

Resource competition and interactive segregation between sympatric whitefish morphs

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Two whitefish morphs have been identified in lakes in northern Norway from a bimodal distribution of gill raker numbers: a sparsely- and a densely-rakered. Habitat choice and feeding ecology of whitefish were studied in five lakes with the two morphs living in sympatry, and in five lakes harbouring only the sparsely-rakered morph. In sympatry, the two whitefish morphs exhibited a strict niche segregation, the sparsely-rakered morph mainly residing in the littoral zone feeding on zoobenthos, whereas the densely-rakered morph predominantly fed on zooplankton and dominated in the pelagic zone. In allopatry, however, the densely-rakered morph exhibited a larger niche width, utilising both the benthic and pelagic habitats and having a diet that included both zoobenthos and zooplankton. Thus, in sympatry with densely-rakered whitefish, the sparsely-rakered morph appears to be relegated from the pelagic zone, resulting in an interactive segregation due to resource competition between the two morphs.

Introduction

Whitefish (*Coregonus lavaretus*) is a highly polymorphic species. Different morphs are usually separated by differences in gill raker numbers, and frequently two or more morphs live sympatrically in the same lake (e.g. Svårdson 1952, 1957, 1979, 1998, Bodaly 1979, Bergstrand 1982, Amundsen 1988a, 1988b, Sandlund & Næsje 1989, Bernatchez *et al.* 1996, Chouidnard *et al.* 1996, Amundsen *et al.* 2002, 2004). Sympatric living morphs often exhibit profound differences in habitat and food selection (e.g. Nilsson 1958, Lindström & Nilsson 1962, Amundsen 1988a, Bernatchez *et al.* 1999). This resource

polymorphism typically includes a benthic morphotype mainly feeding on zoobenthos and a pelagic morph mainly feeding on zooplankton, a pattern also commonly observed in other freshwater fish like charrs (Klemetsen & Grotnes 1980, Walker *et al.* 1988, Malmquist 1992, Skulason & Smith 1995, Adams *et al.* 1998, Bourke *et al.* 1999, Dynes *et al.* 1999), sticklebacks (Lavin & MacPhail 1986, Schluter & McPhail 1993) and sunfishes (Ehlinger & Wilson 1988, Robinson *et al.* 1993).

In lakes in northern Norway, two sympatric living whitefish morphs have been identified from a bimodal distribution of gill raker numbers, including a sparsely-rakered morph with

ca. 20–30 gill rakers and a densely-rakered morph with ca. 30–40 rakers (Amundsen 1988a, Amundsen *et al.* 1997, 1999, 2002, 2004). In sympatry, the sparsely-rakered morph is known predominantly to exhibit a benthic habitat and prey choice, whereas the densely-rakered morph is mainly pelagic and planktivorous (Amundsen 1988a, Amundsen *et al.* 1999, Bøhn & Amundsen 1998, 2001). These differences in resource utilisation between co-occurring morphs may be a result of different morphological adaptations and specializations, but have also been related to competition and interactive segregation (e.g. Nilsson 1958, Lindström & Nilsson 1962). An acid test with respect to the role of competition in resource partitioning is to compare the resource use in sympatry and allopatry under otherwise similar conditions (Nilsson 1967, Schoener 1986, 1989). A similar resource use in sympatry and allopatry of each species or morph would indicate selective segregation through genetically based adaptations, whereas different resource utilization between sympatry and allopatry would suggest interactive segregation as a result of competition. In the present study, we compare the resource use of sympatric living whitefish morphs with the resource utilization of the sparsely-rakered morph living in allopatry. A total of ten lakes were included in the study. Lakes with the densely-rakered morph living in allopatry have not been found, and could therefore not be incorporated in the analysis.

Material and methods

Study area

The study was carried out in ten subarctic lakes located within a 60 × 60 km large area at 69°N, 24°E in Finnmark County, northern Norway (Table 1). Five of the lakes had sympatric populations of the sparsely- and densely-rakered whitefish morphs (referred to as ‘Sympatric’ lakes), whereas in the other five lakes only the sparsely-rakered morph was present (referred to as ‘Allopatric’ lakes; Table 1). The lakes are located in the Kautokeino–Alta watercourse except for Vuoddasjavri, which is located in the Karasjokka–Tana watercourse. The lakes are all oligotrophic with some humic impact, and the ice-free season normally lasts from early June to late October. Whitefish is the dominant fish species in all ten lakes.

Fish sampling and analyses

The lakes included in the study were sampled once during the time period from 1990–2001 (Table 1). In all lakes sampling was carried out during the last week of August. Fish were sampled in benthic and pelagic habitats using standardized gillnets with bar mesh sizes from 10 to 45 mm (knot to knot). Each fish was classified as belonging to the sparsely- or densely-rakered morph by a visual evaluation of the

Table 1. Lake localities sampled for the present study. Sympatry refers to the presence of both the sparsely- and densely-rakered morphs, and allopatry to the presence of only the sparsely-rakered morph. *n* = number of observations (numbers of stomachs examined are given in brackets); SRM = sparsely-rakered morph, DRM = densely-rakered morph.

Lake locality	Morph presence	Area (km ²)	Altitude (m)	Max. depth (m)	Year of study	<i>n</i> SRM	<i>n</i> DRM
Stuorajavri	Sympatry	25	374	30	2000	91 (77)	78 (60)
Suopajavri	Sympatry	2	323	30	1996	101 (48)	87 (83)
Vuolgamasjavri	Sympatry	1.2	301	18	1995	89 (89)	82 (33)
Lahpojavri	Sympatry	7.2	327	25	1993	75 (75)	159 (70)
Vuoddasjavri	Sympatry	2.7	334	24	1994	78 (34)	213 (79)
Jårgajavri	Allopatry	1.9	450	27	1997	96 (55)	0
Durbunjavri	Allopatry	0.3	450	11	1990	123 (88)	0
Guorbajavri	Allopatry	0.7	454	12	1990	142 (53)	0
Jevdesjavri	Allopatry	1.5	360	19	2001	186 (60)	0
Biggejavri	Allopatry	6	381	52	1991	68 (43)	0

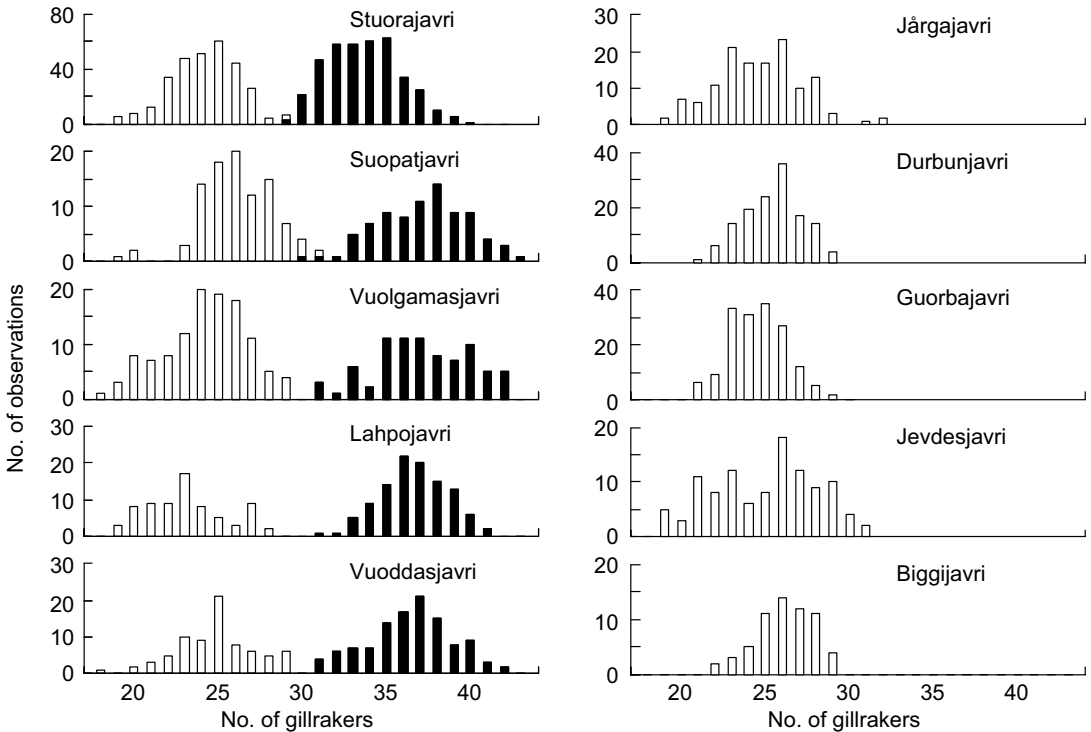


Fig. 1. Distribution of gill raker numbers in whitefish from the investigated lakes. The two morphs are indicated with different colours.

gill raker morphology (*see* Amundsen 1988a, Amundsen *et al.* 2004). The fish were measured for fork length and weight, and gills and stomachs were sampled and conserved in 96% ethanol. Only stomach samples from fish between 15 and 25 cm were used in the study. In the laboratory, the gill rakers on the first left branchial arch were counted under a dissecting microscope. Stomachs were opened and the total fullness was determined, ranging from empty (0%) to full (100%). Food items were further identified and their contribution to the total fullness estimated. The proportion of each diet category was expressed as percent prey abundance (A_i):

$$A_i = (\Sigma S_i / \Sigma S_j) \times 100,$$

where S_i is the stomach fullness composed by prey i and S_j the total stomach fullness of all prey categories (Amundsen *et al.* 1996).

Results

Gill raker distribution

In lakes Stuorajavri, Suopatjavri, Vuolgamasjavri, Lahpojavi and Vuoddasjavri the distributions of gill raker numbers ranged from 18 to 42, and were highly bimodal (Fig. 1). According to the visual classification of fish based on the morphological appearance of the gill rakers, the two morphs separated into each of the two modes in the gill raker distribution, hardly without any overlap in gill raker number (Fig. 1). Some differences in gill raker distributions were observed between the different lakes, but in general the sparsely-rakered morph had less than 30 rakers and the densely-rakered morph more than 30. In Järgajavri, Durbunjavri, Guorbajavri, Jevdesjavri and Biggijavri, in contrast, the distributions of gill raker numbers were unimodal ranging from 19 to 32 (Fig. 1). Thus, only the sparsely-

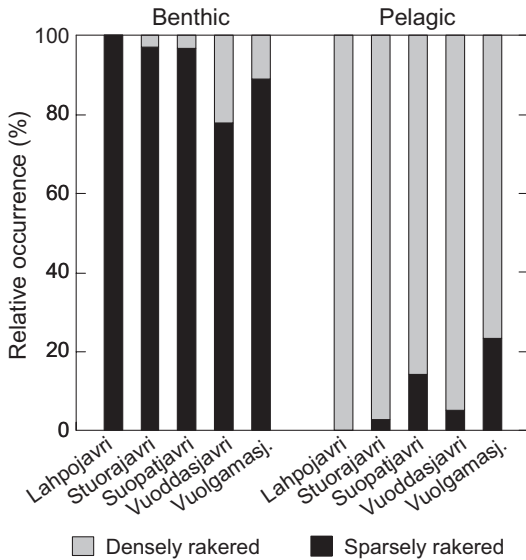


Fig. 2. Relative contribution of the sparsely- and densely-rakered morphs in whitefish catches from respectively benthic and pelagic habitats in the five lakes with sympatric morphs present.

rakered morph appeared to be present in these lakes, a conclusion that was also reached by the visual classification of fish from their gill raker morphology.

Habitat

In all lakes with sympatry of sparsely- and densely-rakered whitefish, the sparsely-rakered morph totally dominated in the benthic catches and the densely-rakered morph in the pelagic catches (Fig. 2). In the allopatric lakes, in contrast, the sparsely-rakered morph occurred commonly both in benthic and pelagic catches. A comparison of the catch per unit effort (CPUE; no. of fish per 100 m² gill net per night) of the sparsely-rakered morph in the pelagic zone, revealed a significantly higher CPUE in the allopatric lakes (Fig. 3; mean 8.8, range 1.9–13.8) than in the sympatric lakes (mean 1.0, range 0–2.9).

Diet

The densely-rakered morph had a diet totally dominated by zooplankton (Fig. 4a), whereas

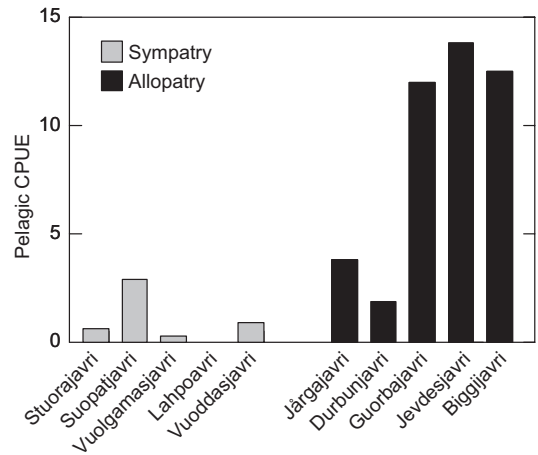


Fig. 3. Catch per unit effort (no. of fish per 100 m² gill net per night) of the sparsely-rakered morph in pelagic catches from sympatric and allopatric lakes.

the sympatric living, sparsely-rakered morph mainly had been feeding on benthic invertebrates, in particular benthic crustaceans, molluscs and insect larvae (Fig. 4b). In allopatry, in contrast, the sparsely-rakered whitefish had a diet dominated by zooplankton, although zoobenthos was also regularly consumed (Fig. 4c). The mean contribution of zooplankton in the diet of the sparsely-rakered morph was 57.4% (range 32%–74%) in the allopatric lakes as compared with 11.0% (range 0%–20%) in the sympatric lakes. The densely-rakered whitefish had a mean zooplankton contribution to the diet of 81.0% (range 59%–96%).

Discussion

The observed distribution of gill raker numbers documents the presence of two sympatric whitefish morphs in lakes Stuurajavi, Suopajavi, Vuolgamasjavi, Lahpojavi and Vuoddasjavi, whereas only the sparsely-rakered morph was present in lakes Jargajavi, Durbunjavri, Guorbajavi, Jevdesjavri and Biggjavri. In sympatry, the two whitefish morphs were strongly segregated with respect to habitat choice, the sparsely-rakered whitefish primarily residing in the benthic habitat and the densely-rakered morph in the pelagic zone. This was also reflected in the diet of the two morphs. The sparsely-rakered white-

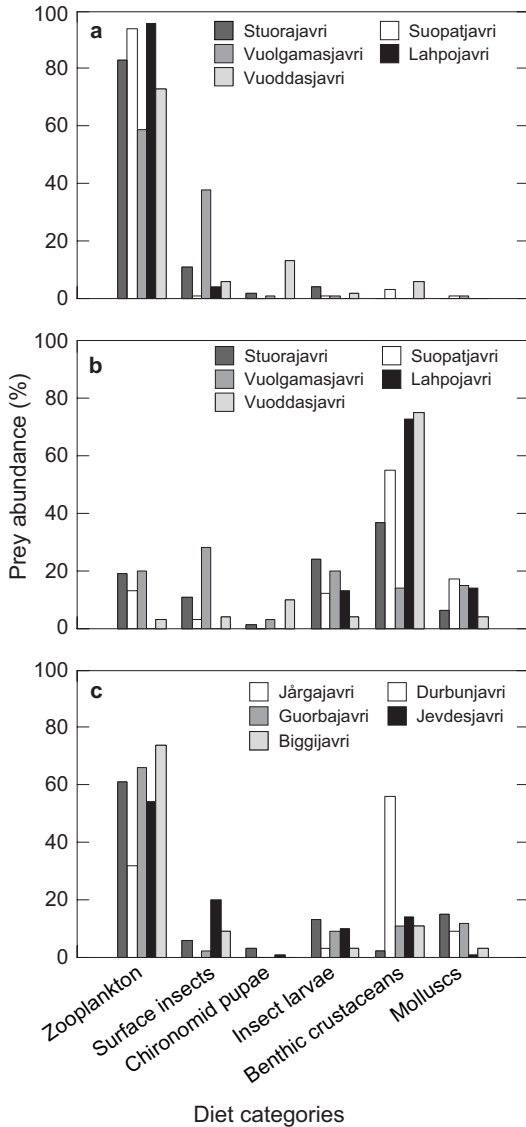


Fig. 4. Diet of the densely-rakered morph in sympatry (a), and the sparsely-rakered morph in sympatry (b) and allopatry (c) in the investigated lakes.

fish had mainly consumed zoobenthos and the densely-rakered morph mainly zooplankton. This resource-partitioning pattern was consistent for all the examined lakes where both morphs were present, and has also commonly been observed in other studies of sympatric whitefish morphs (e.g. Svärdson 1952, 1979, Nilsson 1958, Lindström & Nilsson 1962, Bodaly 1979, Amundsen 1988a, Bernatchez *et al.* 1999). In contrast, when the sparsely-rakered morph occurred in allopa-

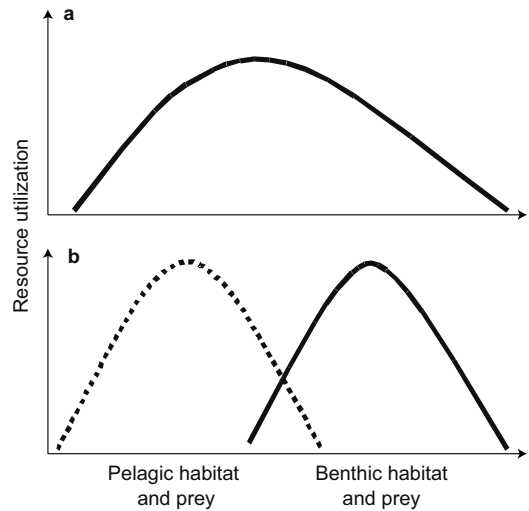


Fig. 5. Schematic niche considerations of the resource utilization of the sparsely-rakered morph (solid lines) in (a) allopatry and (b) sympatry with the densely-rakered morph (dotted line).

try, both the benthic and pelagic habitats were regularly occupied, and the CPUE in the pelagic zone was much higher than for sparsely-rakered whitefish living in sympatry with the densely-rakered morph. Furthermore, zooplankton dominated the diet of the allopatric living, sparsely-rakered morph, although a large proportion of benthic invertebrates was also included.

In terms of the niche concept (Hutchinson 1957, Schoener 1989), the allopatric resource utilization may reflect the fundamental niche of the sparsely-rakered morph, including a comprehensive use of both benthic and pelagic habitat and food resources. In sympatry, on the other hand, there were obvious limitations in resource use due to competition with the densely-rakered morph, which appears to be better adapted for the utilization of pelagic habitat and prey (Amundsen 1988a, Bernatchez *et al.* 1999, Amundsen *et al.* 2004). The sparsely-rakered morph is therefore mainly constrained to the use of benthic resources when living in sympatry with the densely-rakered morph, exhibiting a realised niche that is highly restricted in comparison with the resource utilization in allopatry (Fig. 5). The restricted niche performance of the sparsely-rakered morph in sympatry is thus a result of interactive segregation due to resource

competition with the densely-rakered morph. A similar conclusion was also suggested by Nilsson (1958), and Lindström and Nilsson (1962), but these authors did not have allopatric comparisons to confirm their claims. Lakes with the densely-rakered whitefish living in allopatry have not been found in northern Norway, and comparable studies of this morph unfortunately do not, therefore, exist. In the Pasvik watercourse, Norway and Russia, the densely-rakered morph has however been observed to adopt a benthic habitat and diet after being relegated from the pelagic by invading vendace, *Coregonus albula* (Bøhn & Amundsen 1998, 2001, Amundsen et al. 1999). Hence, also the densely-rakered whitefish appears to have a wide fundamental niche potentially including both pelagic and benthic resources, but in sympatry with the sparsely-rakered morph, the general pattern appears to be a niche constriction and segregation towards utilization of pelagic resources.

In conclusion, the habitat and diet segregation observed between sympatrically living sparsely- and densely-rakered whitefish is an interactive segregation related to resource competition between the two morphs (see e.g. Nilsson 1967), and not a result of selective segregation due to e.g. morphological differences. This is clearly demonstrated by the profound niche shift between allopatry and sympatry by the sparsely-rakered whitefish (Figs. 3, 4 and 5), which in the case of selective segregation should have maintained a similar niche in both situations. Minor selective (i.e. genetic) differences in morphology, behaviour or physiological adaptations may on the other hand play a role for the outcome of competition between the two morphs. Apparently the densely-rakered whitefish are better adapted for feeding on zooplankton in the pelagic, resulting in a relegation of the sparsely-rakered morph into the benthic habitat when the two morphs are living in sympatry.

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