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Gsell, A.S.; De Senerpont Domis, L.N.; Verhoeven, K.J.F.; Van Donk, E.; Ibelings, B.W.

published in

ISME Journal

2013

DOI (link to publisher)

[10.1038/ismej.2013.73](https://doi.org/10.1038/ismej.2013.73)

document version

Peer reviewed version

[Link to publication in KNAW Research Portal](#)

citation for published version (APA)

Gsell, A. S., De Senerpont Domis, L. N., Verhoeven, K. J. F., Van Donk, E., & Ibelings, B. W. (2013). Chytrid epidemics may increase genetic diversity of a diatom spring-bloom. *ISME Journal*, 7(10), 2057-2059. <https://doi.org/10.1038/ismej.2013.73>

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1 **Chytrid epidemics may increase genetic diversity of a diatom spring-bloom**

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12 **Running title:** Parasite epidemics increase host genetic diversity

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33 **Abstract**

34 Contrary to expectation, populations of clonal organisms are often genetically highly diverse. In
35 phytoplankton, this diversity is maintained throughout periods of high population growth (i.e. blooms),
36 even though competitive exclusion among genotypes should hypothetically lead to the dominance of a
37 few superior genotypes. Genotype-specific parasitism may be one mechanism that helps maintain such
38 high genotypic diversity of clonal organisms. Here, we present a comparison of population genetic
39 similarity by estimating the beta-dispersion among genotypes of early and peak bloom populations of
40 the diatom *Asterionella formosa* for three spring-blooms under high or low parasite pressure. The
41 *Asterionella* population showed greater beta-dispersion at peak bloom than early bloom in the two
42 years with high parasite pressure, while the within group dispersion did not change under low parasite
43 pressure. Our findings support that high prevalence parasitism can promote genetic diversification of
44 natural populations of clonal hosts.

45 **Keywords:** beta-dispersion / chytrid / diatom / genetic diversity / parasitism

46 **Subject category:** microbial population and community ecology

47

48 **Introduction**

49 Populations of (predominantly) clonal organisms, such as diatoms, are often genetically highly diverse
50 (Evans *et al*, 2009), even throughout blooms (Rynewson & Armbrust, 2005). Over the short periods of
51 time within which diatom spring-blooms develop, abiotic variation is limited, and competition between
52 genotypes should lead to numerical dominance of few superior genotypes driven by genotype sorting
53 (De Meester, 1996). But biotic interactions, such as parasitism, may increase host population genetic
54 dissimilarity through time-lagged, negative frequency-dependent selection (Bell, 1982) if parasites adapt
55 to- and select against the most common genotypes (Hardin, 1968). This can lead to an increase in
56 genotypic evenness of host populations in infected systems compared to non-infected ones (Wolinska a
57 & Spaak, 2009). To our knowledge, no field study has yet described an increase in genetic dissimilarity in
58 asexual host populations as they are being invaded by a parasite epidemic.

59

60 **Materials and Methods**

61 In Lake Maarsseveen (The Netherlands), the diatom *Asterionella formosa* Hassall regularly forms spring-
62 blooms which are followed by high prevalence parasite epidemics of its fungal parasite, the chytrid
63 *Zygorhizidium planktonicum* Canter (Ibelings *et al*, 2011; Van Donk & Ringelberg, 1983). The *Asterionella*
64 population is genetically very diverse (De Bruin *et al*, 2004) even though it is presumed to reproduce

65 (predominantly) clonally. Sexual reproduction has been hypothesised, but never observed (Mann, 1988).
66 Moreover, gene-flow is expected to be negligible as Lake Maarsseveen is hydrologically isolated, and as
67 the *Asterionella* population is genetically distinct from that of lakes close-by (De Bruin, 2006).
68 Differential susceptibility of host genotypes to the chytrid was shown experimentally (De Bruin et al,
69 2004) suggesting that this parasite can act as selection agent.

70
71 The population development of host and parasites was monitored in weekly intervals during
72 three years (2008-2010). Each spring, genetic diversity of the early and the peak bloom population was
73 sampled at 5m depth in the pelagic zone of Lake Maarsseveen. Single *Asterionella* colonies were isolated
74 from these six sub-populations (three years, early and peak bloom), cultured and AFLP fingerprinted
75 (Vos et al, 1995), for more details on methods see supplementary material. A total of 65 isolates were
76 fingerprinted (2008: n=25 (13 early, 12 peak), 2009: n=26 (13, 13), 2010: n=14 (5, 9)). To measure
77 changes in genetic similarity of the host population we assessed beta-diversity among all subpopulations
78 (Fig 2a,b) and the homogeneity of beta-dispersion for early and peak subpopulation of each year by
79 permutational Analysis of Variance (PERMANOVA) (Anderson et al, 2006) based on pair-wise Jaccard
80 distances (Jaccard, 1901). Beta-dispersion calculates distances from observations to their group
81 centroids and then compares the average of these distances among groups. *P*-values were obtained by
82 999 permutations of the raw data using R package vegan (R, 2011).

83

84 **Results**

85 The spring of 2008 showed no clear host bloom or parasite epidemic (Fig 1a). *Asterionella* was present in
86 low numbers (maximum 14 cells/mL) and parasitized at low levels (maximum prevalence 15%). The 2009
87 and 2010 spring-blooms (Fig 1b,c) showed more typical population maxima (2009: 530 cells/mL ; and
88 2010: 264 cells/mL) and were followed by high prevalence epidemics (maximum prevalence 2009: 77%;
89 and 2010: 80%) (Ibelings et al, 2011). The AFLP analysis yielded on average 32.0 ± 2.2 marker bands per
90 primer pair (128 marker bands; 87.5% polymorphism). Two genotypes occurred twice, all other isolates
91 showed unique fingerprints. Although the six group centroids differed significantly ($F_{5,64} = 6.47$, $P < 0.001$),
92 temporally consecutive populations overlapped to large extent (Fig 2a), suggesting that the host-
93 population was changing over time but remained coherent. The beta-dispersion among all
94 subpopulations was non-homogeneous ($F_{5,59} = 3.71$, $P = 0.005$). Within year analysis of beta-dispersion
95 showed a significantly larger dispersion in the peak bloom subpopulation than in the early bloom
96 subpopulations in the heavily parasitized years 2009 and 2010; 2009: $F_{1,25} = 5.38$, $P = 0.029$; and 2010:

97 $F_{1,13} = 14.33$, $P = 0.002$ (Fig 2b). However, the beta-dispersion of early and peak bloom subpopulation of
98 the low parasitized 2008 bloom showed no difference: $F_{1,24} = 1.33$, $P = 0.24$ (Fig 2b).

99

100 **Conclusions**

101 What mechanisms may maintain host genetic diversity is particularly relevant in spring-bloom
102 phytoplankton species as they form the base of lake food-webs (Sommer et al, 2012). Genetically more
103 diverse host populations are known to be more resistant to disease than genetically poor ones
104 (Altermatt & Ebert, 2008; Whitehorn et al, 2011) since higher host diversity hampers adaptation of the
105 parasite (De Bruin et al, 2008). Paradoxically, high parasite pressure is also expected to increase host
106 genetic diversity through frequency-dependent selection (Little, 2002). Parasite epidemics exert a short-
107 lived albeit strong selective force, while hosts are under different selection forces during the rest of the
108 year. However, our results support the idea that high prevalence parasitism can drive genetic
109 diversification in natural host populations, which then again serves as raw material for selection
110 processes throughout the rest of the year.

111

112 **Acknowledgments**

113 The authors thank Nico Helmsing and Koos Swart for fieldwork support and Suzanne Naus-Wiezer for
114 laboratory assistance. Also, we thank three anonymous reviewers for their constructive and thoughtful
115 comments. ASG is supported by grant 816.01.018 of the Dutch Organization for Scientific Research -
116 Earth and Life Science Foundation (NWO-ALW) to BWI and EvD. LdSD is supported by grant 817.01.007
117 of NWO-ALW.

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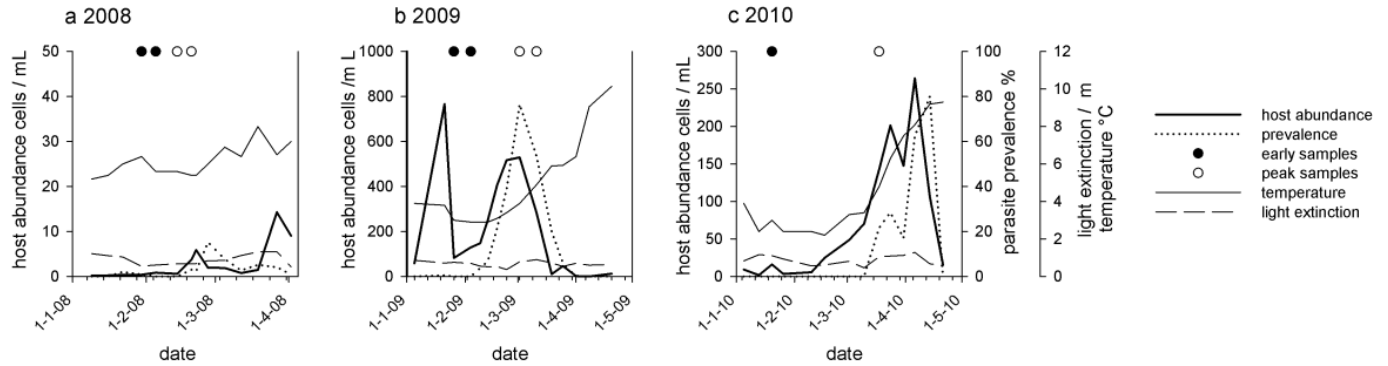
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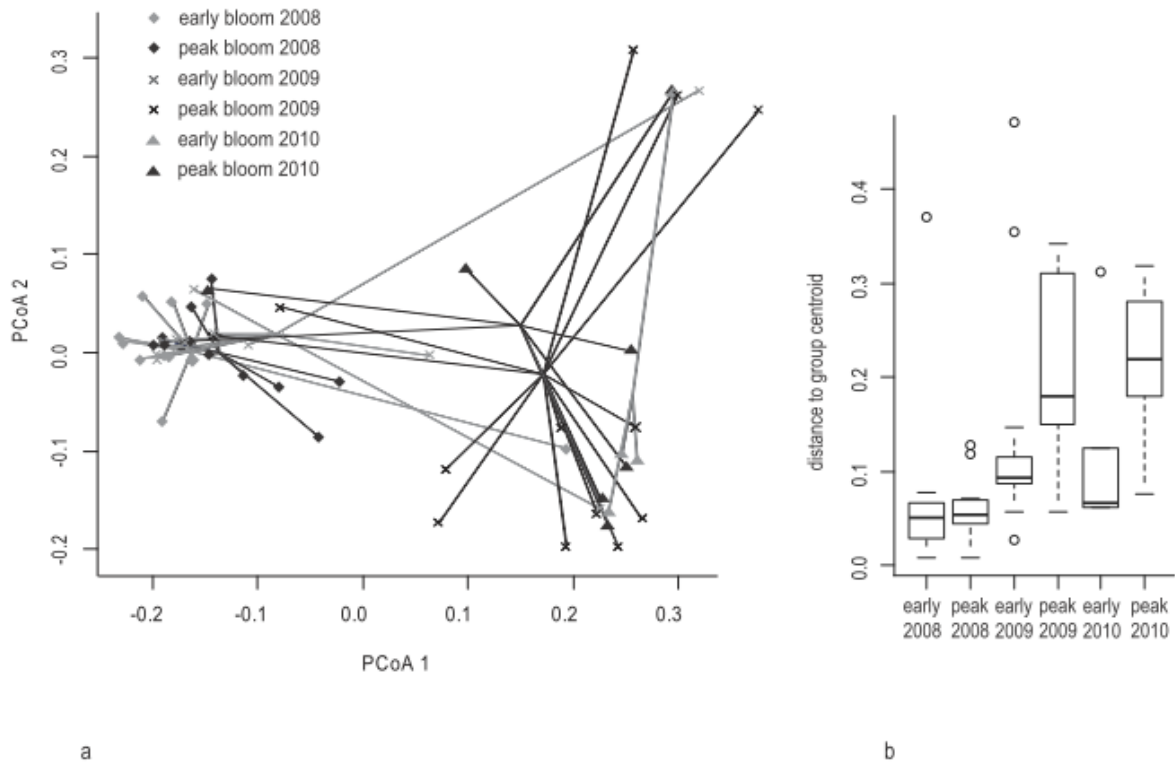
227 **Figures**

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230 **Figure 1:** Host abundance (solid line) and parasite prevalence (dotted line) over the first four months of
 231 the years 2008, 2009 and 2010 at 5m depth in Lake Maarsseveen. The sampling events for population
 232 genetic diversity samples (n=1 or 2 for each subpopulation) are indicated for early bloom (black circles)
 233 and peak bloom (empty circles). In 2008 (panel a) *Asterionella* population density and parasite
 234 prevalence in spring remain low, and winter and spring surface water temperatures remain relatively
 235 high. In 2009 and 2010 (panels b and c) the *Asterionella* spring-blooms show more typical time courses
 236 and are followed by high prevalence parasite epidemics. Winter and spring surface water temperatures
 237 start off cooler but increase over time. Light extinction shows no particular pattern over the observed
 238 time period.



239

240 **Figure 2:** a) Two-dimensional representation of the principal coordinates analysis based on Jaccard's
 241 similarities among AFLP fingerprints of genotypes: grey symbols represent members of the early bloom
 242 populations; black symbols represent members of the peak bloom populations. The plot shows how the
 243 subpopulation centroids shift over time, however, temporally subsequent subpopulations show
 244 considerable overlap. b) Boxplot of beta-dispersion per subpopulation, based on distances of each
 245 genotype to its respective group centroid. The thick line represents the median, the limits of the lower
 246 and upper box are the 25% and 75% percentile, the bars extend to the most extreme values (excluding
 247 outliers), points indicate the position of putative outliers. The beta-dispersion of early and peak bloom
 248 subpopulation shows no significant differences in the low parasitized year 2008. However, the beta-
 249 dispersion of the peak bloom subpopulations in heavily parasitized years 2009 and 2010 is significantly
 250 larger than that of their respective early bloom subpopulation.