Coregonids

17

Konrad Dabrowski,[1] Sergiusz Czesny[1,*] and Malgorzata Matusiewicz[1,†]
[1]School of Natural Resources, Ohio State University, Columbus, OH 43210, USA

Introduction

Whitefish (*Coregonus* sp.) have a northern circumpolar distribution, occurring in North America, Europe and Asia (Bodaly *et al.*, 1991). From the viewpoint of aquaculture, it is a country with no native coregonids (Japan) and countries in the most southern distribution of this genus (Italy) that have shown the greatest interest in the potential of coregonids as a farm-raised fish. Coregonids in Japan originated from pond-cultured *Coregonus lavaretus maraena* and *Coregonus peled* from Czechoslovakia and were domesticated in Saku Station, Nagano Prefecture.

Interest in cage-farming methods increased during the 1970s and 1980s, primarily for the development of propagation programmes to mitigate the negative effects of lake eutrophication and spawning-habitat deterioration for coregonids. Results from these studies suggested that supplementary feeding of juveniles with commercial diets in cages is extremely beneficial to their growth and survival during the episodes of low zooplankton abundance in the epilimnetic layer of lakes (Mamcarz, 1990).

The nutritional requirements of coregonids are little known. Mass rearing of larval coregonids was resolved in 1984 (Dabrowski *et al.*, 1984) and subsequently several authors have reported success in growing coregonids fed formulated practical diets in Japan (Dabrowski *et al.*, 1986), Europe (Rosch and Dabrowski, 1986; Champigneulle, 1988; Dabrowski and Poczyczynski, 1988), the USA and Canada (Drouin *et al.*, 1986; Zitzow and Millard, 1988; Harris and Hulsman, 1991). Furthermore, Shiose *et al.* (1984) and Gillet (1991) reported production of offspring to maturity from semidomesticated whitefish reared on a dry diet in intensive systems in Japan and France, respectively.

Present addresses: *Illinois Natural History Survey, Lake Michigan Biological Station, Zion, IL 60099, USA; †Department of Biochemistry, Medical Academy, Wroclaw, Poland.

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Nutrient Requirements

Protein

Koskela (1995) performed growth studies with European whitefish of 50 g initial body weight fed one of six experimental, fish-meal-based diets containing from 34% to 58.7% crude protein. However, lipid levels decreased from 30.7% to 16.6% as protein level increased, complicating the interpretation of the results. Fish increased body weight threefold during a 75-day-long study at water temperatures of 13.7–18.7°C; however, there were no significant differences in weight gain. The authors concluded that a protein level of 34% is sufficient to sustain growth of whitefish at a high rate, but this may be an underestimation as diet palatability most probably changed dramatically with decreasing fish-oil supplement from 21 to 5.9%.

Fukatsu (1985) has also used diets based on fish-meal with European whitefish domesticated in Japan's Nagano Prefecture for several generations. In these formulations, protein level increased from 27.2 to 46.5%, but the level of supplemented cod-liver oil was only 3.4–5%. Whitefish fingerlings of 4 g body weight were used and, based on the protein efficiency ratio, the optimum protein level was estimated at 34%.

In a study with Lake Erie *Coregonus clupeaformis* raised for 2 years in captivity on formulated, commercial diets, fish were allocated to one of five experimental, fish-meal-based diets with protein levels between 25.5 and 49.9% (Dabrowski, 1995). Diets were formulated (Table 17.1) with increasing proportions of 'basal' protein carrier and balanced for lipids and minerals in such a manner that an increase in 'basal' ingredient accompanied a decrease in fish-oil supplement (from 14 to 6%) and mineral and vitamin mixtures. Consequently, amounts of lipids and minerals in all diets were much more similar than would be the case with simple protein-ingredient replacement. Significant increases in weight gains were found when the dietary protein level was increased from 25.5 to 35% (Fig. 17.1). No significant differences were found in haematological parameters of whitefish fed different protein levels. The optimum protein level for growth of whitefish during the grow-out phase was determined as 36.5%.

In accompanying studies, the concentration of total free amino acids in blood plasma corresponded to fish growth; however, it indicated lower absorption of dietary amino acids in fish fed a diet with 49.5% protein. Several free amino acids in whitefish liver have shown a breakpoint at a dietary protein level maximizing growth (Fig. 17.2), but then the trends markedly differed among individual amino acids. The first panel in Fig. 17.2 may be an illustration of an inappropriate leucine/isoleucine ratio, whereas the panel at the bottom demonstrates a deficiency in methionine.

These results may indicate that methionine is the first limiting amino acid, followed by lysine and arginine (Fig. 17.2). Arzel *et al.* (1995) hypothesized that, at variable levels of protein in the diet, concentrations of some essential amino acids in fish tissues may increase at a protein value inferior to the requirements. This is further interrelated to a variable protein/lipid ratio. Fynn-Aikins *et al.*

Table 17.1. Examples of diet composition used in studies of protein, amino acid requirement and attractant supplements with lake whitefish (*C. clupeaformis*).

Ingredients	Protein requirement study (% dry wt)	Ingredients	Amino acid requirement study (% dry wt) (lysine)	Ingredients	Attractant study (% dry wt)
Basal*	40–80	Casein	20	Casein	7 or 10
Maize starch	12.35–43.75	Gelatin	7.15	Gelatin	3 or 4
Fish-oil	6–14	Dextrin	23.43	Dextrin	23.43
Mineral mix	1–1.4	Cellulose	18.97–21.12	Attractant†	4 or 8
Vitamin mix	0.5–0.7	Amino acid mixture‡	14.05	Amino acid mixture‡	14.05
Choline chloride	0.1	Cod-liver oil	4	Maize starch	10
Vitamin C	0.05	Maize oil	4	Cod-liver oil	4
Vitamin B_6	0.001	Vitamin mix	1	Maize oil	4
		Mineral mix	2	Vitamin mix	1
		Carboxymethyl cellulose	2	Mineral mix	2
				CMC	2
				Choline chloride	0.2
				Vitamin C	0.1
				Cellulose	23.22 or 27.22

*Basal (%): menhaden fish-meal 61.5, maize-gluten meal 16.5, blood meal 11, whey 11.

† Attractant: CPSC, concentrate des proteines soluble des poissons, Soporopeche S.A., Boulogne, France; whitefish muscle freeze-dried; krill meal; menhaden fish-meal

‡ Non-essential amino acids (%): alanine 15.74, aspartic acid 28.77, glycine 5.41, glutamic acid 27.56, proline 1.25, serine 21.27.

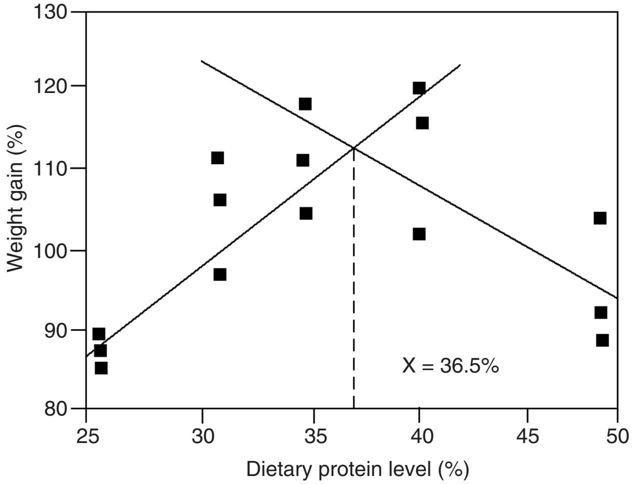


Fig. 17.1. Determination of protein requirement in lake whitefish (*C. clupeaformis*). The optimum level was estimated based on regression analysis at 36.5% (Dabrowski, 1995).

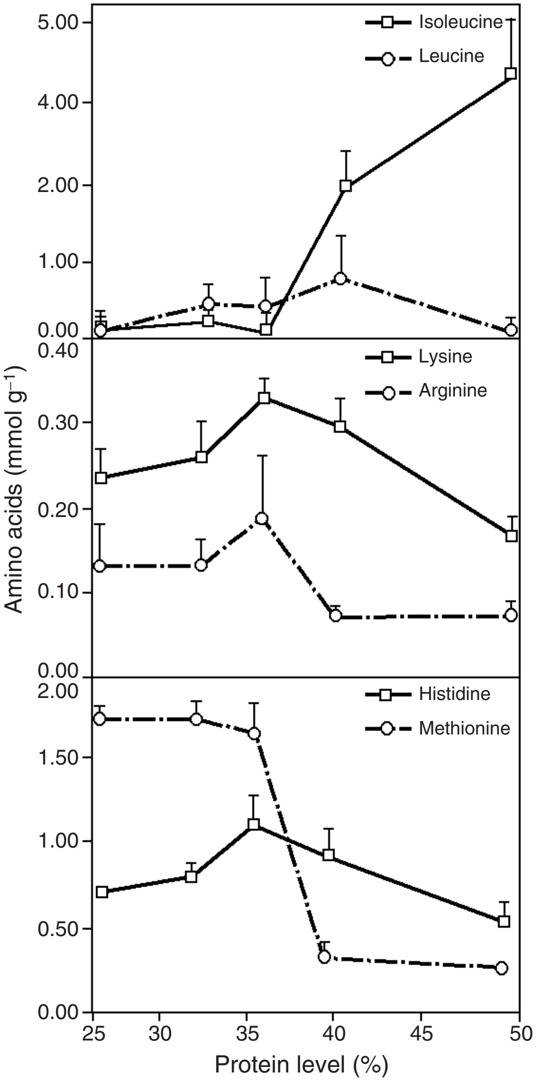


Fig. 17.2. The concentrations of free amino acids in lake whitefish liver following a feeding experiment with different protein levels. See Table 17.1 for diet formulations.

(1995) concluded that amino acid-catabolizing enzymes in salmonid fishes (closely related to coregonids) were not affected by variation in protein level, although different energy sources had a significant impact on protein retention. We examined the aspartate aminotransferase (AspAT) activity in whitefish liver (Ciereszko *et al.*, 1998). We found a significant decrease in AspAT activity only in fish fed a diet with the highest protein level (Dabrowski, 1995).

Preliminary studies were carried out for lysine and arginine requirements in lake whitefish juveniles (Dabrowski, 1995). Basal diets were formulated to contain 35% protein, using purified ingredients (Table 17.1). A mixture of crystalline L-amino acids (except lysine and arginine) was used to provide the balance so that the amino acid profile was similar to that of whole-egg protein (Santiago and Lovell, 1988). At the termination of the 24-week-long experiment, muscle samples from the dorsal part were taken and analysed for free amino acids (Fig. 17.3).

Weight increase analysis did not show significant differences among treatments, although these data subjected to a broken-line method indicated the dietary arginine and lysine requirements at 1.2 ± 0.1 and 1.5 ± 0.1%, respectively. Free amino acids have shown significantly higher concentrations at the dietary lysine level of 1.75% (Fig. 17.3). The latter is very close to an established maximum utilization level of lysine in rainbow trout, *Oncorhynchus mykiss*, 1.85% (Pfeffer *et al.*, 1992), and the requirement suggested for striped bass, *Morone saxatilis*, 1.5% (Griffin *et al.*, 1992).

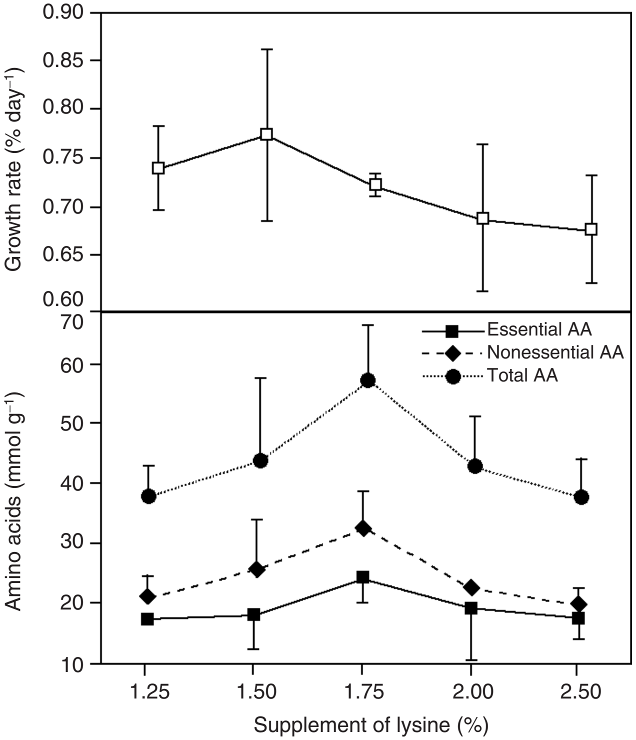


Fig. 17.3. Daily body increments and free amino acids (AA) in muscle of whitefish juveniles fed semipurified diets supplemented with L-lysine. Fish were 5–8 g body weight and were assigned to 30 conical tanks, in triplicate (20 fish) per treatment. Feed was provided twice a day at 2% body weight day^{-1}.

Energy

Different levels of protein offered in the experimental diets (Table 17.1) had no significant effect on the total lipid content in whitefish muscle. However, the polar/neutral lipid ratio in liver differed significantly after 4 and 7 months of feeding as well as between diets with different protein–energy ratios (Fig. 17.4). The high proportion of neutral lipids in the liver corresponds to accumulation of oleic acid (Fig. 17.4B) and saturated fatty acids (Fig. 17.4D). This indicates that more research is required in the area of protein/energy optimization as well as in respect of the detrimental effect of excessive dietary lipids in cases of low dietary protein.

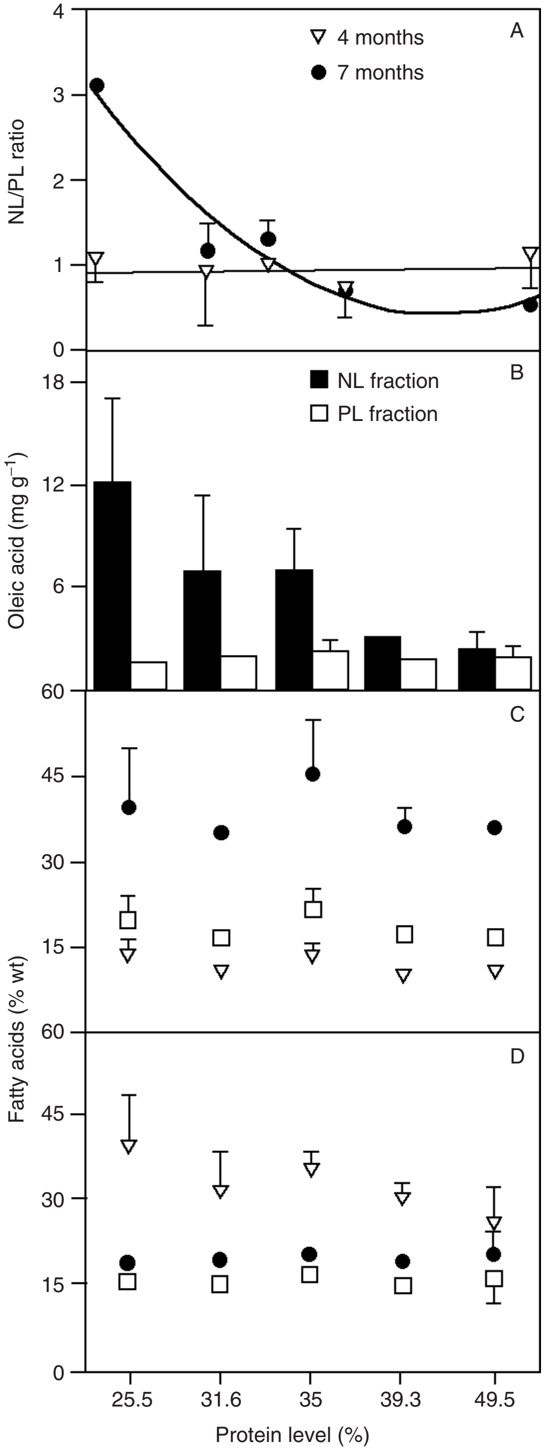
Environmental manipulation can also influence the chemical composition of the body in coregonids. Delayed spawning, enforced by increased day length in the autumn, resulted in an extended period of feeding on high-energy-density diets and had a positive impact on the n-3/n-6 fatty acid ratio in gonad lipids of *C. peled* (Dabrowski *et al.*, 1992). In the deep-water Lake Baikal whitefish (*Coregonus autumnalis migratorius*), a dramatic decrease in the phospholipid–triglyceride ratio was observed with increasing age of the fish. As fish increased in age from 3 to 13 years, the proportion of docosahexaenoic acid (DHA) decreased from 33.2% to 19.7% (Ju *et al.*, 1997). This may indicate that protein–energy utilization changes considerably in coregonid ontogeny.

Lipid and fatty acids

Coregonid muscles contain high levels of lipids (Dabrowski, 1982a,b) and particularly high levels of the polyunsaturated fatty acids (PUFA) DHA, 22:6n-3 (8.4–10.1%) and eicosapentaenoic acid (EPA), 20:5n-3 (6.8–8.2%) (Kaitaranta and Linko, 1979), which are usually most abundant in lipids of marine fish. In addition, coregonid lipids had high proportions of linoleic acid, 18:2n-6 (4–5.2%) and linolenic acid, 18:3n-3 (4.3–5.1%).

Seasonally, the level of PUFA in the phospholipid fraction of coregonid flesh can increase to 39.7% for DHA and 10.3% for EPA (Linko *et al.*, 1992). The same authors also indicated that the plankton fatty acids are transferred into fish lipids without major modifications. The high level of PUFA is consequently reflected in the composition of fatty acids deposited in coregonid eggs and larvae (Soivio *et al.*, 1989). This composition is indicative of the structural importance of PUFA in phospholipid-containing membranes during embryonic development of coregonids in temperatures frequently close to freezing, 0.1–0.5°C (Luczynski *et al.*, 1984).

It has been observed that a difference exists between freshwater and marine fish in the fatty acid desaturation/elongation pathway both *in vivo* and in cultured cell lines (Tocher and Ghioni, 1999). The evidence obtained in studies with domesticated *C. lavaretus* by Watanabe *et al.* (1989) suggests that both n-6 and n-3 are essential for growth of coregonids, although the growth improvement after addition of only n-3 fatty acids to a diet containing exclusively oleic acid was


A
▽ 4 months
● 7 months
NL/PL ratio
4
3
2
1
0
B
■ NL fraction
□ PL fraction
Oleic acid (mg g^{-1})
18
12
6
60
C
45
30
15
60
D
45
30
15
0
Fatty acids (% wt)
25.5
31.6
35
39.3
49.5
Protein level (%)

highly significant. The conclusion drawn here differs from the original made by the authors, who claimed that linoleate 'was ineffective as an essential fatty acid'. Whitefish fed with a mixture of PUFA (34% EPA and 38% DHA) had higher weight gains than fish fed equivalent amounts of dietary linoleic acid, 18:2n-6, and linolenic acid, 18:3n-3. Furthermore, the levels of DHA in the polar lipid fraction of liver in fish fed a PUFA-supplemented diet was 26.9% in comparison with 7.2% in fish fed linoleic and linolenic acids. Therefore, Thongrod *et al.* (1989) addressed specifically the requirement for n-3 in the whitefish diet. Linolenic acid at a 1% level in a casein-based diet resulted in growth equivalent to 0.25% PUFA. This may suggest that the essential value of PUFA for whitefish is four times higher than that of linolenic acid. The efficiency of PUFA in rainbow trout, based on the growth rate and the liver lipid content, was twice as high as that of linolenate (Takeuchi and Watanabe, 1976). This may indicate that whitefish is closer to marine fish in its requirement for PUFA than to salmonids. Neither linoleic acid nor arachidonic acid, 20:4n-6, were included, however, for comparison with n-3 diets.

Takeuchi *et al.* (1983) reported that the saturated fatty acids, such as lauric acid, 12:0, depressed the appetite and reduced growth in Nile tilapia (*Tilapia nilotica*), whereas no such effect was observed in whitefish fed a diet with 4.5% lauric acid in comparison with oleic acid, 18:1n-9. The authors stated that there was no accumulation of lauric acid in liver lipids.

Vitamins and minerals

In all experiments with semipurified diets offered to coregonids, vitamin mixtures contained all required vitamins in accordance with the guidelines for salmonids (Watanabe *et al.*, 1989). However, in experiments with practical diets used for lake whitefish rearing by Zitzow and Millard (1988), lordosis, scoliosis and erratic swimming were observed. Addition of vitamin C to the processed diet eliminated the overt deficiency symptoms. Dabrowski (1990) demonstrated that European whitefish (*C. lavaretus*) fed with diets apparently deficient in vitamin C (9 and 118 mg kg^{-1}) exhibited a gradual decrease in body concentration of ascorbic acid, whereas fish offered feeds with vitamin C levels above 800 mg kg^{-1} maintained body ascorbate concentration at a relatively high level (76–88 μg g^{-1} wet weight).

When juveniles of lake whitefish of approximately 1 g body weight from Lake Erie were fed fish-meal-based diets supplemented with a graded level of ascorbyl monophosphate (Fig. 17.5), there were no significant differences in body-weight

Fig. 17.4. (Opposite) Changes in non-polar/polar (NL/PL) lipids ratio in liver of lake whitefish as a function of dietary protein levels (A). The amount of oleic acid found in both lipid fractions after 3 and 7 months of feeding (B). Polar lipids (C). Neutral lipids (D). □, Total saturated fatty acids; ▽, total monounsaturated fatty acids; ●, total polyunsaturated fatty acids.

gains, but the mortality of fish fed a vitamin C-free diet was considerably increased at week 4. At the end of the study (9 weeks), lordosis and extensive haemorrhages on ventral parts of the body, particularly around gill arches, were observed (K. Dabrowski and M. Matusiewicz, unpublished). We concluded that ascorbyl monophosphate is a bioavailable ester of ascorbic acid in coregonids and the required level in larval–juvenile diets seemed to be above 220 mg kg^{-1}. Coregonids manifested vitamin C deficiency much earlier than did salmonids – at a three- to fivefold body-weight increase in comparison with a 10–20-fold increase in salmonids (Matusiewicz *et al.*, 1994).

Dabrowski *et al.* (1987) demonstrated that, when concentrations of carotenoids varied in vendace (*Coregonus albula*) eggs from 2.57 to 9.15 μg g^{-1} dry weight, the concentration correlated inversely with survival of embryos exposed to visible light. These results in coregonids corresponded to Torrissen's (1984) conclusion that salmon-egg survival was highly dependent on astaxanthin level.

Dabrowski and Schwartz (1985) examined mineral concentration in larval diets for whitefish (*Coreganus shinzi palea*) and indicated that coregonids tolerated a wide variation of macro- and trace elements in their diets. *Artemia* nauplii had a low level of calcium (1.86 g kg^{-1} dry matter) in comparison with freshwater cladoceran zooplankton (30.7 g kg^{-1}), whereas the opposite applied to potassium (K) (14.56 and 2.2 g kg^{-1}, respectively). Trace elements, such as iron and copper, in whitefish juvenile bodies were at much lower levels in fish fed live food in comparison with those fed formulated diets. Excess minerals and interaction with other nutrients may be a concern in diet formulation for coregonids.

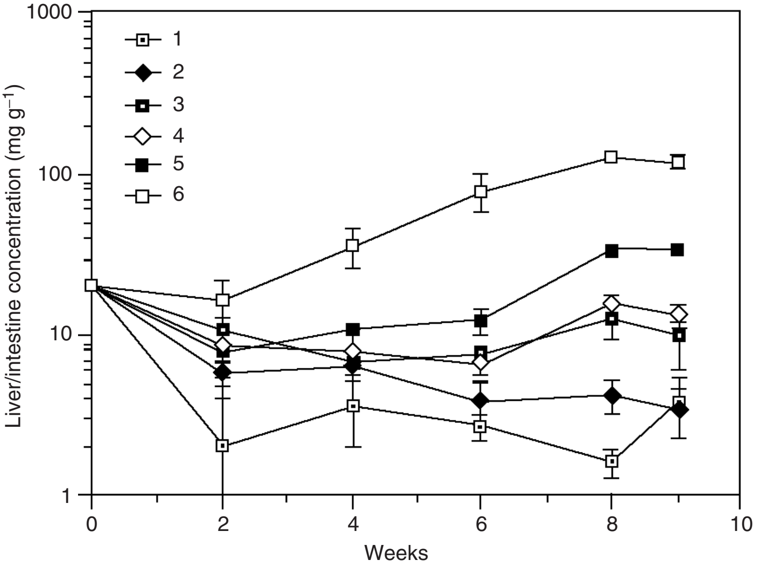


Fig. 17.5. Concentrations of ascorbic acid in tissues (liver plus intestine) of whitefish juveniles fed six experimental diets containing (1) 0, (2) 30, (3) 110, (4) 220, (5) 440 and (6) 870 mg kg^{-1} of ascorbate equivalents in the form of ascorbyl monophosphate.

Practical Diets

The first successful formulation of larval starter diets for coregonids was based on yeast (57%) and freeze-dried pork liver (28%) (Dabrowski *et al.*, 1984). In a subsequent study, Bergot *et al.* (1986) refined a diet formulation for larval whitefish and obtained juveniles of 0.275 g and 92% survival until 54 days of age. The optimized formulation contained 50% yeast, 35% dried beef liver, 5% cod-liver oil and 5% of both mineral and vitamin mixtures.

Watanabe *et al.* (1989) suggested supplementing a 2.47% amino acid mixture containing arginine (1.63), lysine (0.06), tryptophan (0.11), methionine (0.11), cystine (0.28) and histidine (0.28) as a feeding attractant for whitefish diets. However, no controlled experiments were performed to prove or optimize this attractant formulation. Studies performed with juveniles of lake whitefish (*C. clupeaformis*) provided evidence for significant growth enhancement from several animal proteins (Table 17.1; Fig. 17.6). Soluble fish-protein concentrate (CPSP) at 8% of the diet more than doubled the body-weight increase in juvenile coregonids during the 9-week-long experiment. This result was similar to the effect of CPSP in sturgeon diets (Moreau and Dabrowski, 1996).

Segner and Rosch (1990) indicated that large hepatocyte nuclei and well-developed endoplasmic reticulum, in concert with low glycogen stores, in

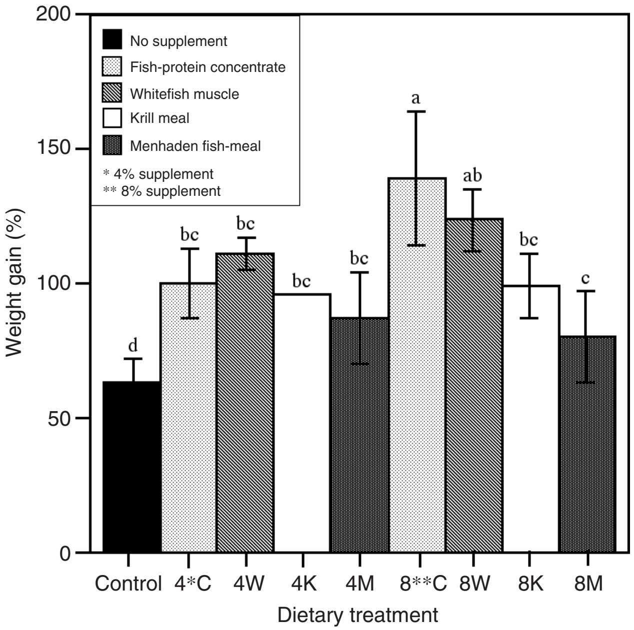


Fig. 17.6. The effect of attractant supplementation at the 4 and 8% level to semipurified diet for juvenile whitefish (Table 17.1). C, CPSP, soluble fish-protein concentrate, Sopropeche, Boulogne sur Mer 62204, France; W, freeze-dried whitefish muscle; K, krill meal; M, menhaden fish-meal. Bars having different letters indicate significant differences are at $P = 0.05$.

whitefish juveniles fed live food in comparison with smaller nuclei in hepatocytes of fish fed dry diets are relevant features for characterizing the nutritional value of the diets.

Feeding Practices

The food intake of coregonid larvae can be considerably improved by a high frequency of feeding (Dabrowski *et al.*, 1984). Bergot *et al.* (1986) enhanced the frequency of feeding by using automatic rotating dispensers, which delivered feed three times every 10 min during 12 h of illumination. At optimum water temperatures of 14°C, survival of larval Lake Leman coregonids was frequently over 95% during the first 54 days of rearing. Other investigators employed continuous feeding of *C. lavaretus* larvae using commercial diets and at lower water temperatures losses were considerably higher (50%), mostly due to mortality of non-feeding. Larvae (Segner *et al.*, 1988). Food dispensed during larval rearing of coregonids must be in excess of 10–15% biomass, as the specific growth rate of fish between 90 and 170 mg (individual weight) can be as high as 7.8% per day (Bergot *et al.*, 1986). Although no direct comparison of the effect of the duration of feeding (illumination) was carried out, an indirect comparison of growth rate in different experiments did not provide conclusive results on the advantage of 24 h illumination with continuous feeding (Dabrowski and Kaushik, 1985).

Growth of coregonid larvae from Late Hallwil (Switzerland) fed a Biokyowa diet (Biokyowa, Inc., Cape Girardeau, MO 63702) for 40 days was significantly better at 13°C than at 5°C; however, cumulative mortality for this experiment was 26% (Enz *et al.*, 2000). Mass rearing of European coregonids exclusively on dry diets throughout the first year is feasible, and larval diets can be gradually replaced with 'starter' salmonid diets (Champigneulle, 1988; Dabrowski and Poczyczynski, 1988). It is accepted that, at an individual weight of 50 mg, a transition can be made from larval diet to commercial, salmonid diets.

North American coregonid larvae (*C. clupeaformis*) were reared using a combination of decapsulated, freeze-dried *Artemia* cysts with commercial diets provided by automatic, vibrating feeders (Sweeney Enterprises, Boerne, TX 78006) (Harris and Hulsman, 1991). In some variants, the Biokyowa-B diet was used exclusively during 57-day-long experiments; however, growth was depressed and a high frequency (86%) of deformed fish, most missing opercular covers, was observed. These skeletal malformations were associated with the salmonid starter diet provided in an increasing proportion from the third to the fifth week of rearing. The authors concluded that a uniformly high survival of coregonids (97–98%) and individual weights obtained in 8 weeks (0.8–1 g) show that large-scale culture of this species are very practical options for farming coregonids.

Larger coregonids (initial weight 60–90 g) consumed over 70% of their daily intake during the first 3 h of feeding (Koskela *et al.*, 1997). Whitefish (*C. lavaretus*) maintained on gradually increasing feeding regimes from 6 to 24 h initially responded by decreased intake and depressed growth rate with the restricted time of feeding. Time-restricted feeding (6 h) apparently leads to an increase in gastric capacity and hypertrophy of digestive-tract tissue. In contrast to salmonids, restricted feeding in coregonids did not lead to the establishment of a feeding hierarchy, i.e. the presence of dominant and subordinate individuals (Jobling *et al.*, 1999). The authors observed that the catch-up growth of individual fish was directly related to the weight-gain decrease during the period of severe feed restriction. The full ration for whitefish of 38–44 g at 14°C amounted to 7–11 g feed kg^{-1} body weight day^{-1}.

Large whitefish (260–520 g) fed either a high-fat (27.5% lipid on dry basis) or a medium-fat (12.6%) diet did not show significant differences in feed intake (3.5–7.6 g kg^{-1} body weight day^{-1}) or growth (Koskela *et al.*, 1998). A high-fat diet increased lipids in the carcass of whitefish following 11 weeks of feeding to 12.7% in comparison with control (10.5%).

Acknowledgements

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