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Estimating Food Consumption by a Heavily Fished Stock of Zooplanktivorous *Coregonus lavaretus*

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Abstract.—The food consumption of adult zooplanktivorous *Coregonus lavaretus* in Lake Constance, Germany, was estimated monthly from May to October 1989 with a bioenergetics model. To achieve fine temporal resolution of lakewide consumption, we scaled the monthly weight increments of fish during the 6-month growing season by the relative weights of the stomach contents of fish sampled around sunset. As a result, the proportion of maximum consumption varied from month to month. When this proportion was held constant, the total consumption estimates were similar but the allocation of consumption to each month differed by up to 30% between the two scenarios. *Bythotrephes longimanus* was the most important prey item from June to October. The average daily consumption of *B. longimanus* amounted to 15.4% of the standing stock, while that of daphnids *Daphnia* spp. and *Leptodora kindtii* was more than an order of magnitude lower. We conclude that adult *C. lavaretus* in Lake Constance may control the population dynamics of *B. longimanus* but not those of other cladocerans.

Quantitative estimates of the consumption of zooplankton by fish are essential for evaluating inter- and intraspecific resource competition (Parrish and Margraf 1990; Rudstam et al. 1994), for analyzing top-down control in the pelagic community (Hülsmann and Mehner 1997; Durbin and Durbin 1998), and for implementing complex ecosystem models (Northcote 1988; Gaedke 1998; Straile 1998). In the large, deep lakes of the northern temperate and subarctic zones, where the fish fauna is often predominated by open water zooplanktivores, such estimates are particularly important for obtaining a better understanding of the structure and function of the lakes' pelagic subsystems. As a case study, we used Lake Constance, a large pre-Alpine lake in southern Germany, where an integrated research program has recently provided new insight into the food web structure and trophic relationships in the pelagic domain (Bäuerle and Gaedke 1998). The role of zooplanktivorous fish in the lake's pelagic food web, however, had not yet been quantified. Therefore, we analyzed fish predation pressure on zooplankton in Lake Constance using data from the time period when most of the other food web studies were conducted.

Powan *Coregonus lavaretus* (generally known as whitefish in Europe) are the predominant zooplanktivores in Lake Constance. They are heavily fished with monofilament gill nets of strictly controlled mesh size and are generally harvested soon after they reach the legal minimum size (Eckmann and Rösch 1998). Only a few studies in which the lakewide food consumption of powan was quantified have been published (Helminen et al. 1990; Rudstam et al. 1994; Tolonen 1999), and none of these dealt with exclusively zooplanktivorous powan. We therefore considered it necessary to explore some of the methodological problems associated with obtaining lakewide estimates for the consumption of zooplankton by powan.

In Lake Constance, powan are intensively exploited with size-selective gill nets. Under these conditions, the fast-growing members of a cohort are removed at younger ages than the slow-growing members, as Nümann (1959) has shown by detailed back-calculation of growth. Therefore, cohort growth cannot be modeled along one representative growth trajectory but must be split into different trajectories, each of which is representative of a particular subcohort.

Furthermore, monthly powan yields vary considerably across the growing season. As a result, monthly estimates of consumption by powan should not be based on a virtual population analysis that assumes a constant coefficient of fishing mortality. Fortunately, because the commercial fishery in Lake Constance is thoroughly controlled and scientists and fishery wardens regularly monitor the stock, monthly estimates of virtual population size (structured by year-classes) are available.

Taking advantage of this almost unique data set and considering the above-mentioned problems,

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we selected the following aims for our study: (1) to analyze the sensitivity of monthly consumption estimates based on bioenergetics to variations in the input parameters, population size, and fish growth and (2) to assess the potential impact of zooplanktivorous powan predation on their predominant prey species.

Methods

Study site.—Upper Lake Constance (Bodensee-Obersee in German) is a large (472 km^2), deep (mean depth, 101 m), warm monomictic pre-Alpine lake situated on the northern fringe of the European Alps (9°18′E, 47°39′N). The lake was originally oligotrophic but underwent pronounced eutrophication during the 20th century. Total phosphorus concentration during winter mixis (TP_{mix}) peaked around 1980 at more than 80 μg/L, when the lake was considered to be mesotrophic (Bäuerle and Gaedke 1998). As a result of sewage treatment, including partial P removal, the lake returned to a more oligotrophic state by the end of the 20th century (TP_{mix} in 2000, 14 μg/L).

Powan are the most abundant zooplanktivores in the lake's pelagic zone. The average yearly harvest of powan was 13 kg/ha during the last three decades. This value lies within the range of yields (from <10 to about 40 kg/ha) of 40 oligotrophic to eutrophic lakes with commercial powan fisheries in Europe and North America (Eckmann 2000). Two powan forms can be distinguished in upper Lake Constance: inshore spawners and pelagic spawners. According to microsatellite analysis, these forms represent distinct gene pools (Douglas et al. 1999). During the growing season, however, both forms coexist as zooplanktivores in the pelagic zone, and fishing regulations are identical for them (Eckmann and Rösch 1998). Powan yields increased from about 300 metric tons annually prior to 1955 to nearly 500 metric tons thereafter. This has been attributed to changes in the lake's trophic state and to the advent of highly efficient monofilament gill nets in the 1950s. Nevertheless, the proportion of powan in the overall fishery yield decreased during the eutrophication process from more than 70% to less than 40%, while the proportion of Eurasian perch *Perca fluviatilis* rose. During the last 15 years this trend has reversed. More details on the Lake Constance fishery can be found in Eckmann and Rösch (1998).

Fish sampling.—Powan were sampled weekly from May to October 1989 in the western part of upper Lake Constance with gill nets of 25-, 32-, 38-, 44-, and 50-mm-bar mesh (yarn diameter, 0.12 mm). Net panels were randomly combined into one fleet 240 m long and 6 m deep, which was suspended with droplines from surface floats. Dropline lengths were frequently modified following the recommendations of professional fishermen in order to obtain high catches during short exposure times. The fleet was set in the pelagic zone from 2 h before until 1 h after sunset.

All fish were measured, weighed, and sexed, and fish selected randomly from all size-groups were aged by scale reading. For consumption analyses, only age-2 and age-3 fish (total length, 29–41.5 cm; wet weight, 220–630 g) were considered, which accounted for 82% of the total catch in terms of numbers. Stomachs from 15 to 20 fish per sample were preserved in a 4% solution of formalin. In total, 627 fish were sampled for stomach analysis. Additionally, the stomachs from 9 to 17 fish per sample (mean, 13.3 fish) were removed and stored on ice for gravimetric determination of stomach fullness.

Diet analyses.—The contents of the formalin-preserved stomachs were quantitatively flushed into a zooplankton counting chamber. Under a dissecting microscope, prey items were identified to species and counted. For *Daphnia galeata* and *D. hyalina*, two size-classes were distinguished (≤1.5 mm and >1.5 mm), while for *Leptodora kindtii* and *Bythotrephes longimanus* randomly chosen specimens were measured. For each sample, fish stomach contents were expressed as mean percentage composition by number (Becker 1992). These values were then converted to percentage composition by biomass by means of length−dry weight relationships (Geller and Muller 1985; Hälbich 1997) and average dry matter content values (Hanson et al. 1997). The mean length of ingested daphnids was 1.9 mm for both species, which corresponded to 40 μg dry weight and 364 μg wet weight at 11% dry matter content. The values for *L. kindtii* were 5.4 mm, 37 μg dry weight, and 925 μg wet weight at 4% dry matter content, and those for *B. longimanus* were 2.1 mm, 56 μg dry weight, and 509 μg wet weight at 11% dry matter content.

Zooplankton samples.—Zooplankton were collected with a Clark–Bumpus sampler once per fishing day immediately after the gill nets had been set, that is, 2 h before sunset. The upper 20 m of water were sampled by two vertical tows of 10 m. Samples were preserved in sugar−formalin and evaluated in the same way as stomach contents. Zooplankton abundance was expressed as individuals per square meter. Finally, a weighted mean abundance was calculated for each month.

Temperature.—Temperature profiles were taken with a temperature-depth probe once per fishing day. Data were registered at 1-m intervals in the upper 10 m of water and at 5-m intervals at greater depths. From these profiles, the average temperature of the depth layer fished by the gill nets was calculated. Several day−night echo surveys during 1989 showed that the pelagic powan did not migrate vertically to any detectable extent during the growing season (our unpublished data). Thus, the overall mean temperature experienced by powan from the beginning of May until the end of October was 12.8°C (range, 8.8–16.7°C), without any seasonal trend.

Growth.—In the mesotrophic upper Lake Constance, powan grew mainly from May to October (Hartmann and Quoss 1982); although this was about 2 months longer than under the previous oligotrophic conditions, we have no indication so far that the growing season has become shorter since nutrient reduction began. We therefore assumed that the entire annual growth occurs between May 1 and October 31.

The mean lengths of powan (males and females combined) 2, 3, and 4 years old were 27.6, 33.8, and 36.7 cm for 1992–1995 (C. Ruhlé, Wildlife and Fishery Administration, St. Gallen, Switzerland, personal communication). These values were converted to approximately 190, 350, and 450 g wet weight, respectively, by means of a length−weight relationship based on our 1989 powan samples (65–620 g, n = 622, r^2 = 0.91).

The cohorts are normally fished out from the 3rd to the 6th year of life, the faster-growing members at younger ages than the slower-growing members (Nümann 1959). Weight at harvest increased slightly during the 1989 growing season. Age-2 fish weighed 290, 340, 350, 360, 390, and 380 g at harvest in the months from May to October 1989, while age-3 fish weighed 400, 410, 425, 435, 450, and 450 g, respectively. For simplicity, we assumed that the weight of age-2 fish that were harvested in October had increased from 190 to 380 g over the 6 months and that that of age-3 fish had increased from 350 to 450 g.

Since we had no precise data on monthly weight gain for the different age-classes of powan in Lake Constance, we needed to model their growth trajectory during the growing season. We used stomach fullness values from the fish sampled around sunset as proxies for food consumption and hence growth. Stomach fullness, however, may not always be directly related to growth, and particularly so if food quality and digestibility differ considerably across time. In spite of this uncertainty, and taking into account the strong seasonal variation of zooplankton abundance in Lake Constance (Straile and Geller 1998), we considered it more appropriate to scale monthly growth by stomach fullness than to assume linear growth over the entire growing season.

TABLE 1.—Mean monthly stomach fullness of powan (generally known as whitefish in Europe) in Lake Constance, Germany (stomach content wet weight as a percentage of fish wet weight based on samples collected at sunset) during the 1989 growing season. The total yearly growth (190 g for age-2 fish and 100 g for age-3 fish) was allocated to the 6 months of the growing season according to stomach fullness.

Month	Stomach fullness (%)	Monthly weight gain (g)	
		Age-2 fish	Age-3 fish
May	1.10	52	27
Jun	0.81	38	20
Jul	0.72	34	18
Aug	0.66	31	17
Sep	0.47	23	12
Oct	0.25	12	6

The stomach fullness index decreased from 1.1% (wet weight basis) in May to 0.25% in October (Table 1). When we scaled weight gain over the growing season by these values, the monthly growth of age-2 fish decreased from 52 g in May to 12 g in October and that of age-3 fish from 27 to 6 g (Table 1). The growth trajectories of those fish that were fished out earlier in the year were calculated backwards, starting with the weight at catch and subtracting the monthly weight increments that had been established for the fish harvested in October. As a result, growth curves for the subcohorts of age-2 and age-3 fish, which were fished in different months, run parallel (Figure 1).

In addition to the fish that were harvested during 1989, other fish in the lake also consumed plankton that year. Almost all age-3 fish that were not harvested in 1989 were fished out at age 4 in 1990. As their weighted mean weight at capture (427 g) was only 2 g higher in 1990 than in 1989, we assumed that these fish had grown from 190 to 380 g in 1989. Part of the 1987 year-class was caught in 1990 at a weighted mean weight of 410 g, and we assumed that these fish had also grown from 190 to 380 g in 1989. The monthly growth of these groups of fish was modeled according to the growth of the cohorts fished in October 1989. Other subcohorts of the 1987 year-class were fished in 1991 and 1992 at average weights of 410 and 414 g. These most slowly growing members of the

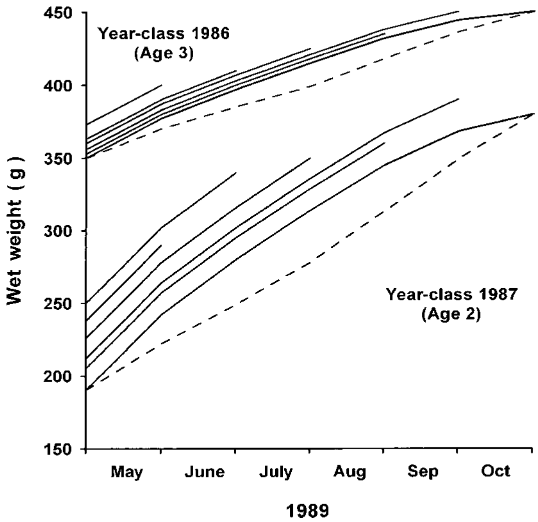

FIGURE 1.—Monthly growth (solid lines) of adult powan (generally known as whitefish in Europe) subcohorts from the 1986 and 1987 year-classes during the 1989 growing season in upper Lake Constance, Germany. The monthly weight gain for the age-2 subcohort that was fished out in October (the October cohort) was scaled according to relative stomach content weight. Monthly growth for all other age-2 subcohorts was back-calculated from the weight at harvest by subtracting the monthly weight gains of the October cohort. The same procedure was followed for age-3 fish. The dashed lines show growth curves calculated with a coefficient of maximum consumption that was held constant from May to October.

1987 year-class probably weighed less than 200 g in 1989. Fish of this size have a different food spectrum from larger individuals (Becker 1992), but our samples were too small to describe their diet quantitatively. These fish and the 1988 cohort (age 1 in 1989) were excluded from the zooplankton consumption estimates, which systematically biased our data towards low values.

Population size.—The age composition of commercial powan catches is regularly assessed through internationally coordinated test fishing with gill nets of legal mesh size. Additionally, professional fishermen report monthly on commercial yields in terms of total weight. From these data, the number of fish of a particular year-class that are removed from the lake can be calculated month by month until the cohort is fished out. By cumulative addition of the yields in terms of numbers, starting with the last harvest of a cohort and moving back until the cohort was first recruited into the fishery, monthly estimates of virtual population size are obtained. These data, however, do not account for losses to natural mortality. We assumed that the instantaneous rate of natural mortality is constant for powan of age 2 and older and chose a value of 0.2/year based on published estimates of natural mortality (Meng et al. 1986; Reckahn 1992; Mills et al. 1998). Virtual population estimates were then corrected for mortality losses by assuming (1) that the number of fish decreased exponentially during 1 month due to natural mortality and (2) that the fish that were harvested were all removed at the end of that month.

These population estimates are only available for the pelagic-spawning powan. Both the pelagic- and inshore-spawning forms are, however, fished with identical mesh sizes, so that their weight at capture is similar. Since we had no indication that the growth rates of the two forms differ, we assumed that their age compositions were the same. In 1989, the harvest in terms of weight of inshore-spawning powan was 36% of that of the pelagic-spawning form, so we obtained a population estimate for both forms combined by adding 36% to the estimate for the pelagic-spawning form.

Consumption estimates.—We used the Wisconsin bioenergetics model (Hanson et al. 1997) to estimate zooplankton consumption by powan. The physiological parameter values for the generalized coregonid model are largely based on benthivorous bloater *C. hoyi* but also on lake whitefish *C. clupeaformis*, while the weight exponent of the consumption equation has been derived from experiments on the consumption of zooplankton by Lake Constance powan (Rudstam et al. 1994). We used the default parameter values of the Wisconsin model since the model has not yet been parameterized for exclusively zooplanktivorous powan (Helminen et al. 1990; Tolonen 1999). Energy content was held constant for predators (13,060 J/g wet mass) and prey (2,513 J/g wet mass for both daphnid species and *B. longimanus*, 949 J/g wet mass for *L. kindtii*) during the simulation period since data on seasonal energy content were not available. Lake powan are fully mature at age 2, but the gonadosomatic index of females is less than 10% until late September (Rösch 2000). Therefore, the assumption that powan energy content remains constant seems reasonable for all months except October. For this month we probably underestimated consumption due to the increased energy content of maturing females. However, Bartell et al. (1986) have shown that bioenergetics models

TABLE 2.—Mean numbers of the four predominant prey species in the stomachs of adult powan from upper Lake Constance during the 1989 growing season. Fish were sampled around sunset and 15–20 stomachs were analyzed per sample.

Date	*Daphnia hyalina*	*Daphnia galeata*	*Leptodora kindtii*	*Bythotrephes longimanus*
May 2	5,155	14	1	23
May 9	4,087	37	5	8
May 16	7,829	120	8	87
May 22	1,904	123	12	89
Jun 8	162	2,056	32	465
Jun 12	0	110	7	3,012
Jun 20	32	681	480	1,716
Jul 3	5	814	500	1,358
Jul 10	7	883	316	1,016
Jul 17	2,314	180	44	417
Jul 24	14	340	109	2,460
Aug 9	3	69	55	1,860
Aug 14	11	844	81	2,755
Aug 21	1	332	53	2,311
Aug 29	7	869	3	205
Sep 4	70	169	21	833
Sep 11	1	110	20	3,254
Sep 18	116	899	17	746
Sep 25	25	60	19	210
Oct 2	8	40	5	514
Oct 17	198	90	36	361
Oct 25	143	17	29	181

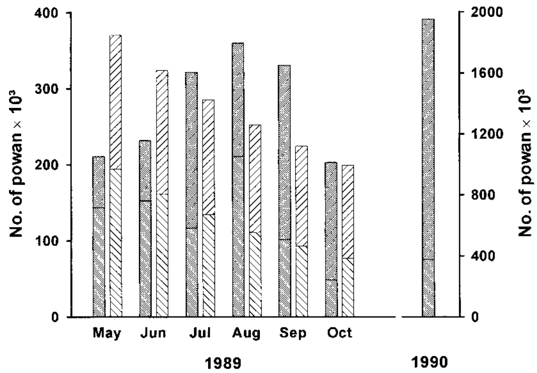

FIGURE 2.—Powan harvests in upper Lake Constance from the 1986 (backward slashes) and 1987 (forward slashes) year-classes during the 1989 growing season (left scale) and in 1990 (right scale). Pelagic- and inshore-spawning powan are combined. Values indicated by the first bar for each month and that for 1990 were calculated from the original monthly harvest data; those indicated by the second bar for each month were calculated with a constant coefficient of fishing mortality from May to October 1989.

are not highly sensitive to changes in energy densities.

For each subcohort of age-2 and age-3 fish, (i.e., those fish that were harvested in different months in 1989), we obtained monthly consumption estimates based on their weight increment (Figure 1) and diet composition (Table 2) during that month. Similarly, consumption was estimated for age-2 and age-3 fish that were harvested in 1990. The total consumption of zooplankton was calculated by summing consumption across subcohorts and age-classes for each month from May to October.

Sensitivity analyses of the bioenergetics model.— To evaluate the sensitivity of the bioenergetics consumption estimates to variations in the input parameters, temperature, population size, and fish growth, we performed three sensitivity analyses in addition to obtaining our baseline estimate of zooplankton consumption. First, we calculated total zooplankton consumption for a powan growing from 190 to 380 g in 6 months at the actual temperatures at the fishing depths, at a constant temperature of 12°C, and at an overall mean temperature at the fishing depths of 12.8°C. In all cases, the fish's diet was the same, that is, it corresponded to the stomach contents from the sunset samples. Second, we created a data set in which the total harvest during the 6-month growing season was allocated to the different months according to a coefficient of fishing mortality that was held constant across time (Figure 2). And third, we modeled fish growth with a constant proportion of maximum consumption (p-value) throughout the growing season, that is, without scaling monthly weight gain to stomach fullness. Thus, the monthly weight increments ranged from 26 to 35 g (p-value = 0.345) for age-2 fish and from 12 to 20 g (p-value = 0.267) for age-3 fish (Figure 1).

TABLE 3.—Absolute (metric tons wet weight) and percentage contributions of the 1986 and 1987 year-classes to the total monthly zooplankton consumption by adult powan in upper Lake Constance during the 1989 growing season.

Year-class/year of harvest	May		Jun		Jul		Aug		Sep	
	Tons	%	Tons	%	Tons	%	Tons	%	Tons	%
1986/1989	564	19.3	464	17.5	362	14.6	261	12.5	112	6.7
1987/1989	780	26.6	692	26.0	628	25.2	437	20.9	301	18.1
1986 + 1987/1990	1,586	54.1	1,504	56.5	1,498	60.2	1,390	66.6	1,253	75.2
Total	2,930		2,660		2,488		2,088		1,666	

Results

Diet

The powan in Lake Constance consumed *D. galeata*, *D. hyalina*, *L. kindtii*, and *B. longimanus* in varying proportions throughout the growing season (Table 2). The number of cyclopoid copepods in the fish's diet decreased from 10% on May 2 to 2.8% on May 22 and was insignificant thereafter. *Eudiaptomus* spp. and *Bosmina* spp. were only found occasionally. Hence, copepods and *Bosmina* were excluded from consumption estimates.

D. hyalina dominated the powan diet in May, were almost absent from the stomachs from June to September, and formed an increasing proportion of the diet in October (Table 2). The only exception to this pattern was observed on July 17, when *D. hyalina* accounted for almost 73% of the average stomach contents in terms of biomass. Apart from this unique event, *B. longimanus* was by far the most important food of powan from June to early October, followed by *D. galeata* and to a lesser extent *L. kindtii*.

Population Size

The 1986 and 1987 year-classes accounted for more than 99% (in terms of number) of all pelagic-spawning powan harvested in 1989. Taking both forms together, 802,500 fish from the 1986 year-class and 970,900 fish from the 1987 year-class were nominally harvested from May to December 1989. In 1990, 374,000 fish from the 1986 year-class and 1,579,000 from the 1987 year-class were harvested. The 1989 monthly harvest values are depicted in Figure 2, which also shows the monthly harvest values that were calculated with a constant coefficient of fishing mortality from May to October 1989.

Zooplankton Consumption

According to bioenergetics estimates, age-2 and older powan consumed 2,930 metric tons of fresh-weight zooplankton in May 1989 and consumption decreased steadily to 1,306 metric tons in October (Table 3). The contribution of age-2 and age-3 fish to overall consumption decreased from 26.6% to 10.5% and from 19.3% to 3.7%, respectively, as these age-groups were fished out during the year, while the contribution of fish that were not harvested until the following year increased from 54.1% to 85.8%.

TABLE 3.—Extended.

Year-class/year of harvest	Oct		Total tons
	Tons	%	
1986/1989	48	3.7	1,811
1987/1989	137	10.5	2,975
1986 + 1987/1990	1,121	85.8	8,352
Total	1,306		13,138

In May, when the abundance of *B. longimanus* had just started to increase, the contribution in terms of biomass of this species to the powan diet was low (4.3%), while *D. hyalina* accounted for 86.4% of powan consumption of zooplankton. From June to October, however, *B. longimanus* accounted for 51–75% of their monthly consumption. *B. longimanus* was thus by far the most important food of adult powan throughout the growing season.

The daily consumption of zooplankton by adult powan is compared with monthly averages of zooplankton standing stock in Table 4. The overall mean consumption of *B. longimanus* was 15.4% of the standing stock, while that of *L. kindtii* and both daphnid species was more than an order of magnitude lower. Since these data suggest that adult powan in upper Lake Constance control the population dynamics of *B. longimanus* but not of daphnids, our sensitivity analyses focused on the consumption of the former.

The influence of different temperature scenarios on total consumption estimates was weak. When we input the actual temperatures at the fishing depths, total consumption was 3,808 g wet weight; at a constant temperature of 12°C it was 3,712 g, and at an overall mean temperature at the fishing depths of 12.8°C it was 3,789 g. The contribution of different zooplankton species to total consumption differed by a maximum of 1.4% between the constant- and fluctuating-temperature scenarios, and the allocation of consumption to the 6 months of the main growing season differed by a maximum of 3.0%. The second alternative scenario, in which powan were removed from the lake according to a constant coefficient of fishing mortality (Figure 2), underestimated the consumption of *B. longimanus* only slightly as compared with the baseline calculation (Table 5). In the third scenario, however, in which powan growth was modeled with a constant *p*-value across the 6-month growing season, there was considerable deviation from the baseline values (Table 5).

Discussion

The bioenergetic model parameters that we used were based on benthivorous bloater and lake

TABLE 4.—Average zooplankton standing stock (10^3 individuals/m^2) from 0 to 20 m depth in upper Lake Constance and daily consumption by adult powan as a percentage of the average standing stock during the 1989 growing season. Abbreviations are as follows: B.l. = *Bythotrephes longimanus*; D.g. = *Daphnia galeata*; D.h. = *Daphnia hyalina*; and L.k. = *Leptodora kindtii.*

Month	Zooplankton standing stock				Consumption of standing stock (%)			
	B.l.	D.g.	D.h.	L.k.	B.l.	D.g.	D.h.	L.k.
May	0	139.9	151.9	0.1		<0.1	0.3	1.3
Jun	3.6	62.8	54.4	2.6	5.2	0.2	0.1	1.2
Jul	1.5	55.2	12.0	12.8	12.2	0.1	0.6	0.2
Aug	2.4	84.0	4.1	1.1	8.7	0.1	<0.1	0.6
Sep	1.4	20.7	3.0	0.5	12.1	0.3	0.4	1.1
Oct	0.3	2.3	3.7	0.5	38.6	0.7	1.2	1.8
Average					15.4	0.2	0.4	1.0

whitefish as well as Lake Constance powan (Rudstam et al. 1994) and may therefore not be entirely appropriate for purely zooplanktivorous powan. However, since bioenergetic model parameters have not been estimated specifically for zooplanktivorous powan (Helminen et al. 1990; Tolonen 1999), we relied on the generalized coregonid model (Hanson et al. 1997).

We observed that the different temperature scenarios had only a slight influence on total consumption, the contribution of the main prey species to total consumption, and the allocation of consumption to the 6 months of the growing season. Since temperature fluctuations were random and did not show any seasonal trend, we considered it appropriate to run all simulations at the overall mean temperature at the fishing depths of 12.8°C.

For analyzing the impact of zooplanktivorous fish on their prey, fine temporal resolution of prey population dynamics and fish consumption is required. Estimates of the latter two essentially depend on reliable estimates of population size and growth rate, both of which are structured by size-classes. When weight-at-age data are available at sufficiently short time intervals, consumption can be estimated for each growth interval (e.g., Helminen et al. 1990). In this case, the *p*-value can be adjusted to the observed weight gain for each time interval. When only year-end weight data are available, consumption estimates are generally obtained with the *p*-value held constant across time (e.g., Rudstam et al. 1994). Even though overall consumption will be correctly estimated in this way, the allocation of consumption to shorter time intervals might be incorrect. In our case, weight at harvest was fairly well known, but precise data on weight gain across time were lacking. We assumed that the sunset stomach content weight, which represents the maximum stomach content weight observed during each 24-h period, can be taken as a proxy for food consumption. Furthermore, since powan were assumed to experience the same temperature throughout the growing season, stomach content weight can be used as an indication of growth rate. Under these assumptions, the total zooplankton consumption of an age-2 powan growing from 190 to 380 g over 6 months was 3,956 g. If the *p*-value was held constant at 0.345, the total consumption was 3,775 g. For an age-3 powan growing from 350 to 450 g, the respective values were 3,828 and 3,756 g (*p*-

TABLE 5.—Daily consumption of *Bythotrephes longimanus* by adult powan during the 1989 growing season estimated according to three different scenarios and *B. longimanus* mortality. All values are given as individuals·m^{-2}·d^{-1} except those in parentheses, which are percentages of baseline consumption. The baseline scenario was based on monthly harvest figures and monthly growth rates scaled by stomach content weight. In the constant-*F* scenario, monthly harvests were calculated with a constant coefficient of fishing mortality. In the constant *p*-value scenario, the proportion of maximum consumption was held constant. For further details, see text.

Variable	May	Jun	Jul	Aug	Sep	Oct
Consumption						
Baseline	17	189	183	209	170	116
Constant *F*	18 (101)	181 (96)	170 (93)	194 (93)	163 (96)	116 (100)
Constant *p*-value	13 (76)	156 (83)	162 (89)	210 (100)	196 (115)	150 (130)
B. longimanus mortality rate	307	566	157	142	47	89

value = 0.267). The total consumption estimates thus matched fairly well. The allocation of consumption to the 6 months of the main growing season, however, differed considerably between the two scenarios. When we compared the monthly consumption estimates for the entire adult powan population, the constant-*p*-value scenario underestimated our baseline model data by 24% in May and overestimated them by 30% in October (Table 5). As long as no better estimates of powan growth across time are available, we feel that our baseline approach is more realistic than simply adopting a constant *p*-value for the entire growing season.

As with the growth rate, size-structured data on fish population size are crucial for analyzing the predation impact of fish on zooplankton. When estimates of fish population size are only available for certain points in time or harvest data are integrated over longer periods (e.g., one fishing season), population sizes can be calculated by back-extrapolation across time, adapting the coefficients of natural and fishing mortality accordingly (Helminen et al. 1990). Because monthly harvest data are available for the Lake Constance powan fishery, the virtual stock size can easily be calculated month by month. However, the magnitude of natural mortality is unknown. When we incorporated a natural mortality coefficient of 0.0167/month, the estimates of total zooplankton consumption increased by amounts ranging from 3% in October to 9% in May. We included this estimate of natural mortality in our baseline calculation. Next, we analyzed the importance of explicitly considering monthly harvest data instead of using a constant coefficient of fishing mortality. The latter scenario underestimated our baseline values only slightly (Table 5). These small deviations will, however, eventually increase owing to the errors that are introduced by other parameter estimates. We therefore suggest that the best available estimates of stock size across time should be used for consumption estimates.

A major source of uncertainty lies in the consumption estimates for fish that were not recruited into the fishery in 1989. The monthly consumption of these fish ranged from 54.1% to 85.8% of the total consumption by the adult powan stock. Any error in either the abundance or growth estimates for the prerecruits will have a considerable impact on the overall consumption estimates. For a more refined, temporally explicit analysis of powan–zooplankton interactions, a detailed study of the prerecruits' diet and growth is necessary. It should be noted, though, that the 1987 year-class, which accounted for more than 80% of the prerecruits of age 2 and older in 1989, was a very strong one. The virtual size of this year-class was 1.8×10^6 individuals (natural mortality excluded), while the average virtual year-class strength for the years 1962–1988 was 0.9×10^6 individuals. If we had assumed that the 1987 cohort was an average one and set the number of prerecruits to 50% of the observed value, their contribution to the overall consumption of zooplankton would still have ranged from 37% in May to 75% in October. Therefore, even under this scenario better knowledge of the prerecruits' growth is deemed necessary.

The role of *B. longimanus* as an important prey for planktivorous fish, including coregonids, has been demonstrated repeatedly (Giussani 1974; Nilsson 1974; Langeland 1978; Fitzmaurice 1979; Mookerji et al. 1998), but quantitative estimates of *B. longimanus* consumption by powan have not been reported so far. Our monthly estimates agree fairly well with independently derived estimates of *B. longimanus* mortality rates (Table 4) calculated according to Paloheimo (1974) and Saunders et al. (1999) (D. Straile, Limnological Institute, University of Konstanz, personal communication). We do not argue that this is final proof for the validity of our approach, however, since both our fish consumption and zooplankton mortality rate calculations are constrained by certain assumptions and uncertainties in the parameter estimates. Nonetheless, fine temporal resolution of fish consumption does provide the opportunity to analyze fish−zooplankton interactions in a very detailed fashion.

We conclude from our analyses that adult powan in upper Lake Constance may control the population dynamics of *B. longimanus* from June to October but not those of daphnids and *L. kindtii* (Table 4). Since this result is based on monthly consumption estimates, we are confident that our conclusion is valid for the entire growing season. In particular, adult powan apparently did not contribute to the collapse of the *D. galeata* stock at the end of the clearwater phase in June, since the daily consumption by powan amounted to only 0.2% of the standing stock (Table 4). A more detailed analysis of *B. longimanus* population dynamics will probably improve our understanding of the top-down control of this carnivorous cladoceran by planktivorous powan.

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