

Gill raker morphology and feeding ecology of two sympatric morphs of European whitefish (*Coregonus lavaretus*)

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Received 10 Sep. 2002, revised version received 31 Dec. 2002, Accepted 17 Feb. 2003

Amundsen, P.-A., Bøhn, T. & Våga, G. H. 2004: Gill raker morphology and feeding ecology of two sympatric morphs of European whitefish (*Coregonus lavaretus*). — *Ann. Zool. Fennici* 41: 291–300.

European whitefish is a polymorphic species where different morphs often are identified by differences in their gill raker numbers. Gill rakers may play an important role in food-particle retention, particularly with respect to zooplankton feeding. Possible associations between feeding ecology and gill raker number and morphology were studied in European whitefish in the Pasvik watercourse. The numbers of gill rakers exhibited a bimodal distribution pattern, demonstrating the presence of two sympatric forms, including a sparsely-rakered morph with 18–30 and a densely-rakered morph with 28–42 rakers. The morphology of the gill rakers was correlated to the raker number and exhibited distinct differences between the morphs; sparsely-rakered whitefish having shorter, thicker and less densely packed rakers than the densely-rakered morph. Differences in habitat choice and trophic ecology between the two morphs appeared to be correlated to gill raker number and morphology. Densely-rakered whitefish exhibited a diet dominated by zooplankton and other pelagic prey, whereas the sparsely-rakered morph mainly fed on zoobenthos. Within the morphs, however, the feeding ecology of individual fish was not correlated with number and morphology of the gill rakers. Thus, whereas gill raker number and morphology appear to be a reliable marker for identifying ecologically and genetically different European whitefish morphs, the functional role with respect to the feeding performance of individual fish is less obvious.

Introduction

European whitefish (*Coregonus lavaretus*) and its North-American sibling, the lake whitefish (*Coregonus clupeaformis*), are highly polymorphic species. Different morphs are often separated by differences in gill raker numbers (Svärdson 1952, 1957, 1979, 1998, Bodaly

1979, Lindsey 1981, 1988, Bergstrand 1982, Amundsen 1988a, Sandlund & Næsje 1989, Bernatchez *et al.* 1996), and the differences have also been shown to have a genetic basis (Svärdson 1952, 1979, Bernatchez *et al.* 1996). Frequently two or more morphs live sympatrically in the same lake (Svärdson 1952, 1957, 1979, Bodaly 1979, Bergstrand 1982, Amund-

sen 1988a, 1988b, Bernatchez *et al.* 1996), and co-existing morphs often exhibit profound differences in habitat and food selection (e.g. Nilsson 1958, Lindström & Nilsson 1962, Amundsen 1988a, Bernatchez *et al.* 1999). The feeding habits of sympatric whitefish morphs have commonly been found to correlate with the number of gill rakers. Morphs with the lowest gill raker numbers are usually benthivorous whereas those with high gill raker numbers are planktivorous (Svärdson 1952, 1957, 1979, Nilsson 1978, Bodaly 1979, Bergstrand 1982, Amundsen 1988a, Bernatchez *et al.* 1999). It is suggested that morphs with high gill raker numbers are better adapted to zooplankton feeding because dense gill raker spacing is assumed to be more efficient for retaining small prey in the mouth cavity (O'Brien 1987, MacNeill & Brandt 1990, Link & Hoff 1998). Exceptions to this pattern do however exist (e.g. Svärdson 1950, Kliewer 1970, Chouinard *et al.* 1996), and the role of gill rakers in zooplankton feeding has been questioned (Seghers 1975, Wright *et al.* 1983, Langeland & Nøst 1995).

In lakes in northern Norway, two sympatric morphs of the European whitefish have been identified from a bimodal distribution of the gill raker numbers; one mode ranging from approx. 20–30 and the other from approx. 30–40 gill rakers (Amundsen 1988a, Amundsen *et al.* 1997, 2002, 2004, and unpubl. data). Individuals of the two morphs may also be separated visually by examining the morphology of the gill rakers; the morph with the lowest raker numbers having shorter, thicker and more widely spaced rakers, as compared with the longer, slender and more densely spaced rakers of the other morph (Amundsen 1988a). This subjective classification of morphological differences has, however, previously not been examined and tested quantitatively. The two morphs appear to have a diet and habitat choice correlated to their gill raker numbers: the sparsely-rakered morph predominantly having a benthic habitat and food choice; and the densely-rakered morph mainly being pelagic and planktivorous (Amundsen 1988a, Bøhn & Amundsen 1998, 2001, Amundsen *et al.* 1999).

In the present study, two sympatric morphs of European whitefish in the Pasvik watercourse, northern Norway and Russia, have been com-

pared with respect to gill raker number and morphology to scrutinize the assumed differences in length, breadth and distance of the rakers. It was hypothesized that the two morphs exhibit distinct quantitative differences with respect to gill raker morphology. Habitat choice and feeding ecology were further compared with gill raker number and morphology both at the population (i.e. morph) and individual levels, hypothesizing that fish with more numerous and densely packed gill rakers exhibit a stronger tendency for pelagic and planktivorous behaviour. Thus, the high-rakered morph was expected to be predominantly planktivorous, and the low-rakered form mainly benthivorous. Similarly, within each of the two morphs, the individuals with more numerous rakers were expected to be more pelagic and planktivorous than those with a lower raker number.

Study area and fish communities

The Pasvik watercourse belongs to three countries. It originates from Lake Inari (1102 km²) in Finland, runs into Russia and then defines the border between Norway and Russia for a length of about 120 km. The Norwegian–Russian part of the river system has a total area of 142 km², a catchment area of 18 404 km² and a mean annual water flow of about 175 m³ s⁻¹. There are altogether seven water impoundments in the watercourse. Most rapids and waterfalls have disappeared, and lakes and reservoirs currently dominate the former river system. The water level fluctuations are small, usually less than 80 cm. The ice-free season in the lakes and reservoirs lasts from late May or early June, to the end of October or early November. The lakes and reservoirs in the watercourse are oligotrophic with some humic impact; the Secchi-depth ranges from 2 to 6 m. The geology in the region is dominated by bedrock, mainly containing gneiss. The catchment area is dominated by birch- and pinewoods intermingled with stretches of bogs. Annual mean air temperature is low (−0.3 °C) and minimum and maximum monthly mean temperatures are −13.5 °C and +14.0 °C, respectively. The precipitation in the area is low, with an annual mean of 358 mm.

Two different lakes in the watercourse were investigated, Ruskebukta in the upper part and Skrukkebukta in the lower. Ruskebukta (69°13'N, 29°14'E; 52 m a.s.l.) has an area of 5.3 km², and a maximum depth of 15 m. Skrukkebukta (69°33'N, 30°7'E; 21 m a.s.l.) has an area of 6.6 km², and a maximum depth of 19 m. Both lakes are dimictic and oligotrophic with humic impacts.

Altogether 15 different fish species have been recorded in the Pasvik watercourse, but the most commonly occurring species in the lakes are European whitefish (*Coregonus lavaretus*), Eurasian perch (*Perca fluviatilis*), northern pike (*Esox lucius*), burbot (*Lota lota*), 9-spined sticklebacks (*Pungitius pungitius*) and brown trout (*Salmo trutta*). Vendace (*Coregonus albula*) has recently invaded the Pasvik River system, after being introduced to lake Inari in the 1960s (Amundsen *et al.* 1999, Bøhn & Amundsen 2001). Prior to the invasion of vendace, European whitefish was the dominant fish species in the pelagic, profundal and littoral habitats of the lakes and reservoirs in the Pasvik watercourse (Amundsen *et al.* 1999). The European whitefish consists of two different morphs, differentiated by the morphology and number of gill rakers, and referred to as densely- and sparsely-rakered whitefish (Amundsen *et al.* 1997, 1999), or, with reference to their predominant food and habitat choice, as pelagic and benthic whitefish (Amundsen 1988a, 1988b, Amundsen *et al.* 2002), respectively. In the pelagic zone, the densely-rakered whitefish on average constituted > 95% of the total catches prior to the vendace invasion, whereas sparsely-rakered whitefish, brown trout, Eurasian perch and northern pike occasionally were caught (Amundsen *et al.* 1997, 1999, Bøhn *et al.* 2002). After the invasion of vendace, the European whitefish has been partially displaced from the pelagic zone where vendace has now become the dominant species (Bøhn & Amundsen 1998, 2001, Amundsen *et al.* 1999, unpubl. data). In the profundal zone, both densely- and sparsely-rakered whitefish frequently occur and dominate the catches, which also include burbot and Eurasian perch. Densely- and sparsely-rakered whitefish are, together with Eurasian perch, also the dominant species in the littoral, but northern pike and burbot are also regularly caught.

Material and methods

Fish sampling

Sampling for the present study was carried out in lakes Ruskebukta and Skrukkebukta during 12–18 June, 5–11 August and 15–21 September in 1998. In both lakes, the same patterns were revealed with respect to gill raker number and morphology and feeding ecology and habitat choice. Data from the two localities have therefore been integrated in the result presentation. European whitefish were sampled both in benthic and pelagic habitats using gillnets with bar mesh sizes from 10 to 45 mm (knot to knot). Each fish was subjectively classified as belonging to the sparsely or densely-rakered morph from a visual evaluation of the gill raker morphology (*see* Amundsen 1988a). The fish were measured for fork length and weight, and gills and stomachs were sampled and preserved in 96% ethanol. Only fish larger than 140 mm were used in the analyses, since gill raker development appears to be incomplete and raker number may increase with increasing size in juvenile fish (Todd 1998, Sandlund *et al.* 2002, Yu. S. Reshetnikov pers. comm.). In the present study, the gill raker number was independent of fish size at lengths > 140 mm (Linear regression; $p > 0.05$).

Analyses of gill raker number and morphology

In the laboratory, the first left branchial arch was cut off from the rest of the gill, and the number of gill rakers (including rudiments) counted under a dissecting microscope. The gill arch was further mounted with the gill rakers perpendicular to the base of the arch, and a digital photographic image was taken under the microscope. From the digitalised images were measured: (1) the gill raker length from tip to base of the longest and the next two ventral rakers, (2) the distances between these rakers, and (3) the breadth at the base of the longest and the next ventral raker. The parallel measurements of raker length, distance and breadth exhibited strong correlations (Linear regression; $p < 0.001$, $r^2 \geq 0.87$, $n = 278$ for all tests), and the average measurements for each individual fish

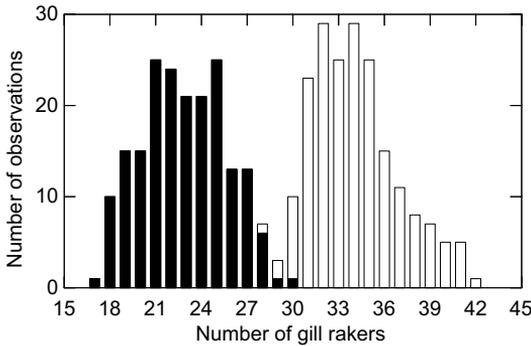


Fig. 1. Distribution of gill raker numbers of European whitefish from the Pasvik watercourse. The two morphs are indicated with different colouring based on the visual classification of gill raker morphology.

have therefore been used in the further analyses. All three measurements increased with increasing length of the fish (linear regression: $p < 0.001$), and the measurements were therefore standardized to a fish of 200 mm fork length using the equation:

$$M_{200} = M(\text{FL}_{200}/\text{FL})^b,$$

where M is the original morphological measure, M_{200} the standardized measure, FL the original fork length of the fish, FL_{200} the standardized fork length (200 mm), and b the slope in a linear regression between $\log M$ and $\log \text{FL}$ (Ihssen *et al.* 1981, Adams *et al.* 1998). The standardized morphological measurements were independent of fish length (linear regression: $p > 0.05$).

Stomach analyses

Stomachs were opened and the percentage degree of 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 in percent as prey abundance (A_i):

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

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).

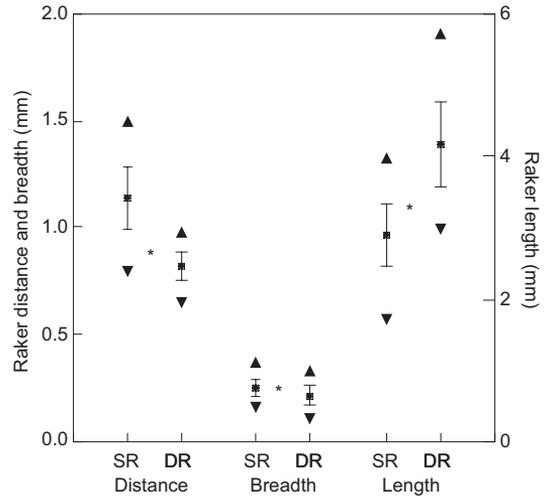


Fig. 2. Comparisons of gill raker distance, breadth and length between the sparsely-rakered (SR) and densely-rakered (DR) morphs. Error bars represent standard deviation and arrows indicate the total range of the distributions. Significant differences between the morphs are indicated by asterisks ($p < 0.001$).

Diet overlap was quantified using the percentage overlap index (Krebs 1999):

$$D = \sum \min(A_{ij}, A_{ik}),$$

where D is the diet overlap, and A_{ij} and A_{ik} are the prey abundance of prey i for predator j and k , respectively. The overlap is considered to be significant when the index value exceeds 60% (Wallace 1981).

Statistical methods

Liliefors test (Zar 1999) revealed no significant differences from the normal distribution both for number, distance, length and breadth of the gill rakers. Statistical comparisons of means were performed with Student's t -test. The Dunn-Sidak adjustment was used with multiple testing (Sokal & Rohlf 1994). Linear regression was used for examining relationships between the morphometric parameters and fish size and gill raker numbers. Multivariate discriminant analysis was used to determine if the *a priori* (i.e. by eye) grouping of the two morphs could be distinguished on

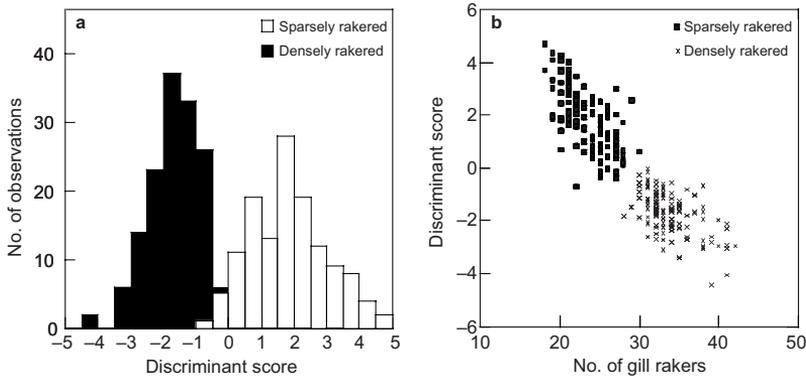


Fig. 3. — **a:** Frequency distribution of discriminant function scores of sparsely and densely-rakered whitefish from analysis of gill raker distance, length and breadth. The discriminant function analysis was highly significant for the differences between the two morphs (Wilks' $\lambda = 0.2446$, $p < 0.001$). — **b:** Plot of discriminant function score against gill raker number.

the basis of the quantitative morphometric gill raker data.

Results

Gill raker number and morphology

The European whitefish from the Pasvik watercourse exhibited a bimodal distribution of gill raker numbers (Fig. 1), confirming the presence of two different morphs in the watercourse. According to the visual classification of the two morphs based on the morphological feature of the gill rakers, the sparsely-rakered morph had from 18 to 30 gillrakers (mean 23.3) and the densely-rakered morph from 28 to 42 rakers (mean 33.7).

The two morphs exhibited large and significant differences both in length, distance and breadth of the gillrakers (Fig. 2). The densely-rakered morph had longer and narrower rakers with a shorter distance between the rakers as compared with those of the sparsely-rakered morph. The differences were highly significant for all three measures (t -test: $p \leq 0.001$), but were most profound and with the least overlap for length and distance. A discriminant analysis of length, distance and breath of the gill rakers showed that the *a priori* visual classification of the two morphs was strongly in accordance with the morphometric measurements. The

distribution of the discriminant function scores was highly bimodal with only a minor overlap between the two morphs (Fig. 3a), and in total, 98% of the fish had been correctly classified with respect to morphological differences of the gill rakers (Table 1a). Furthermore, plotting discriminant scores against gill raker numbers, the points were separated into two distinct groups representing each of the two morphs (Fig. 3b). Similarly, expanding the discriminant analysis also to include raker numbers, 100% of the fish had been categorized correctly from the *a priori* visual classification (Table 1b).

Table 1. Classification of European whitefish morphs by jackknife discriminant analyses of (a) gill raker distance, length and breadth, and (b) gill raker number in addition to the three parameters used in part a. SRM = Sparsely-rakered morph, DRM = Densely-rakered morph.

Discriminant analysis grouping	<i>A priori</i> grouping		
	SRM	DRM	Total
a			
SRM	125	0	125
DRM	6	147	153
% Correctly assigned	95	100	98
b			
SRM	131	0	131
DRM	0	147	147
% Correctly assigned	100	100	100

Habitat distribution

In the samples of European whitefish from the benthic habitat, the sparsely-rakered morph had a higher prevalence than the densely-rakered morph (Table 2). The densely-rakered morph, in contrast, totally dominated the pelagic habitat, where only a few sparsely-rakered fish were caught. There were no significant differences in gill raker number and morphological measures for the sparsely-rakered morph between individuals caught in the benthic and pelagic habitats, respectively (Fig. 4a). For the densely-rakered whitefish small but significant differences were observed; the number and length of the gill rakers were significantly larger in fish caught in benthic habitats, whereas the distance between the rakers was smallest in the pelagic caught fishes (Fig. 4b).

Diet

The diet of the sparsely-rakered morph was dominated by zoobenthos such as molluscs, benthic crustaceans and insect larvae throughout all sampling periods and exhibited moderate seasonal variations (Fig. 5a). Zooplankton was almost absent from the diet in June and August and gave only a minor contribution (9.7%) in September. The densely-rakered whitefish had in contrast a diet dominated by pelagic prey types (zooplankton, chironomid pupae and surface insects), but zoobenthos also gave a significant contribution to the diet (Fig. 5b). Chironomid pupae were the most important prey in June, whereas zooplankton exhibited an increasing importance towards autumn and dominated in September, constituting 73.9% of the diet. In June, the two morphs exhibited a high percentage overlap in the diet

Table 2. Relative composition (%) of the sparsely and densely-rakered morphs in European whitefish catches from the benthic and pelagic habitats in the Pasvik watercourse.

	Sparsely-rakered morph	Densely-rakered morph	<i>n</i>
Benthic catches	59.2	40.8	439
Pelagic catches	3.5	96.5	85

($D = 70.7\%$), but the overlap decreased towards autumn and was 54.5% and 31.0% in August and September, respectively (Fig. 6).

Comparisons of the diet within each of the two morphs between fish with respectively low and high raker number (18–23 versus 24–30 rakers for the sparsely-rakered morph, and 28–34 vs. 35–42 for the densely-rakered morph) revealed a high diet similarity within each of the morphs (Fig. 6; Diet overlap always > 60%), suggesting that the number of gill rakers did not have any significant impact on intra-morph variations in prey choice. Furthermore, the contribution of zooplankton and pelagic prey to the diet did not exhibit any increase with increasing gill raker number within the morphs, whereas a distinct increment was observed in the transition between the two morphs, i.e. going from 28 to 30 gill rakers (Fig. 7). Finally, comparisons were also carried out for number, distance and length of gill rakers within the two morphs between: (1) individuals that had a predominantly pelagic respective to a predominantly benthic diet, and (2) individuals that had a predominance of small respective to large prey in their stomachs. None of these comparisons revealed any significant differences (t -test: $p > 0.05$), supporting the conclusion that intra-morph diet choice was not correlated to gill raker number or morphology.

Discussion

The data presented here on gill raker number and morphology confirms the existence of two discrete European whitefish morphs in the Pasvik watercourse. The two morphs exhibit distinct differences both in gill raker number, distance, length and breadth; the densely-rakered morph having the longest, most closely packed and narrowest rakers. Furthermore, it is shown that a visual classification based on gill raker appearance successfully distinguishes between individuals of the two morphs. Thus, the two morphs are easily and precisely separated by a brief *in situ* examination of the gills, and laborious gill raker counting is not a necessity for morphotype identification. The two morphs recorded in the Pasvik watercourse closely resemble the European whitefish morphs that have been described from

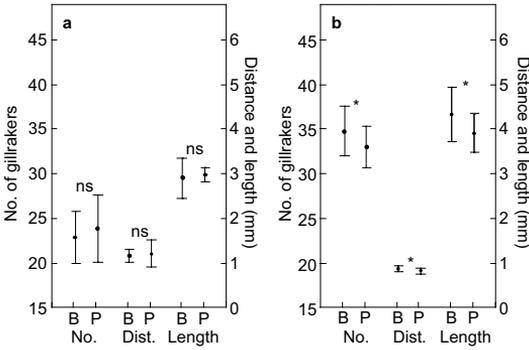


Fig. 4. Comparisons of gill raker numbers, distance and length between individuals caught in benthic (B) and pelagic (P) habitats. — **a:** Sparsely-rakered morph, — **b:** Densely-rakered morph. Error bars = S.D., * = significant differences ($p < 0.05$), ns = no significant differences.

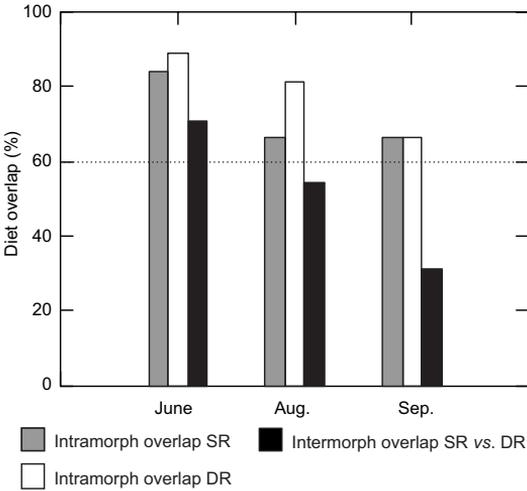


Fig. 6. Intra-morph diet overlap between individuals with low and high raker numbers, respectively (sparsely-rakered morph (SR): 18–23 vs. 24–30 rakers; and densely-rakered morph (DR): 28–34 vs. 35–42 rakers), and inter-morph diet overlap between the sparsely and densely-rakered morphs.

other lake localities in northern Norway (Amundsen 1988a, 1988b, Amundsen *et al.* 2002, 2004). Identification of different whitefish morphs from the numerical distribution of gill rakers has commonly been accomplished (e.g. Svårdson 1950, 1957, 1979, 1998, Lindsey 1981, 1988, Heinonen 1988, Sandlund & Næsje 1989, Bernatchez *et al.* 1996), but this is to our knowledge the first documentation of distinct inter-morph differences in gill raker morphology.

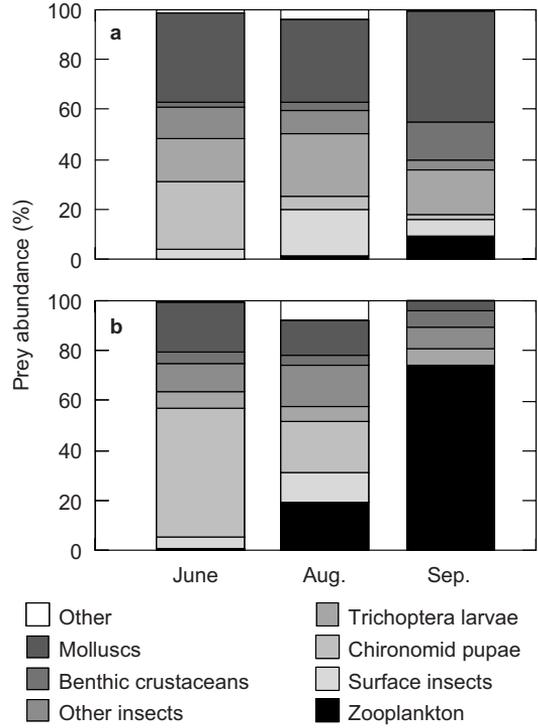


Fig. 5. Comparison of the diet of (a) sparsely-rakered and (b) densely-rakered whitefish morphs.

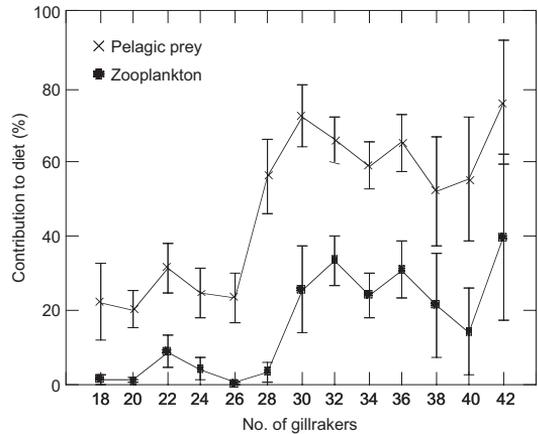


Fig. 7. The relationship between number of gill rakers and the contribution of zooplankton and total pelagic prey to the diet. Error bars = standard error.

The two European whitefish morphs in the Pasvik watercourse are ecologically dissimilar. The densely-rakered morph dominated in the pelagic zone, whereas the sparsely-rakered whitefish was most prevalent in the benthic habitat. Similarly, the densely-rakered morph

had mostly been feeding on zooplankton, especially in the autumn, or other pelagic prey like surface insects and chironomid pupae in early summer. For the sparsely-rakered morph, in contrast, typical benthic prey such as molluscs, Trichoptera larvae and benthic crustaceans dominated the diet. A similar resource-partitioning pattern has frequently been found in other systems with sympatric whitefish morphs (e.g. Nilsson 1978, Bodaly 1979, Amundsen 1988a, Bernatchez *et al.* 1999). The diet and habitat segregation between the two sympatric morphs in the Pasvik watercourse was however less distinct than observed in other lake systems in northern Norway (Amundsen 1988a, Amundsen *et al.* 2004, and unpubl. data), because the densely-rakered whitefish also utilised benthic habitats to a large extent and fed on typical benthic prey. This may partly be related to the riverine characteristics of the Pasvik watercourse that has a morphometry dominated by fairly narrow and shallow lakes with a short distance between pelagic and benthic habitats. However, the main reason for the benthic component in the ecology of the densely-rakered morph seems to be the recent invasion of vendace in the watercourse (Amundsen *et al.* 1999). The vendace invasion has relegated European whitefish from the pelagic zone into benthic habitats (Bøhn & Amundsen 2001), whereas prior to the vendace invasion the segregation between the two European whitefish morphs was more profound. However, even in the presence of the zooplanktivore specialist vendace in the pelagic zone, there was a strong segregation between the two European whitefish morphs in autumn, when the food resources are known to be most limited in sub-arctic lake systems (Nilsson 1967, Amundsen & Klemetsen 1988, Amundsen 1989). At this time, zooplankton totally dominated the diet of the densely-rakered morph, whereas the sparsely-rakered whitefish mainly consumed zoobenthos.

The resource polymorphism observed in European whitefish in the Pasvik watercourse appears to be related to the phenotypic differentiation in gill raker number and morphology of the two morphs; the morph with the most numerous and densely-spaced gill rakers being planktivorous. A similar relation

has also been suggested from other studies of both whitefish (e.g. Heikinheimo-Schmid 1985, Amundsen 1988a, Bodaly *et al.* 1992, Bernatchez *et al.* 1999) and other fish species (e.g. Lavin & McPhail 1986). A link between morphology and resource-use specialization (*see e.g.* Wikramanayake 1990, Schluter 1995, Wainwright & Barton 1995, Wainwright 1996) may, therefore, also apply to gill rakers and zooplankton feeding. Gill raker number and morphology may thus be adaptive traits mediating the resource use of sympatric morphs through a functional role of gill rakers in zooplankton retention, and resource competition may suggestively be a driving force in the phenotypic divergence between morphs. On the other hand, given a strong link between gill raker characteristics and the ability for zooplankton feeding, a distinct intra-morph variation in resource use could also be expected in relation to the variability in gill raker counts and morphology. In the present study, however, despite distinct ecological differences between the two morphs, no effect of gill raker number and morphology was found with respect to the feeding ecology within each morph. The role of gill rakers in the feeding performance of individual fish therefore remains dubious. It should on the other hand be kept in mind that both gill raker number and morphometric measurements exhibit a strong bimodality, and the discriminant analysis further demonstrated a distinct segregation in morphological traits between the two morphs. This might illustrate the presence of adaptive peaks (*see e.g.* Eldredge 1989) with respect to gill raker morphology and the utilization of respectively pelagic and benthic resources, and potentially also involving disruptive selection and a low fitness of individuals with an intermediate gill morphology (*see e.g.* Lu & Bernatchez 1998). Hence, large differences in the ecological performance should mainly be found between morphs, and not between individuals within the morphs. But these aspects are however still open to speculation. Thus, in conclusion, the gill raker number and morphology appear to be reliable markers for identifying ecological and genetically different European whitefish morphs, whereas the functional role with respect to the feeding performance of individual fish is less obvious.

Acknowledgements

Thanks are due to Laina Dalsbø and Jan Evjen for assistance during field and laboratory work.

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