Menge et al. 1993; Bazzaz 1996; Kim 1997).

In the high rocky intertidal zone of wave-exposed areas of outer Barkley Sound, on the west coast of Vancouver Island, Canada, natural disturbances may result from dislodgement of rock surfaces through wave action and (or) wide temperature changes, impact from floating logs, and lethal bleaching of algae. Macroorganisms that frequently occur at these sites are perennial algae, such as Mazzaella cornucopiae (Postels et Ruprecht) Hommersand (Rhodophyta) and the fucoids Fucus gardneri Silva and Pelvetiopsis limitata Gardner (Phaeophyceae), ephemeral algae, barnacles (Balanus glandula Darwin and Chthamalus dalli Pilsbury), limpets (Lottia spp.), herbivorous (Littorina spp.) and carnivorous (Nucella sp.) snails, a few mussels (Mytilus trossulus Gould), and isopods and amphipods (Kim and DeWreede 1996a, 1996b; Kim 1997). The magnitude and seasonality of disturbances have been experimentally demonstrated to affect the successional pathway observed during recolonization at these sites (Kim and DeWreede 1996a; Kim 1997).

This research focuses on the recolonization of one of the dominant species of this community, the clonal red alga M. cornucopiae, and is part of a larger project on selected aspects of the population ecology of this species (Scrosati 1997, 1998; Scrosati and DeWreede 1997, 1998). A thallus of M. cornucopiae is composed of a crustose, perennial holdfast and several foliose fronds, which have higher turnover rates than holdfasts (Abbott 1971; Scrosati 1998); see a photo of a mature stand in Scrosati and DeWreede (1997). Preliminary observations indicated that there are two mechanisms of recolonization of M. cornucopiae after disturbances: recruitment from spores and vegetative growth of perennating holdfasts from the margins of a disturbed area. By completely clearing experimental quadrats in the field, both processes were quantified and their relative importance for recolonization assessed.

There are few studies of the demography of recruits during a growing season for plants in general (Bazzaz 1996). For *M. cornucopiae*, successive cohorts of recruited thalli were identified and monitored for 2 years after disturbances. The effects of season on the recruitment and mortality rates of recruits (genets) were evaluated. The demography of fronds (ramets) from recruits was also studied. Simultaneous studies of genet and ramet demography are rare for clonal red algae (e.g., Dyck and DeWreede 1995), mainly because of the great difficulty in identifying genets from mature, crowded stands of many species (Bhattacharya 1985; Santos 1994; Scrosati and DeWreede 1997). Finally, quadrats that had been cleared at different seasons previous to this study (Kim and DeWreede 1996*a*) were monitored for an additional 2 years to determine the rate of complete recovery for *M. cornucopiae* after disturbances.

## **Methods**

The study site was the east side of Prasiola Point (48°49'N, 125°10'W), located in southern Barkley Sound (near Bamfield Marine Station), on the west coast of Vancouver Island, British Columbia, Canada. This area belongs to the cold-temperate northeastern Pacific region (Lüning 1990): mean monthly sea surface temperature oscillates between 8.6°C (winter) and 16.1°C (summer) near Prasiola Point (Scrosati 1997). The east side of Prasiola Point is exposed to moderate wave action, whereas the west side receives the direct impact of the large waves from the open ocean. Mazzaella cornucopiae occurs in the high intertidal zone, about 3-4 m above the lowest normal tide (based on Canadian Chart Datum) at the east side. The tidal regime is mixed in this area; the lowest of the two daily low tides occurs mostly during daytime in spring and summer and mostly during nighttime in late fall and winter. At the study site, M. cornucopiae is a codominant alga together with F. gardneri and P. limitata, whereas it is the only dominant perennial alga in the high intertidal zone of the high wave-exposure site (Scrosati 1997). Important biological interactions that shape the structure and dynamics of this community, such as competition and herbivory, have been studied recently (Kim and DeWreede 1996a, 1996b; Kim 1997).

Physical disturbance was experimentally generated on 6 June 1993 by chiseling out the surface rock of six 100-cm<sup>2</sup> quadrats randomly located in the study site. Previous experimental clearings in the same area (Kim and DeWreede 1996a) showed that recolonization rates of Mazzaella cornucopiae during the first 2 years were similar in 100-cm<sup>2</sup> versus 25-cm<sup>2</sup> cleared quadrats. No recolonization of *M. cornucopiae* occurred, however, in larger (400 cm<sup>2</sup>) cleared quadrats during the same period. The quadrats cleared for the present study were regularly monitored at about bimonthly intervals during 2 years: 17 August 1993, 17 October 1993, 26 February 1994, 28 April 1994, 24 June 1994, 21 August 1994, 7 October 1994, 4 December 1994, 30 January 1995, 30 March 1995, 16 May 1995, and 13 July 1995. Using a 100-cm<sup>2</sup> sampling frame with 100 subdivisions, the percent cover of thalli that developed vegetatively from the surrounding perennating thalli and of thalli recruited from spores was determined as the number of subdivisions per quadrat with more than 50% of their area occupied by M. cornucopiae. Recruits that appeared close to the margins of clearings were distinguished from thallus areas that resulted from vegetative growth of bordering holdfasts on the basis of physical separation between recruits and vegetatively generated holdfasts. Percent cover of recolonizing M. cornucopiae was regularly compared with the percent cover of natural stands. This was measured in six, undisturbed 100-cm<sup>2</sup> quadrats randomly located in the same area, which were repeatedly monitored during the study.

The position of recruited thalli was regularly mapped in the cleared quadrats, so successive cohorts could be identified and recruitment and mortality rates determined. An operational definition of recruitment was adopted for this study: the number of new thalli that were visually detected on each sampling date. This method failed to quantify mortality rates between spore settlement and visual detection of recruits, but this was unavoidable because of the inability to visually detect juveniles in the field before they had reached a certain minimum size (see Caley et al. 1996). The smallest recruits detected had only one frond, which was 1–2 mm long. A recruit was recorded as dead when neither fronds nor the holdfast were detected where the recruit had been previously seen.

**Fig. 1.** Temporal variation of percent cover (mean + SE) of *Mazzaella cornucopiae* from control quadrats (CO, n = 6, undisturbed stands) and from quadrats cleared in June 1993 (CL, n = 6, recruitment + vegetative recolonization). No CL data are available for December 1993.



The number of fronds per recruit was also determined on successive sampling dates to study frond demography.

Data were analyzed through t tests and one-way, repeatedmeasures ANOVAs (Howell 1992), as detailed in Results. The ANOVAs were done through randomization tests with 1000 random permutations (Edgington 1987; Manly 1991) because of the violation of the assumptions of data normality and homoscedasticity. The normality assumption was checked with the "Probability Plot-Normal" option in SYSTAT, version 5.2.1 for Macintosh (Wilkinson et al. 1992), whereas the homoscedasticity assumption was considered to be violated if the highest variance was higher than four times the lowest variance (Howell 1992). The t tests were done with SYSTAT and the ANOVAs were done with the program "Randomization Tests" for DOS, developed by E.S. Edgington (University of Calgary, Calgary, Alta.).

To determine the rate of complete recovery of M. cornucopiae after physical disturbances, the same 100-cm<sup>2</sup> quadrats cleared at the east side of Prasiola Point referred to in Kim and DeWreede (1996a) were monitored. The quadrats were cleared in summer (August 1992), fall (October 1992), winter (February 1993), and spring (April 1993) (corrected from Kim and DeWreede 1996a, J.H. Kim, personal communication). Fifteen quadrats had been initially cleared in each season, and they had been last examined in August 1994 (Kim and De Wreede 1996a). For the present study, the quadrats were examined on 26-27 October 1995 and on 20-21 October 1996. Total percent cover of M. cornucopiae (including recruited thalli and thalli extending into the quadrat from vegetative growth of bordering holdfasts) was measured with a 100-cm<sup>2</sup> sampling frame with 100 subdivisions. The distinction between both mechanisms of recolonization could not be made for these quadrats, because it was not specifically recorded during the first years. To compare the percent cover of M. cornucopiae from disturbed quadrats with that from natural, undisturbed stands, 15 additional 100-cm<sup>2</sup> quadrats were randomly located along the original transect in October 1995. Biological assemblages at one of the extremes of the original transect (two ninths of its full length) were

**Fig. 2.** Temporal variation of percent cover (mean + SE, n = 6) of *Mazzaella cornucopiae* from quadrats cleared in June 1993. RE, thalli recruited from spores; VE, thallus areas originated vegetatively from perennating holdfasts bordering the quadrats. RE data are missing for December 1993, and VE data are missing for December 1993, February 1994, and April 1994.



different than in the rest of the transect, apparently because of differences in elevation, so quadrats located in those two ninths of the transect were not considered for the present analysis.

Percent cover for the four clearing treatments (seasons) was compared with the controls separately for October 1995 and October 1996 through one-way ANOVAs (Howell 1992). Because of the lack of normality and homoscedasticity, both ANOVAs were done through randomization tests with 1000 random permutations. Percent cover was compared between the different clearing treatments and the controls only for 1995, because the ANOVA for 1996 was nonsignificant (see Results). For this, independent *t* tests were carried out through randomization tests. The validity of performing a group of *t* tests after an ANOVA is a controversial topic among statisticians; I followed Soto and Hurlbert (1991).

## Results

#### Mechanisms of recolonization

Recolonization of *M. cornucopiae* occurred by recruitment from spores and by vegetative growth of perennating holdfasts (with the subsequent production of fronds) that bordered disturbed quadrats. Despite the operation of both mechanisms, the recolonization was slow: total percent cover of *M. cornucopiae* from cleared quadrats was much lower than percent cover of mature, undisturbed stands during the 2-year study (Fig. 1). For cleared quadrats, cover data are missing for recruits for December 1993 and, for vegetative recolonization, for December 1993, February 1994, and April 1994. For the rest of the monitored period, mean percent cover of vegetatively generated thalli was always higher than that of recruits in cleared quadrats, but owing to a relatively large spatial variability (among quadrats) for vegetative recolonization, there were not significant dif-



ferences in percent cover between the two mechanisms (p > 0.05, separate *t* tests for each month; Fig. 2).

#### **Demography of recruits (genets)**

Recruits were first detected in the cleared quadrats about 4.5 months after disturbances occurred. The temporal pattern of recruit density was highly spatially variable (Fig. 3), so a one-way, repeated-measures ANOVA done through a randomization test did not detect significant differences in recruit density among months (F = 1.11, p = 0.345), despite an apparent seasonal pattern. The turnover rate of recruits was high (Fig. 4). If the age of a recruit is estimated as the time between its first sighting and the middle of the sampling interval in which it died, a recruit lived an average of  $2.6 \pm 0.3$  months (mean  $\pm$  SE, n = 55).

Recruitment rates were also very variable among quadrats (Fig. 5), so a one-way, repeated-measures ANOVA done through a randomization test also failed to show significant differences among months (F = 1.03, p = 0.437). However, a certain degree of seasonality is apparent, since no recruitment at all occurred in August 1993 and August 1994 (summer), the highest total number of new recruits was recorded during spring months, and intermediate values were recorded in fall and winter (Fig. 4).

Mortality rates also varied greatly spatially (Fig. 6). No ANOVA could be done to test for a possible temporal pattern for mortality rates, because sample size varied widely among months (some quadrats did not have new recruits at certain sampling dates, so there was no possible mortality to record at the following respective sampling date). Mortality rates, however, were apparently higher in summer or between late spring and summer than in the rest of the year: 71% percent of recruits died between June and August 1994, and 60% died during May and July 1995 (Fig. 4), which were the two highest mortality values for any of the 2-month intervals.

#### **Demography of fronds (ramets)**

As a result of the high spatial variability of the temporal pattern of recruit density, the temporal pattern of frond density was also highly spatially variable (Fig. 7). A one-way, repeated-measures ANOVA done through a randomization test did not detect significant differences among monthly means of frond density (F = 0.66, p = 0.829). For the number of fronds per recruit, no ANOVA could be performed to test for a possible temporal pattern, because sample size had a great variation among months (recruits were not present in all of the quadrats at all of the sampling dates). Recruits had, apparently, more fronds in average during summer time (Fig. 8).

#### Time to complete recovery

There were significant differences between percent cover of *M. cornucopiae* among the different clearing (seasonal) treatments in October 1995 (F = 2.85, p = 0.023, one-way ANOVA). From a statistical perspective, a complete recovery was observed in quadrats cleared in August 1992 (summer), October 1992 (fall), and February 1993 (winter) (p >0.05, independent t tests against controls), but quadrats cleared in April 1993 (spring) still had a significantly lower percent cover than control areas (p = 0.009, independent t test; Fig. 9). In October 1996, all of the clearing treatments had control levels of percent cover (F = 1.27, p > 0.05, oneway ANOVA; Fig. 9). However, percent cover for quadrats cleared in April 1993 did not change between October 1995 and October 1996 (Fig. 9). The statistical similarity of April 1993 cleared quadrats with control quadrats was a result of a significant decrease in percent cover of control quadrats between October 1995 and October 1996 (p = 0.001, paired t test).

### **Discussion**

The size of a disturbed area is one of the factors that affect the capacity for recolonization of organisms. This study agrees with Kim and DeWreede's (1996*a*) in that 100-cm<sup>2</sup> disturbances begin to be recolonized by *M. cornucopiae* a few months after they occur. Larger areas (e.g., 400-cm<sup>2</sup> quadrats) were not recolonized by *M. cornucopiae* at least during 2 years after disturbances occurred, perhaps as a result of increased heat and desiccation stress, short dispersal distances of *M. cornucopiae*, or a lower perimeter-to-area ratio for clearings (Kim and DeWreede 1996*a*). Higher recruitment in the smaller disturbed areas could also result from reduced water motion owing to the closer presence of mature algal stands, which might enhance spore settlement (Foster 1975). These hypotheses require experimental validation.

The two mechanisms of recolonization of M. cornucopiae, spore dispersal and vegetative growth of perennating holdfasts from the margins of a disturbed area, contributed in a similar proportion to recolonization. The spatial variability (among quadrats) was relatively large for vegetative recolonization. This difference resulted from the dispersal distance of spores being greater than the distance gained by





**Fig. 5.** Temporal variation of recruitment rates for *Mazzaella cornucopiae* (new recruits per 2 months/100 cm<sup>2</sup>, mean + SE, n = 6) from quadrats cleared in June 1993. No data are available for December 1993.



vegetative growth of perennating holdfasts. This makes vegetative recolonization more dependent on the proximity of mature thalli to a clearing than recolonization by spores. Spores would become crucial for recolonization only when mature thalli are relatively distant from a disturbed area. However, the distance that spores can be effectively dispersed (possibly with aid from invertebrates; see Buschmann and Bravo 1990, Buschmann 1991), remains to be determined for *M. cornucopiae*. For other species of *Mazzaella*, such as *Mazzaella flaccida* (Setchell et Gardner) Fredericq from central California (Foster 1982, as *Iridaea flaccida*) (Setchell et Gardner) Silva and *Mazzaella splendens* (Setchell

**Fig. 6.** Temporal variation of mortality rates of recruits of *Mazzaella cornucopiae* (percentage of recruits dead per 2 months/100 cm<sup>2</sup>, mean + SE, n = 6) from quadrats cleared in June 1993. No data are available for December 1993.



et Gardner) Fredericq from sites near Prasiola Point (Phillips 1994, as *Mazzaella lilacina*) (Postels et Ruprecht Leister), the relative importance of bordering, mature holdfasts for recolonization of disturbed areas is much lower than that of spores. This can be attributed to the fact that their mature holdfasts are much smaller than those of *M. cornucopiae* and do not grow as continuously in time.

The temporal pattern of recruit density, recruitment rates, and mortality rates of recruits of *M. cornucopiae* were highly variable on a spatial scale, so possible seasonal differences were not detected with the statistical tests per-

**Fig. 7.** Temporal variation of the density of fronds (referred to quadrat area) from recruits of *Mazzaella cornucopiae* (fronds/100 cm<sup>2</sup>, mean + SE, n = 6) from quadrats cleared in June 1993. No data are available for December 1993.



Fig. 9. Total thallus percent cover of *Mazzaella cornucopiae* from control, undisturbed quadrats and from quadrats cleared in August 1992 (summer), October 1992 (fall), February 1993 (winter), and April 1993 (spring), as observed in October 1995 and October 1996.



formed. However, some temporal trends can still be identified for recruit demography. All of the clearings were progressively colonized during the first 2 years after disturbances occurred, although recruits had high turnover rates.

Both recruitment and mortality rates showed a mild seasonal pattern. The absence of recruitment in the first two summer seasons and the occurrence of the highest mortality **Fig. 8.** Temporal variation of the number of fronds per recruit of *Mazzaella cornucopiae* (mean + SE, n = 6) from quadrats cleared in June 1993. No data are available for December 1993.



rates between late spring and summer probably resulted from the high desiccation and irradiance typical of the lowest tides during these seasons (Scrosati and DeWreede 1998). Experimental thinning of mature stands of M. cornucopiae in the spring resulted in a higher degree of frond bleaching and subsequent biomass loss in the summer than in undisturbed stands, and indirect evidence suggested that high desiccation and irradiance were involved (Scrosati 1997; Scrosati and DeWreede 1998). Young recruits in recently disturbed areas are directly exposed to sunlight and air during low tides, since they lack the protection of a canopy of fronds. Recruits cannot recover from strong bleaching and biomass losses simply because they are tiny. In fact, the upper portion of fronds of the few surviving recruits observed during the summer of 1994 were bleached. High desiccation and irradiance do not occur in the fall and winter, since the lowest tides mostly occur during dark hours. Negative temperatures and increased rain during low tides could constitute stressful factors for recruits, but apparently are less important than the late spring - summer stresses.

The absence of recruitment during the first two summer seasons could also respond to the lack of spore production a few months before. Cystocarpic and tetrasporic (fertile) fronds of *M. cornucopiae* appeared only during fall and winter at the same site during the study period (Scrosati 1998). This reproductive pattern may also explain the detection of the highest number of new recruits in spring months and, secondarily, in fall and winter. The sole detection of reproductive structures does not predict imminent recruitment, because of variations in maturation stage, among other factors (Scrosati et al. 1994; Santelices and Martínez 1997). However, cystocarps and tetrasporic sori looked healthy and were mostly dark red for *M. cornucopiae*, which suggests that spores were viable and able to germinate.

If postsettlement stages survive for long periods without attaining a visible recruit stage, forming part of a bank of microscopic stages (Chapman 1986; Hoffmann and Santelices 1991; Santelices et al. 1995), recruitment dynamics may be uncoupled from the reproductive season of an alga. The survival of microscopic, prerecruit stages between reproductive seasons appears to have been unlikely or numerically unimportant for *M. cornucopiae*. Since the strongest mortality of recruits occurred between late spring and summer, the mortality of prerecruit stages due to desiccation, irradiance, and (or) heat should have been even stronger because of their small size. Uncoupling between reproduction and recruitment was recorded for some intertidal seaweeds, such as Fucus gardneri from Vancouver, B.C. (Ang 1991, as F. distichus) and F. vesiculosus L. from the Isle of Man, Great Britain (Creed et al. 1996).

Density-dependent mortality of recruits appears not to have occurred during the study period because of the large spatial separation among recruits. At later stages, even if crowding increased as thalli grew, mortality (i.e., selfthinning) probably would not increase. Sporeling coalescence occurs for red algae similar to *M. cornucopiae* (Tveter and Mathieson 1976; Tveter-Gallagher and Mathieson 1980; Maggs and Cheney 1990; Santelices et al. 1996), and this could minimize competition among neighboring thalli. However, whether the degree of coalescence is important for older (larger) thalli is still unknown, which needs further research.

The demography of fronds of *M. cornucopiae* was also very variable on a spatial scale, following the spatial variation observed for recruit demography. The only apparent seasonal pattern was that fronds per recruit were increasing in number between winter and summer. This paralleled the temporal pattern of frond density for mature stands (Scrosati and DeWreede 1997). The apparent decrease of the mean number of fronds per recruit between summer and winter could be explained by the high mortality of recruits in summer, which were being progressively replaced by new, smaller recruits.

The complete recovery of *M. cornucopiae* after a 100-cm<sup>2</sup> disturbance, through both mechanisms of recolonization combined, took between 2.7 and 3.5 years in the quadrats cleared by Kim and DeWreede (1996a) at Prasiola Point. A more precise estimation is not possible, since measurements were taken only in October 1995 and in October 1996. A comparison of Fig. 1 of this study with Fig. 3 in Kim and DeWreede (1996a) suggests that the complete recovery of *M. cornucopiae* in the quadrats cleared by myself may take longer. The two groups of quadrats are located on the east side of Prasiola Point, separated by about 20-30 m, and were cleared with a difference of 2-10 months. This suggests that the year of disturbance could be another source of variation for recolonization rates for M. cornucopiae, which would add to season of disturbance, size of disturbed area, and the exact location where a disturbance occurs within a site.

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