Vertical niche separation between two closely related planktonic flagellate species (*Rhodomonas lens* and *Rhodomonas minuta* v. *nannoplanctica*)

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Abstract. *Rhodomonas minuta* v. *nannoplanctica* Skuja and *Rhodomonas lens* Pascher et Ruttner were found to perform vertical migrations. From sunrise until afternoon they adjust their vertical position to an optimum light-intensity, which is for *R. minuta* 2.5 times higher than for *R. lens*. The spatial separation of both species is increasing throughout the whole light phase. The species distinction between them has been questioned recently, but can be maintained not only because of morphological differences but also because they are occupying different niches within the plankton community.

Introduction

The closely related species *Rhodomonas lacustris* Pascher et Ruttner, *R. lens* Pascher et Ruttner, *R. minuta* Skuja and *R. pusilla* (Bachmann) Javornicky were described as one species by Javornicky (1976), *R. lacustris* Pascher et Ruttner. He has suggested, that a gradual morphological transition exists between those species, and that they should not therefore be considered distinct species. In Lake Constance however, two clearly distinct forms exist, which exactly resemble the original drawings and descriptions of Pascher (1913) and Skuja (1948) of *R. lens* and *R. minuta* v. *nannoplanctica* (cf. Lund 1962). Here I give both morphological and ecological evidence that both forms are valid species, and are not only morphologically different but also occupy different niches within the phytoplankton community.

Material and methods

As part of a round-the-year sampling programme, diel variations in the vertical distribution of phytoplankton were studied on May 20th and 21st 1980 in the Überlinger See, which is a 147 m deep bay of Lake Constance (with a total length of 14 km and an average width of about 4 km). The weather was calm. The phytoplankton spring bloom had almost disappeared due to heavy zooplankton grazing. One week later phytoplankton were eliminated almost entirely leading to a so called "clear water stage" which regularly occurs in Lake Constance in late spring (Lampert & Schober 1978, Geller 1980).

Samples were taken with 9 l van Dohrn bottles at depths of 0, 1, 2, 3, 4, 5, 6, 8 and 10 m, the last one being about the limit of the euphotic zone (1%-light-level). Sampling times were 0500, 0700, 0900, 1200, 1500, 1700, 2200, 0200 and 0500 h mid-European time.

Samples were preserved in Lugol's solution and counted according to
Utermöhl's (1958) method with an inverted microscope (WILD M40). At least 400 individuals of each species were counted per sample. In total the linear dimensions of 100 individuals of each species were measured.

The subaquatic light intensity was measured by a quantum-scalar irradiance meter (Biospherical Instruments, San Diego, CA). Underwater light was measured only once during the day, whereas surface light intensity was recorded continuously. The underwater light intensities were calculated assuming that the vertical light attenuation coefficients within the water column did not change during the day.

Dissolved orthophosphate, which is usually the limiting nutrient in Lake Constance (Stabel & Tilzer 1981), was measured according to the method of Lennox (1979), and dissolved nitrate according to the method of Wilhelms & Bernhardt (1969).

Results

No intermediates between the two forms of *Rhodomonas* mentioned above were found in Lake Constance (see insert in Figure 2). In the type resembling Pascher's *R. lens* both ends of the straight cell are pointed. The caudal refractive grain is small. Very often there are two bigger refraction grains in the apical third of the cell. The average cell size is $14 (± 2) \times 7 (± 2) \text{µm}$, the average cell volume $300 \text{µm}^3$. The type resembling Skuja's description of *R. minuta v. nannoplanctica* has a sharply pointed caudal end and a rounded flagellar end. The cell is curved and the caudal refractive grain large. The average cell size is $10 (± 2) \times 4.5 (± 1.5) \text{µm}$, the average cell volume is only about $80 \text{µm}^3$. The dimensions of both types are within the ranges of the original descriptions. Therefore in the following the original species names will be used.

*R. minuta v. nannoplanctica* occurs in the phytoplankton of Lake Constance throughout the year with a biomass maximum during the spring-bloom (usually in May), and forms high proportions of the total algal biomass between October and July. By contrast, *R. lens* only occurs in the winter plankton and during the spring-bloom (Sommer 1981). Both species contribute significantly to the spring bloom. Combined, their biomass comprises 40 to 75% of the total phytoplankton-biomass.

Whenever both species occur together and stratification of the water allows vertical gradients of cell-numbers and biomass, *R. minuta v. nannoplanctica* has its biomass peak closer to the surface than *R. lens*, thus indicating vertical niche separation.

During the light-period, both species show a tendency to concentrate in different layers, increasing their separation from each other. During the night time, when the stimulus for phototactic migration is lacking, the depth distribution of both species is more even (Figure 1).

In order to analyze the pattern of migration of both species the median depth (i.e. the depth below and above which 50% of the population is located) has been calculated and discussed together with the isopleths of the photosynthetically active radiation (PAR) and the gradients of dissolved P and N (Figure 2). In *R. minuta v. nannoplanctica* the median depth between 0900 and 1700 hours oc-
Vertical niche separation of two *Rhodomonas* species

Fig. 1. Diel changes of the vertical distribution of *Rhodomonas lens* (left side of the diagram, white) and of *Rhodomonas minuta* v. *nannoplancica* (right side, grey). The units are % of the total population of each species in the euphotic zone. The arrows indicate the main tendency of migration.

cured at a PAR of 480-680 μE.m$^{-2}$.s$^{-1}$, whereas in *R. lens* the median depth between 0900 and 1500 was at PAR level of 220-260 μE.m$^{-2}$.s$^{-1}$. Thus the average light intensity to which *R. minuta* was exposed was roughly 2.5 times higher than that of *R. lens*. After that period, when the median depth of both species kept at a fairly constant light level by vertical compensatory movements (compare Tilzer 1973), both species moved downward and thus were exposed to significantly lower light intensities. At 1900, PAR in the median depth of *R. minuta* was 68 μE.m$^{-2}$.s$^{-1}$ and for *R. lens* 15.5 μE.m$^{-2}$.s$^{-1}$ (the median depths differ by a factor of 4.4).

The more the species were concentrated at certain light levels the less was their spatial overlap. A quantitative measure of the overlap in depth was calculated according to an equation of Pianka (1973), which was first used for phytoplankton depth distribution by Wall & Briand (1980):

$$\alpha_{ij} = \frac{\sum p_i \cdot p_j}{\sqrt{\sum p_i^2} \cdot \sqrt{\sum p_j^2}}$$

$\alpha_{ij}$: degree of overlap: 0 = no overlap; 1 = total overlap

$p_i$: relative proportion in volume of species i in each sample

The values for $\alpha_{ij}$ are given in Table 1.

The concentrations for dissolved orthophosphate-phosphorus varied between 27 and 33 μg.l$^{-1}$, for dissolved nitrate-nitrogen between 309 and 526 μg.l$^{-1}$ (Figure 2), and probably neither nutrient was limiting.

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Fig. 2. Development of the median depth of *Rhodomonas lens* (solid line) and of *Rhodomonas minute v. nanoplanctica* (dotted line) during the 24-h cycle from May 20th to 21st. The isopleths of the light-intensity are at 1, 10, 100, 200, 500 and 1000 μE m⁻² s⁻¹. Insert: Both species in lateral and dorsal view. Right part: Gradients for dissolved orthophosphate-phosphorus and nitrate-nitrogen in μg l⁻¹.

Table 1. Degree of overlap between *Rhodomonas minute v. nanoplanctica* and *Rhodomonas lens* (α)

<table>
<thead>
<tr>
<th>time</th>
<th>α</th>
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<tbody>
<tr>
<td>0500</td>
<td>0.85</td>
</tr>
<tr>
<td>0700</td>
<td>0.77</td>
</tr>
<tr>
<td>0900</td>
<td>0.73</td>
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<tr>
<td>1200</td>
<td>0.65</td>
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<tr>
<td>1500</td>
<td>0.57</td>
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<tr>
<td>1700</td>
<td>0.61</td>
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<tr>
<td>1900</td>
<td>0.47</td>
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<tr>
<td>2200</td>
<td>0.67</td>
</tr>
<tr>
<td>0200</td>
<td>0.67</td>
</tr>
<tr>
<td>0500</td>
<td>0.65</td>
</tr>
</tbody>
</table>

The temperature was measured 7 times at 1 m intervals during the 24-h cycle. There were no indications of vertical shifts of the water masses. At 10 m the temperature was always 9.0°C. The surface temperature warmed up from 11.0°C to 11.8°C during daytime, while at a depth of 2 m it increased only from 9.9°C to 10.2°C. For *R. lens* the temperature of the median depths varied from 9.2°C to 9.9°C, for *R. minute v. nanoplanctica* it varied from 9.6°C to 10.2°C.
In addition to the morphological differences between both forms of *Rhodomonas*, there is also ecological evidence that they are valid species. Both behave as independent populations showing active segregation as long as the light gradient allows orientation in their movement. As the common nutrient concentrations are at the same level and probably nonlimiting throughout the whole euphotic zone, and as there is only a very small difference in temperature between the median depths of both species, light seems to be the dominant environmental factor characterizing the different niches of *R. lens* and *R. minuta v. nannoplanctica*. The independence of depth distribution for temperature is also indicated by the observations from the 1981 spring-bloom in Lake Constance, when both species bloomed at much higher water temperatures (up to 16°C) than in 1980. In the first phase of the day both species adjust their position to a certain light intensity, a pattern of migration behaviour of phytoflagellates that has been described by Talling (1971) and Tilzer (1973). The downward movement of both species in the afternoon has also been observed by Berman & Rodhe (1971) for *Peridinium* and by Harris, Heaney & Talling (1979) for *Ceratium hirundinella*. As there is no increase of dissolved nutrients in the lower parts of the euphotic zone, it is only possible to describe this pattern of behaviour, leaving the explanation to further experimental research.

**References**


