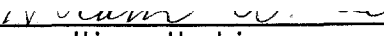


AN ABSTRACT OF THE THESIS OF

Dennis R. Lassuy for the degree of Doctor of Philosophy
in Fisheries Science presented on August 10, 1990

Title: Herbivory by a North Temperate Stream Fish,
Acrocheilus alutaceus (Agassiz & Pickering)

Redacted for privacy

Abstract approved: 
Hiram W. Li

Documentation of the seasonal feeding habits and ability to assimilate algae are presented for the first time for a North American grazing stream fish. The chiselmouth, *Acrocheilus alutaceus*, begins feeding on algal matter in early spring and has deposited large fat reserves prior to an early summer spawning season. A sharp decline in body fat content is then associated with a reduction in food intake at the onset of spawning. A subsequent increase in food intake, possibly with a higher energy value due to the inclusion of animal material, quickly restores fat reserves which then remain high through a period of almost exclusive herbivory (particularly on diatoms) in the late summer and fall. With the onset of winter, the diet of *A. alutaceus* shifts toward omnivory. Diatoms of the genera *Cymbella*, *Gomphoneis*, *Synedra*, and *Melosira* form the bulk of the diet. Both diatom and green algal food sources were

assimilated by A. alutaceus, but at relatively low efficiency. The efficiency of assimilation of Ulothrix varied inversely with ration size, while the assimilation of diatoms was unaffected by ration size. Fiber was not assimilated. The protein fraction was assimilated more efficiently (44%) than total energy (33%).

The order of preference evidenced in A. alutaceus feeding trials was: diatom > bluegreen > green > "mix" > moss. The ratio of digestible protein to digestible energy (P/E) in the food sources proved an excellent descriptor of observed preference. However, a linear combination of fiber content (as a negative factor) and gross P/E (as a positive factor) provided an analytically simpler descriptor and also predicted the correct order of preference.

Chiselmouths apparently live much longer (22+ yrs) than was previously known (6 yrs). Formation of the opaque zone, generally recognized as indicating a growth period, is most evident on A. alutaceus otoliths from July through October. This coincides with the period of highest food intake and peak contribution of diatoms to the natural diet.

Herbivory by a North Temperate Stream Fish,
Acrocheilus alutaceus (Agassiz & Pickering)

by
Dennis R. Lassuy

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*It matters only that you love
For in the end, the act of loving anyone
is the act of loving God.*

*The good in us is all the God there is
And loving is a contribution to that good,
and to that only God.*

(Adapted from CREED, Rod McKuen)

It is a simple creed, but I like it. To believe much more is either enlightened or arrogant - enlightenment is lonely, arrogance wasteful. To believe much less is to abandon hope - and we cannot live without hope.

What I have hoped for has changed throughout my life, but the source of strength for its pursuit has been the unchanging love and encouragement of my mother and father and their complete commitment to the family they raised. Because of their commitment, I have also been blessed with the constant love of seven wonderful sisters and brothers - Mary Pat, Peggy, Suzi, Tim, Teresa, Elizabeth, and Joe. Each, at some point or another, has amazed me with their insight, surprised me with their humor, and inspired me by their confidence. I am also especially indebted to my Godparents Uncle Denny and Aunt Madeline and to Unc. However, the entire extended family from Hoopeston to Pensacola, Phoenix to Arlington has been important. To all of you - I love you; I cannot thank you enough; and I pray that God blesses your every step along life's path.

The path of my educational journey has resembled that of a pinball - Illinois, Arizona, Florida, Guam, British Columbia, Louisiana, and Oregon under the guidance of folks from Sister Mary Petra, Mis'swatson, and Dr. Mrs. Cornelius, to a bearded T.A. playing *Uca* on the mudflats of Mexico (thanks Ric!), a Master's advisor with a banjo and a Mickey Mouse suit, and a thoughtful PhD advisor who was as indignant and irascible as I am (thanks Hiram!). All of these mentors and all of the many friends who have shared my journey (among them, Steven L Stone, Cam & Terri Sharpe, M. Stone Fitzpatrick, Pat "Huleyjimbobby" Hullett, Debra Tiner Bills, Noel Wiggins, Amy Crook, Lorraine Josephine Colavito, Rich Berry, Paul Bentzen, Delsa Catunao, Barry D. Smith, Terry Arndt, Tim Sullivan, and even Shilly-filly!) have been very important to me. Your friendship and help came with no strings attached, it was simply given. May your honesty be repaid by God's giving hands with the many, many blessings you deserve.

Merci a dieu, Dad - let's go fish'n!

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HERBIVORY BY A NORTH TEMPERATE STREAM FISH, *Acrocheilus alutaceus* (Aggasiz & Pickering)

I. GENERAL INTRODUCTION

BACKGROUND

Early recognition of the importance of herbivory in tropical fishes and invertebrates led to a mass of published information on these systems (Vine 1974, Ogden & Lobel 1978, Montgomery & Gerking 1980). Large stands of algal biomass are found in temperate marine systems. However, even in these systems herbivory had been largely downplayed (Quast 1968, Bakus 1969) until others provided clear evidence of the assimilation of plant material and the important functional roles of herbivorous fishes and invertebrates (Paine & Vadas 1969, Montgomery 1977, Edwards & Horn 1982).

In a review of autotrophy in stream systems, Minshall (1978) saw the importance of instream autotrophy to lie primarily in its role in the production of detritus. However, extensive information now exists on the use of primary producers by benthic invertebrates as a direct food source and on the impact of such grazing on the producer assemblage (Cummins & Klug 1979, Benke & Wallace 1980, Lamberti & Resh 1983). Grazers may also provide a direct link, through predation, or an indirect link, through fecal production, between primary producers and other members of the stream community. Shepard and Minshall (1984) presented experimental evidence that "the fecal component [from invertebrate grazers] of fine-particulate organic detritus can play an important role in maintaining homeostasis in stream benthos communities." Similar research on stream fishes has been conspicuously lacking.

The presence of algae in the diets of at least some stream fishes has long been known (Kraatz 1923, Nikolskii 1954). However, it was not until a recent series of publications on the stoneroller, Campostoma anomalum, that the direct impacts of grazing fishes on algal community structure in streams have been demonstrated (Power 1983, Power et al. 1984, Matthews et al. 1987). Even in these extensive studies, however, the actual assimilation of algal matter was neither demonstrated nor cited. All conclusions regarding nutritional value of the various apparent algal food sources were based on assumptions drawn from the interpretation of studies of a variety of different animals from vastly different environments.

In the one study that I have found of the nutritional value of direct herbivory in a temperate stream fish, Moodie and Lindsey (1972) concluded that "large amounts of filamentous algae are ingested but not digested" by the chiselmouth, Acrocheilus alutaceus. This conclusion was based on measurements of crude cellulose in stomach and lower intestine samples. They suggested instead, solely on the basis of visual evidence, that epiphytic diatoms "provide the principal nutrition."

Lobel (1981) clearly demonstrated that the release of cell content is not dependent upon disruption of the cellulosic fraction of cell walls. The method of Moodie and Lindsey (1972) also fails to account for the release of cell content from those cells disrupted by trituration. As Lobel (1981) and Horn (1989) have noted, the mechanical disruption of cell walls is particularly important in stomachless fishes with well-developed pharyngeal mills, such as A. alutaceus. To date then, I have not found a valid test of herbivory in a native temperate stream fish. Some authors

have studied herbivory in exotic species introduced into North American streams (Van Dyke & Sutton 1977, Buddington 1979). However, while these studies have been useful, it is difficult to frame the significance of work on such species in an historic or coevolutionary perspective.

Assessment and prediction of the food value of plant matter has been approached in a variety of ways. Many early studies based their predictions of the food value of plant matter on surveys of the digestive enzymes of fishes (Stickney & Shumway 1974, Prejs & Blaszyk 1977). The results of such surveys can be misleading. Bayon and Mathelin (1980) studied the digestive tracts of larval insects and concluded that the failure to detect cellulolytic activity "is not compelling evidence against the digestion of cellulose." Conversely, the detection of some level of activity did not invariably infer the ability to digest cellulose. Other characterizations of food quality have used whole plant or cell size (Porter 1977, Ogden & Lobel 1978), presence or absence of toxins (Arnold 1971), and degree of calcification (Lassuy 1980).

Perhaps because of an early association of optimization theory with energetics (Lotka 1922) and an interpretational basis formed by much of the fine early work in biological energetics (Lindeman 1942, Brody 1945), energy content has been the most widely used indicator of food quality (Emlen 1966, Paine & Vadas 1969). The use of energetics as a basis of comparison has also underlain much of optimal foraging theory (MacArthur & Pianka 1966, Dill 1978, Schoener 1983). However, strict adherence to the use of energy as the currency of optimization has been criticized by others (Westoby 1974, Schluter 1981, Horn 1983). Particularly among grazers and detritivores, nitrogen or protein content has been identified

as an important nutritional constraint (Boyd & Goodyear 1971, White 1978, Bowen 1979). Bowen (1982) later tied his findings more specifically to the combined roles of protein and energy in determining food quality for herbivorous fishes.

As suggested by Montgomery and Gerking (1980), perhaps the most promising studies are those that combine investigations of the digestive capacities of the grazers with investigations of the properties of the algal resource. An excellent series of papers by Michael Horn and his associates (Edwards & Horn 1982, Horn et al. 1982, Horn 1983, Horn et al. 1986), has contributed greatly to this approach.

This series of papers essentially represented a progression from the simple observation of apparent herbivory in a temperate intertidal stichaeid blenny to a complex comparison of the results of an ensuing series of investigations with the precepts of optimal foraging theory. The value of any one study in the series rested in its ability to contribute to understanding the consumer:food source system of interest; to address the utility of current theory in predicting or interpreting results; and to serve as a justifiable basis from which to address hierarchically higher or lower level questions. Such was the perspective from which my own studies were framed.

The utility of this perspective is exemplified in looking at two previous food quality studies. Boyd and Goodyear (1971) detailed the biochemical composition of a wide variety of plants. Hamada et al. (1983) reported on the growth efficiencies of silver carp, Hypothalmichthys molitrix, when fed a range of algal food sources. Both are useful in their own right. Boyd and Goodyear provided data from which to compare

source management for maximizing growth in an aquacultural species but yielded no deeper understanding of the characteristics of the food sources that had been responsible for rendering nutritive quality. A single, reasonably detailed study of both food source characteristics and consumer capacities would greatly increase our understanding of the subject species; could test the utility of intermediary food quality hypotheses; and serve as a justifiable basis from which to address both higher and lower level questions of interest. It is an integrative, intermediate level study of this type that was intended in my investigations of the chiselmouth, Acrocheilus alutaceus.

THE SUBJECT SPECIES

The chiselmouth, Acrocheilus alutaceus, is the most abundant grazing fish native to Oregon streams. However, only sparse information exists on its life history and feeding habits (Moodie & Lindsey 1972), distribution (Bisson & Bond 1971), or systematics (Miller & Smith 1972). Wydoski and Whitney (1979) suggested that chiselmouths "may serve as a major link" between primary producers and piscivorous fishes.

A. alutaceus is limited in distribution to the Fraser and Columbia River systems and the Harney Basin of eastern Oregon. Within this general distribution, chiselmouths tend to occur in the relatively larger, warmer streams and occasionally also in lakes. Moodie and Lindsey (1972) examined the diet of A. alutaceus during the summer in Wolfe Lake, British Columbia and the Okanagan River, Washington. They concluded that small chiselmouths (<100 mm FL) fed primarily on insects, while filamentous algae and diatoms formed the bulk of the diet of larger fish. As its

examined the diet of A. alutaceus during the summer in Wolfe Lake, British Columbia and the Okanagan River, Washington. They concluded that small chiselmouths (<100 mm FL) fed primarily on insects, while filamentous algae and diatoms formed the bulk of the diet of larger fish. As its common name suggests, the lower jaw of A. alutaceus bears a sharply edged cartilaginous plate, almost straight in adults, which is used for scraping algae-covered surfaces. The peritoneum of A. alutaceus is very dark and the digestive tract in adults is several times the length of the body. Typical of the cyprinids, A. alutaceus lacks a true stomach but has well-developed pharyngeal teeth. In the chiselmouth, these teeth are slightly curved, stout, and have a grinding surface (Bond 1979). Clearly, the chiselmouth appears to be morphologically well-suited for grazing on films of benthic algae.

II. SEASONAL PATTERNS IN FEEDING HABIT, FAT CONTENT, AND GONDADAL DEVELOPMENT OF A GRAZING STREAM FISH, Acrocheilus alutaceus

INTRODUCTION

Direct consumption of primary producers is well documented in a wide variety of temperate and tropical marine species (Horn 1989). However, autotrophy in freshwater streams has been viewed primarily as a source of autochthonous detritus (Minshall 1978). Consequently, consumption of autochthonous primary producers by temperate stream fishes remained largely unstudied until a recent series of papers on the grazing minnow, Campostoma anomalum, demonstrated that direct consumption not only occurs but can play a significant role at least in short-term stream community dynamics (Power & Matthews 1983, Matthews et al. 1987, Power et al. 1988).

Knowledge of the feeding habits of fishes, particularly in temperate regions, may be fairly well developed for the summer months but very limited or entirely unknown during the winter months. Angermeier (1982) and Cunjak et al. (1987) provide recent examples of seasonal diet analyses for temperate stream fishes, but both studies involved carnivorous species. I know of no studies that have investigated the feeding habits of a North American grazing stream fish over an entire annual cycle.

The chiselmouth, Acrocheilus alutaceus, is the most abundant grazing fish native to Oregon streams. Wydoski & Whitney (1979) suggested that A. alutaceus may in fact "serve as a major link" between primary producers and piscivorous fishes. Chiselmouths may also serve as a link to other members of the stream community through fecal production (see Chapter 3). However, only sparse information exists on its life history (Moodie & Lindsey 1972), distribution (Bisson & Bond 1971), or systematics (La

Rivers 1962, Miller & Smith 1972). A. alutaceus is limited in distribution to the Fraser and Columbia River systems and the Harney Basin of eastern Oregon. Within this general distribution, chiselmouths tend to occur in the relatively larger, warmer streams and occasionally also in lakes and reservoirs.

Moodie and Lindsey (1972) limited their investigations of A. alutaceus feeding habits to a brief period during the summer months. They were unable, therefore, to comment on seasonal variation. From their summer analyses, they concluded that small chiselmouths (< 100mm FL) fed primarily on insects, while adults fed most heavily on filamentous algae and diatoms. In this study, I analyzed the gut contents of adult chiselmouths from all twelve months of the year to determine whether or not herbivory was maintained over an entire annual cycle.

Concurrent knowledge of body condition and gonadal development has often proven useful in the interpretation of seasonal feeding pattern (Bulow et al. 1981, Guillemot et al. 1985, Rimmer 1985b). Determinations of seasonal patterns in body fat content and gonadosomatic index (gonad weight/body weight) were therefore included in the study as was an analysis of diel feeding pattern and daily consumption rate.

METHODS

All fish used in this study were collected from the Willamette River between Peoria and Corvallis, Oregon. Fish were collected at monthly intervals by electroshocking, usually within the final week of the month, between May of 1984 and April of 1985. Unsuccessful mid-winter sampling

in the first year required that December through February samples be collected the following winter of 1985-86. Water temperature was recorded at the time of collection and corresponding river flow condition was later estimated from nearby United States Geological Survey stations (USGS 1986, 1987, 1988).

Whenever possible, five to ten fish were held live and the remaining fish placed immediately on ice for transport back to the laboratory. Upon return to the laboratory, those fish held on ice were weighed, and fork length (FL), sex, and gonad weight determined. For fish over 180 mm FL, the weight of the contents of the entire gut was recorded and the contents of the anterior two centimeters of the gut (always prior to the first bend) were separated for diet analysis. Live fish were held for a 24-hr period to allow gut clearance and then killed for use in the determination of fat content. Fat content was measured according to the method of Bligh and Dyer (1959) as an indication of body condition.

Contents of the anterior gut were placed in a 5-ml vial of distilled water and shaken briskly to separate often "stringy" clumps and to randomize their constituents. Subsamples were removed with a wide-mouthed pipet and placed on a glass slide for viewing at 200X magnification on a microscope equipped with a camera lucida. A digitizing pad was placed beneath the camera lucida so that the projected image of its moveable crosshairs overlaid the microscopic view of the gut contents. Volume of each dietary item was estimated by measuring its length, width, and height (as needed) and calculating the volume of a similarly shaped geometric solid. Similar methods have been reported by Johannsson and Beaver (1983) and Ahlgren (1990).

Food sources were assigned to one of the following six categories; diatoms (Bacillariophyta), blue-green algae (Cyanobacteria), green or yellow-green algae (Chlorophyta & Chrysophyta), nonalgal plant matter (e.g., moss, duckweed), detritus (e.g., leaf litter and unidentifiable particulate organic matter), or animal matter (e.g., cladocerans and larval and adult dipterans). Matter identifiable as inorganic (e.g., sand) was not included in the analysis. A total of 300 food items were measured for each month. The number of items from any one fish therefore varied with the number of specimens available for that month while the total dietary sample size for each month remained constant. Differences in seasonal feeding habits were analyzed by Kruskal-Wallis ANOVA by ranks.

On October 4th and 5th, 1986, a single 24-hr field study was undertaken to determine the diel feeding pattern of *A. alutaceus* and to provide a field estimate of daily consumption rate for comparison with laboratory feeding experiments being run at a similar temperature (see Chapter 3). Daily consumption rate was estimated according to method of Elliott and Persson (1978). Mean river temperature at the time of this analysis was 15.5°C.

RESULTS

The months from November through March were designated as winter months because of the sharp changes in temperature which preceded and followed this period. All other months are referred to as non-winter. The most evident pattern in the data on feeding habits is the dominance of diatoms as a food source and the pronounced decrease in their

contribution during the winter months (Table 2.1, Fig. 2.1). Diatoms averaged only 31.5% of the diet in winter, significantly less (K-W ANOVA, $P < .01$) than the 80.1% of dietary volume attributable to diatoms during non-winter months. In a separate study (see Chapter IV), A. alutaceus showed a significant preference for diatoms over other plant food sources.

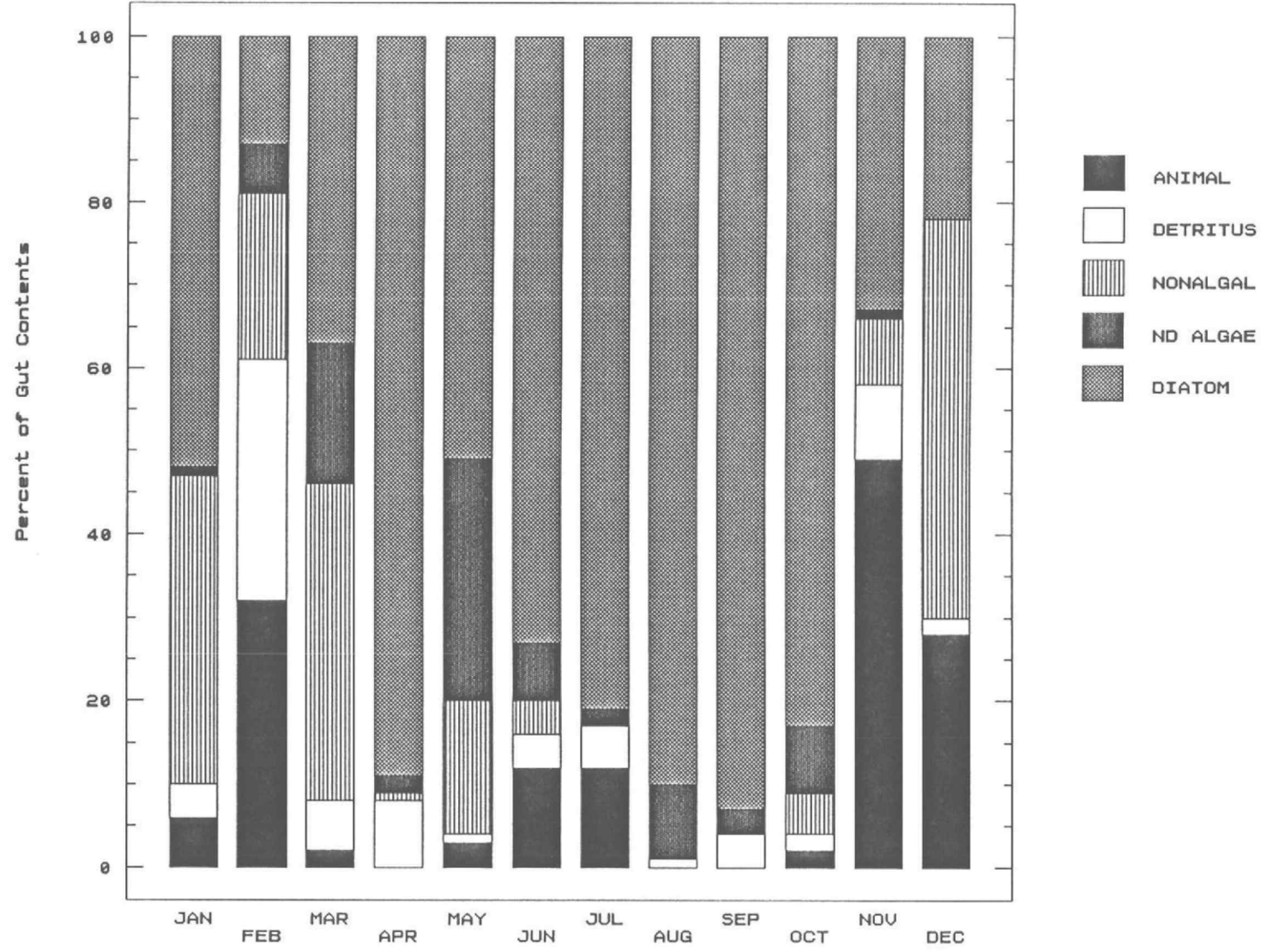
Within the diatom component of chiselmouth gut contents, species from the four genera, Cymbella, Gomphoneis, Synedra, and Melosira were the most consistent contributors. Cymbella was an abundant contributor in all 12 monthly samples and dominated from August through October. Gomphoneis was the leading contributor from March through July and was absent from only the January and February samples. Synedra also occurred in 10 of 12 monthly samples but dominated only the January sample. Melosira was the leading contributor in February and occurred in all subsequent months through August, but was largely absent from September through January. Other diatoms that occasionally contributed significantly to the diatom fraction of chiselmouth gut contents included: Hannaea (February through June), Nitzschia (October), Diatoma (October and November), and Cocconeis (November and December). Rhoicosphenia was also common in several months but was never a major contributor to dietary volume. Fragilaria was not common in most months, but formed the bulk of the diatom fraction in the month of November.

Nonalgal plant matter, primarily moss (Fontinalis), also showed significant seasonal differences ($P < .01$). The winter average for nonalgal plant matter was 30.4% of the diet, non-winter 3.7%. Duckweed (Lemna) accounted for nearly all of the nonalgal plant matter in October.

Table 2.1. Summary of monthly dietary composition (% volume) and concurrent data; river flow (cms*100), temperature (°C), fat content (% body wt, wet), gonadosomatic index (gonad wt/body wt, wet), and gut contents (% body wt, dry).

SOURCE	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
Diatom	52.2	13.4	36.9	88.8	51.1	73.3	81.3	89.7	93.0	83.2	32.7	22.4
Green	0.6	5.7	17.6	1.4	27.5	6.7	2.0	9.3	2.7	7.4	1.4	0.0
Bluegreen	0.0	0.0	0.0	0.7	1.5	0.1	0.0	0.1	0.0	0.1	0.0	0.0
Nonalgal	37.9	20.0	38.0	0.7	15.9	4.4	0.0	0.0	0.0	4.9	8.0	48.3
Detritus	3.8	29.4	5.7	8.3	1.0	3.7	5.0	0.9	4.3	2.4	9.3	1.3
Animal	5.6	31.5	1.8	0.0	3.0	11.8	11.7	0.0	0.0	2.0	48.6	28.1
River flow	5.2	14.7	4.5	2.3	4.2	3.0	1.4	1.8	2.5	3.4	9.5	3.3
Temperature	7.0	7.2	6.8	11.3	12.2	15.2	19.1	15.8	14.4	12.7	8.5	4.2
Fat Content	7.3	10.7	9.9	8.6	4.8	9.6	9.3	8.9	10.1	10.0	10.4	7.6
GSI (male)	0.7	0.9	1.7	5.2	3.9	1.9	0.5	0.4	0.9	0.7	1.1	0.5
GSI (female)	4.3	4.0	3.5	11.2	13.3	2.3	1.3	0.9	1.3	2.9	3.4	3.8
Gut Content	0.5	0.9	1.1	1.3	0.3	1.1	2.9	2.2	2.0	2.1	0.2	0.1

Figure 2.1. Seasonal feeding habits (percent of gut contents based on volume) of adult A. alutaceus from the Willamette River, Oregon. Plant = nonalgal living matter (e.g., moss and duckweed), Algae = cyanobacteria, green and yellow-green algae, Detritus = leaf litter and unidentified particulate organic matter.



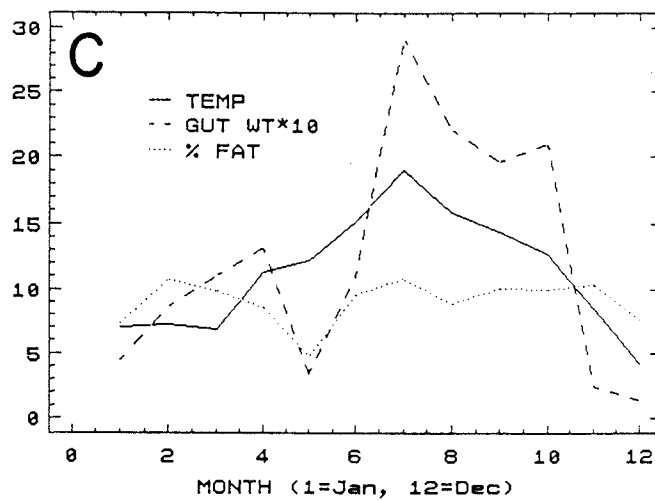
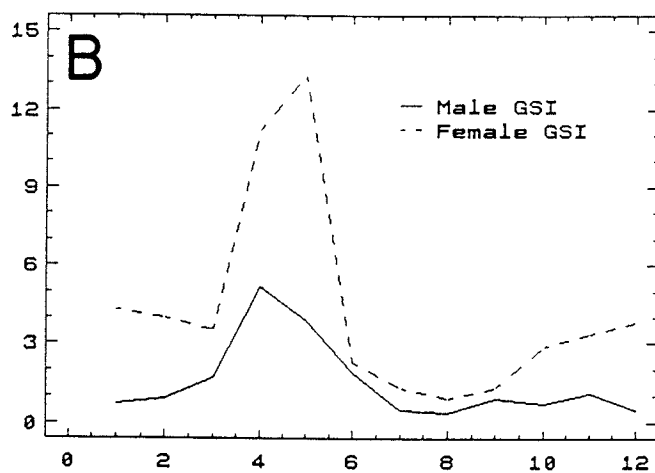
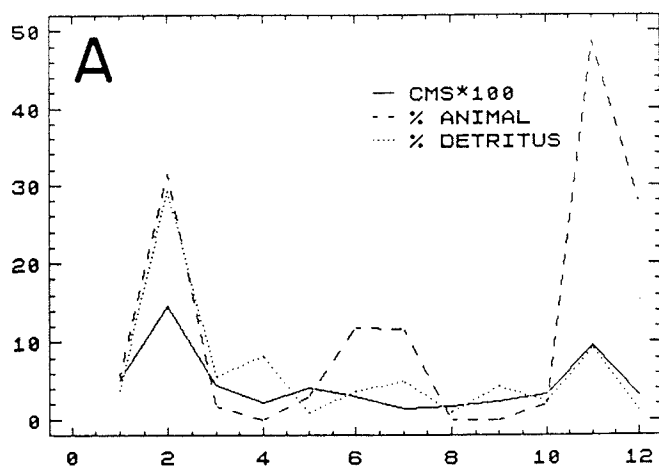
Though previously considered unimportant in the diet of adult chiselmouths, animal material occasionally contributed a surprisingly high percentage of dietary volume. Peak contributions of animal material occurred during November (48.6%) and February (31.5%). Interestingly, these are also the two months during which flood events coincided with collection dates (Table 2.1, Fig. 2.2A). Unfortunately, the November value is based on only a single specimen.

Animal matter was often completely absent and contributed only 3% or less in non-winter months with the exception of the late June and July samplings. During these consecutive months, animal material constituted just under 12% of dietary volume. Despite the apparently high month-to-month variation, mean winter contribution of animal material (23.1%) was significantly greater than for non-winter months (4.1%, $P < .05$).

Cyanobacteria also showed statistically significant seasonality in dietary contribution ($P < .05$), but never constituted a major component of the diet with a peak of only 1.5% in May. One fish in the May sample had apparently fed on a patch of Stichococcus. However, this is the only time when this taxon was seen. Phormidium was a consistent, but minor contributor for the 3-month period from April through June and was also present in the August and October samples.

Other sources of algae in chiselmouth diets, primarily green algae, showed no significant seasonal pattern dietary contribution ($P = .19$), averaging 5.1% in winter and 8.1% in non-winter months. Stigeoclonium and Ulothrix formed the bulk of the contribution of green algae during non-winter months, particularly in May. Cladophora and Rhizoclonium were

Figure 2.2. Seasonal trends in: (A) river flow and selected dietary components; (B) gonadosomatic index (GSI = gonad wt/body wt, % wet wt); (C) temperature, mean weight of gut contents (% body wt, dry), and fat content (% body wt, wet) for A. alutaceus from the Willamette River, Oregon.



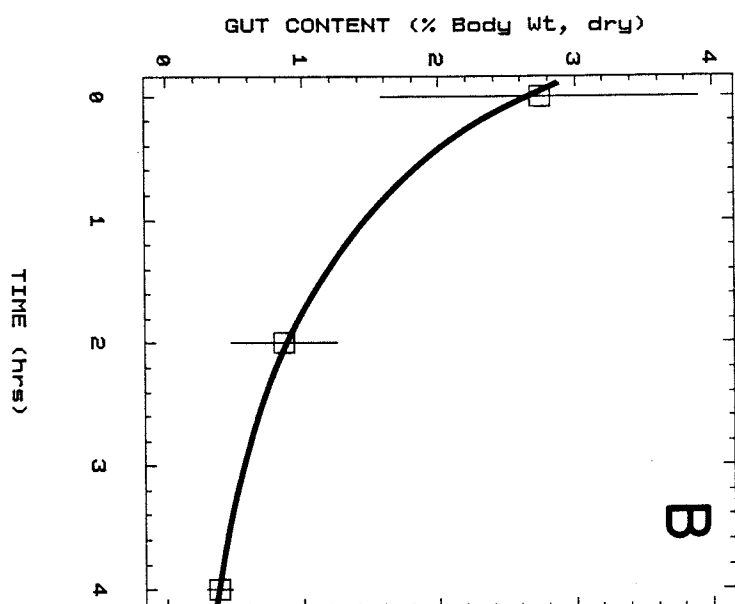
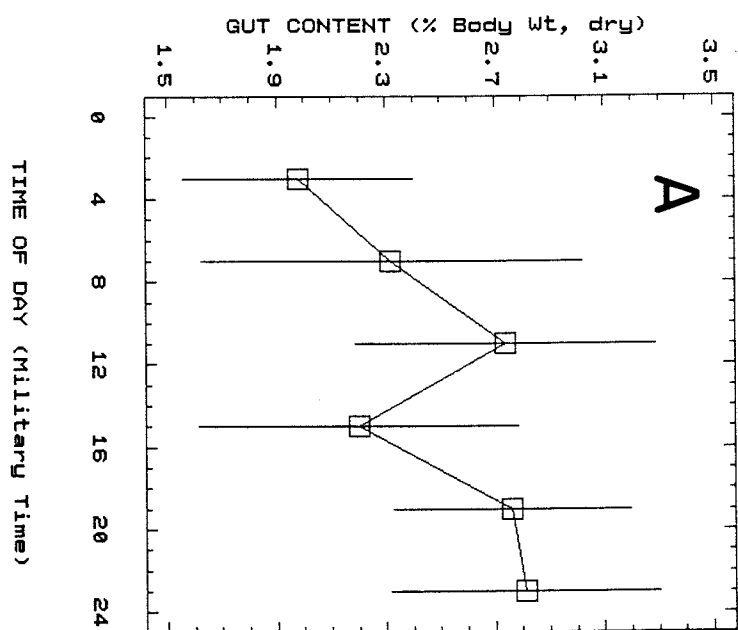
minor contributors in July and August, while Oedogonium was common in October and November samples.

Detrital material was present during all months of the year but usually constituted less than 10% of dietary volume. The one exception to this (29.4%) was in the month of February. Again, this coincided with a peak river flow that was nearly twice the level of any other month in this study (Table 2.1, Fig. 2.2A). Though less pronounced a peak, the second highest contribution of detritus to chiselmouth gut contents was in November (9.3%), the only other month with a notable flood event. Winter and non-winter means (9.9% and 3.6%, respectively) were not significantly different ($P = .17$).

During the diel feeding study in October, adult A. alutaceus apparently fed throughout the diel cycle (Fig. 2.3A). Gut contents averaged 2.43% of whole body weight (dry wt:dry wt) for all samples combined. Sample period means varied from a high of 2.8% at 2300 hrs to a low of 2.0% at 0300 hrs. Though there is some suggestion of a decrease in nocturnal feeding rate, none of the sampling period means was significantly different from any other. Serial sacrifice of fish collected at the final sampling period (1100 hrs) indicated an exponential decrease in gut content weight (Fig 2.3B) at a constant relative rate of gut evacuation (R) of 0.47. Subsequent analysis of the diel feeding information according to the method of Elliott and Persson (1978, Eq. 9) yielded an estimated daily consumption rate of 27.8% of whole body weight (dry wt:dry wt).

For most monthly samples, the fat content of adult chiselmouths remained fairly constant at about 10% of wet weight (Table 2.1, Fig.

Figure 2.3. (A) Diel feeding pattern in adult A. alutaceus from the Willamette River, Oregon at water temperature of 15.5°C. (B) Weight of contents (% body wt, dry) remaining in gut tract at time of capture (1100 hrs), two hours, and four hours after capture. Plotted data are means \pm standard errors.



2.2C). There were, however, two notable exceptions to this pattern. The first was a sharp decline to less than 5% body fat in late May. This represented a significantly lower fat content than both prior and following monthly samples. A smaller decline to approximately 7.5% was apparent for the December and January samples. Unfortunately, because of the difficulty of collecting in a large and murky river system, winter sample sizes were generally quite low. This winter decline, therefore, while consistent with observed patterns of body condition in other temperate species (Guillemot et al. 1985, Cunjak et al. 1987), was not significantly less than the values for the preceding and following months. The gonadosomatic index (GSI) expresses gonad weight as a percentage of whole body weight (wet wt:wet wt) and has been shown to be a sensitive indicator of spawning time (Hay & Outram 1981). The seasonal pattern of gonadal development in A. alutaceus is depicted in Fig. 2.2B. Mean GSI for males peaked at 4-5% in the late April and May samples and at 11-13% for females in these same months. The duration of gonadal development in males was longer than in females.

By late June, GSI in males had dropped to about one-third and in females to about one-fifth of maximum values. A preponderance of ripe fish in the late May sampling and the presence of only a few ripe and running fish in the late June sampling suggests that spawning had occurred primarily in mid-June. River temperature at this time was approximately 15°C, slightly below the temperature that Moodie and Lindsey (1972) had suggested was necessary to cue spawning in populations of A. alutaceus from British Columbia lakes. For both sexes, GSI remained quite low for three to four months following the apparent spawning season.

DISCUSSION

The results of this study suggest the following seasonal pattern of feeding, body condition, and gonadal development. Adult A. alutaceus in the Willamette River apparently begin feeding on algal food sources in early spring and have deposited significant fat reserves prior to an early summer spawning season. A sharp decline in body fat content is then associated with a reduction in food intake at the onset of the spawning season. A subsequent increase in food intake, possibly with a higher energy value due to the inclusion of animal material, quickly restores fat reserves which then remain relatively high through a period of high food intake and almost exclusive herbivory (particularly on diatoms) in the late summer and fall. With the onset of winter, the diet of adult A. alutaceus then shifts toward omnivory. Food intake during the winter months is greatly reduced, but decreased metabolic demand and the inclusion of a higher portion of animal material in the diet may prevent a significant decline in fat content and allow overwintering in relatively good condition.

Elliott (1972) showed that the rate of gastric evacuation (R) increased exponentially with increasing temperature. It is likely, therefore, that the use of mean gut content weight as an indicator of feeding rate exaggerates the contribution of winter months to the annual total while that of the warmer months are underestimated. In other words, the dominance of diatoms in the diet of adult A. alutaceus is even greater than indicated and the relative contribution of animal and detrital material is reduced.

This does not necessarily suggest, however, that detrital and animal material are unimportant to chiselmouth nutrition. Ahlgren (1990b), for example, has shown that detrital material can be of significance to the nutrition of consumers not generally regarded as detritivorous. The pattern of inclusion of animal material in diet of A. alutaceus suggests that it may also play an important dietary role.

Animal material is often of greater energetic value than algal or other plant material (Cummins & Wuychek 1971, Schroeder 1977). Consumption of a higher proportion of animal material may therefore maintain or rebuild energy reserves. Since availability was not investigated in this study, it is not known whether the inclusion of animal material in the diet of A. alutaceus was the consequence of a directed effort or simply a reflection of resource availability. However, while investigating community structure in an Oklahoma stream, Power and Stewart (1987) noted a sharp reduction in algal abundance following a flood event. It may be suggested then that the association of higher proportions of animal and detrital material with months in which flood events occurred is consistent with reduced algal availability.

Daily ingestion rate estimated in this study (27.8% of body weight) is much higher than the maintenance ration (5.6-5.9%) estimated by Gerking (1980) for the marine herbivore Sarpa salpa. This species, however, also assimilated a very high proportion (60-80%) of its food source. Data presented by Prejs (1984, Table 7) indicate daily consumption rates of 10-20% were common for two European cyprinids. Hofer and Scheimer (1981) reported a daily consumption rate of 24.1% for Sarotherodon mossambicus

and daily ingestion rates of 50-100% body weight have been reported in aquacultural settings (Cassani & Caton 1983).

Separation of individual dietary items for direct measurement of biomass is difficult, if not impossible, in analyzing the gut contents of microphagous consumers such as A. alutaceus. While the direct estimation of volume in this study is certainly less abstract than often-used occurrence or point system techniques, others have taken volumetric estimates a step further by converting to dry (Lawrence et al. 1987) or ash-free dry weight (Ahlgren 1990a). Conversions from volume to biomass suffer the drawback of additional assumptions about the uniformity of the food items to which they are applied. However, the utility of the approach taken by Ahlgren (1990a) lies in its representation of a more biologically meaningful value than volume, i.e., available organic material. The nutritional value of the ash fraction is assumed to be insignificant. When dealing with herbivorous fishes, fiber (cellulose, lignin, and cutin) may also represent a large and essentially unavailable fraction of the food source. For A. alutaceus, in particular, fiber has been shown to be unassimilable (Chapter III).

Since feeding by A. alutaceus is apparently constant over the diel cycle, mean gut content weights (Table 2.1) may be assumed to reflect the rate of food intake on the date of collection. In compiling an annual summary of dietary composition (Table 2.2), monthly samples were therefore weighted by mean gut weight for that month. Chiselmouth dietary composition is expressed as relative volumetric, ash-free dry weight (AFDW), and ash- and fiber-free dry weight (A&FFDW) contribution. Conversion from volume to AFDW and A&FFDW for four of the six categories

Table 2.2. Annual summary of dietary composition by volume, ash-free dry weight (afdwt), and ash- and fiber-free dry weight (a&ffdw).

	% VOLUME	%AFDW	% A&FFDW	Source of conversion data
Diatom	73.1	65.9	74.2	This study (Chapters III & IV)
Green	7.0	10.5	8.9	This study (Chapters III & IV)
Bluegreen	0.1	0.1	0.1	This study (Chapters III & IV)
Plant	8.8	12.2	7.3	This study (Chapters III & IV)
Detritus	5.1	6.6	4.0	Naiman & Sedell (1979), Ward (1986), Ahlgren (1990)
Animal	5.8	4.5	5.5	Cummins & Wuychek (1971), Ahlgren (1990)

was based on data gathered in this and related studies (Chapters III & IV) while the remaining two were based on literature values.

Conversion to AFDW noticeably decreased the apparent contribution of diatoms and animal matter while other items generally increased. The additional step to A&FFDW, intended to be most representative of the biologically available organic contribution, had essentially the reverse effect. None of the categories, after conversion to A&FFDW, varied more than 2% from its original relative composition value based on volumetric estimation. At least in this study, therefore, volumetric estimation seems a sufficient descriptor of dietary contribution without the need to incur the burden of assumptions associated with additional conversions.

III. ALGAL ASSIMILATION IN A NATIVE RIVERINE CYPRINID, Acrocheilus alutaceus (Aggasiz & Pickering)

INTRODUCTION

Grazers may provide both direct and indirect linkages, through predation and fecal production, between primary producers and other members of the community. Despite their abundance in many North American systems and the potential to constitute such linkages, scant attention has been paid to grazing stream fishes. The presence of algae in the diets of stream fishes has long been known (Kraatz 1923), but quantitative demonstration of the importance of such herbivory in stream ecosystems, or indeed validation of the actual assimilation of algal matter, has until recently been extremely sparse.

Matthews et al. (1987) reviewed the results of an exciting series of studies of the grazing minnow Campostoma anomalum in streams throughout the Midwest. These studies showed clearly that grazing fishes can play an important functional role in the structuring of stream communities and even elucidated higher order interactions which may modify this function. Even in these extensive studies, however, actual assimilation of algal matter was neither demonstrated nor cited.

In one investigation of direct herbivory in a North American stream fish, Moodie and Lindsey (1972) concluded that "large amounts of filamentous algae are ingested but not digested" by the chiselmouth, Acrocheilus alutaceus. This conclusion was based on an apparent lack of reduction in cellulose along the length of the gut. No mention was made of how this pattern was quantified, nor the taxa of algae consumed.

Regardless, the release of cell content is not contingent upon assimilation of the cellulosic fraction of the cell wall. This is particularly the case in stomachless fishes, such as A. alutaceus, that often depend on specialized morphologies for the trituration of cell walls (Lobel 1981, Horn 1989). On the basis of a visual inspection of foregut and rectal samples, Moodie and Lindsey (1972) concluded that diatoms "provide the principal nutrition" of adult A. alutaceus. No estimate of assimilation efficiency was reported.

A. alutaceus is distributed throughout the relatively large, warm tributaries and mainstem of the Columbia River system. An abundant population of chiselmouths in the Willamette River near Corvallis, Oregon provided an excellent opportunity to investigate the ability of a grazing stream fish to assimilate algal matter and to directly test the conclusions of Moodie and Lindsey (1972).

METHODS

Though Moodie and Lindsey (1972) did not mention the taxa of filamentous algae observed in the guts of A. alutaceus, it is likely that they were referring to filamentous green algae. Algal food sources used in this study were a filamentous green alga and an assemblage of diatoms. Ulothrix zonata is an abundant alga that occurs in dense, relatively pure stands on the cobble and boulders of many Western Oregon streams. Cobblestones were collected from the South Santiam River, returned to the laboratory, and scrubbed and rinsed until microscopic analysis of subsamples revealed only Ulothrix filaments. The diatom food source was

grown in laboratory streams (Lamberti et al. 1987) on 15 X 15 cm unglazed clay tiles. These same tiles were used for feeding preference experiments (see Chapter IV) and determined to be constituted of 97% diatoms, less than 1% filamentous greens, and about 2% detrital material. The diatom assemblage was heavily dominated by Synedra ulna and Achnanthes lanceolata.

Chiselmouths collected from the nearby Willamette River were held for 7 days in 90-L, constant-flow aquaria equipped with a shaded hiding place, necessary to calm the fish, and maintained with a combination of Oregon Moist Pellets and unscrubbed rocks with Ulothrix. Aquaria were placed in a constant temperature chamber at 14-15°C with a 12L:12D daily photoperiod to approximate conditions at the collection site. Each aquarium held a single fish. In order to allow gut clearance without reingestion, food was withheld and a false bottom installed 24 hours prior to the introduction of experimental food sources.

At the time that assimilation studies began, I had assumed that adult A. alutaceus feeding activity was limited to daylight hours. Fish in the first trial were therefore allowed to feed *ad libidum* only during the 12-hr light period, afterwhich all food was removed. Since natural diel feeding habits were not actually known at that point, it was decided that fish in the second trial would be allowed to feed *ad libidum* for the entire diel cycle.

Food intake during the feeding trials was estimated by subtracting the biomass remaining on the tiles at trials end from the initial value of replicate food sources. In each trial, feces were collected by siphoning at 4 to 6-hr intervals. Feces from individual fish were not

kept separate but combined for each food type by 12- or 24-hr feeding trial. Fish used in this study ranged from 194 to 243 (\bar{x} =217) mm fork length. *A. alutaceus* of this size have adult digestive morphology and feeding habits but are still in a phase of relatively rapid growth (Moodie & Lindsey 1972, and see Chapters II and V).

Both food and feces were analyzed for protein, lipid, carbohydrate, fiber, ash, and energy contents. Protein, lipid, and carbohydrate were analyzed according to the methods of Kochert (1978 a,b,c). Ash content was determined by ignition of dried sample at 550°C for 4 hours. Energy content was measured with a Parr microbomb calorimeter. Fiber (cellulose, lignin, and cutin) was analyzed by a modified Goehring and Van Soest (1970) technique. The pellet remaining after fiber analysis was then ashed as above to yield hydrolysis-resistant ash (HRA) content for use as a reference marker in determining assimilation efficiency.

Assimilation efficiency has been estimated in two general ways, mass balance and reference marker techniques. In mass balance techniques, the initial food source, all remaining food at trials end, and all fecal material must be collected quantitatively and analyzed for the component(s) of interest. Because of the meticulous logistical requirements of this technique and because it cannot be used in field research, some variation of reference marker is often used instead. The marker is a non-assimilable substance, either indigenous to the food source or introduced in known proportion, to which the particular organic moiety of interest can be compared. Assimilation efficiency is then calculated by the change in ratio of moiety to marker between food and

feces. The technique does not require quantitative collection and is usable in either field or laboratory settings.

Conover (1966) described a marker technique that used indigenous ash content for the estimation of assimilation efficiency in zooplankton. Ash has since been used in a large number of studies (reviewed by Horn 1989), but the assumption of non-assimilability has been questioned (Buddington 1980). Since some herbivorous fishes have been shown to be capable of lysing algal cell walls in a low pH gut environment (Moriarty 1973, Payne 1978, Lobel 1981), several authors have used the ash remaining after treatment with harsh acids as a more suitable alternative (Bowen 1981, Atkinson et al. 1984). Unless demonstrated, however, non-assimilability even for this fraction remains an assumption. Fiber, or a similar fraction, has also been used as a marker in a variety of assimilation studies (Buddington 1980, Klumpp & Nichols 1983). Though fishes in general are not apparently equipped to assimilate fiber (Stickney & Shumway 1974, Prejs & Blasczyk 1977), the ability to digest cellulose has been demonstrated for some species (Lewis 1984, Rimmer & Wiebe 1987).

The general formula for calculation of assimilation efficiency (AE) was:

$$AE = (1 - ((AC/M)_{feces}/(AC/M)_{food})) \times 100,$$

where AC is the algal component of interest (e.g., protein) and M is the reference marker. Both HRA and fiber content of food and feces were measured in this study and could therefore be compared for their utility as markers.

RESULTS

Consumption rate for the 24-hr trial was roughly double that of the 12-hr trial, clearly suggesting that A. alutaceus feeds throughout both day and night. This was later confirmed in field studies (see Chapter II) that also provided a daily consumption rate estimate of 27.8% of body weight (dry wt:dry wt) at a river temperature of 15.5°C. Consumption of diatoms in the laboratory feeding trials (at 14-15°C) was 20-21% of body weight over 24 hours and 11% over 12 hours.

Consumption of Ulothrix for 24- and 12-hr trials was 10% and 4% of body weight, respectively. In terms of dry weight then, diatoms were consumed at 2-3X the rate of Ulothrix over the same period. Consumption rates were very comparable in terms of organic weight consumed in both 12-hr (diatom = 3.9%, Ulothrix = 3.5%) and 24-hr trials (diatom = 7.1%, Ulothrix = 8.8%) because of the high ash content of diatoms (Table 3.1).

Before proceeding with comparisons of assimilation efficiencies between algal food sources and among organic moieties, we must first look at the analyses of fiber and HRA. The assimilation of each was calculated by using the other as the reference marker. In all variations of food source and ration size (Table 3.2), assimilation efficiencies of fiber and HRA were not significantly different from zero, nor from each other. This suggests either that both are assimilated at the same efficiency or the more likely alternative that neither component is assimilable. If the latter is the case, either component would be suitable for use as the reference marker. HRA was chosen simply because results would be more directly comparable with the greater number of studies that have used some

Table 3.1. Macromolecular composition (% dry wt) and energy content (kJ/g afdw) of diatom and Ulothrix food sources.

FOOD SOURCE	COMPONENT					
	Protein	Lipid	Non-fiber Carbohydrate	Fiber	Ash	Energy
DIATOM	12.8	6.6	6.0	6.5	64.9	22.3
±S.E.	±0.26	±0.37	±0.28	±0.66	±0.94	±0.58
(n)	(6)	(10)	(10)	(8)	(7)	(5)
<u>Ulothrix</u>	15.7	10.5	22.6	29.9	12.2	20.1
±S.E.	±0.33	±1.74	±1.02	±2.10	±1.13	±0.39
(n)	(6)	(7)	(6)	(7)	(6)	(5)

Table 3.2. Means and standard errors of triplicate analyses of assimilation efficiency (% with HRA marker) of adult *A. alutaceus* fed diatoms and *Ulothrix* at two feeding levels. HRA assimilation efficiency calculated based on fiber marker.

		COMPONENT					
FOOD SOURCE		Protein	Lipid	Non-fiber Carbohydrate	Fiber	HRA	Energy
DIATOM:	12-hr	48.4	37.5	46.3	-1.1	1.1	35.4
	±S.E.	±2.0	±2.7	±3.2	±1.0	±1.0	±2.1
	24-hr	43.9	33.3	41.5	-2.1	1.8	30.3
	±S.E.	±3.4	±3.5	±7.1	±3.4	±3.4	±3.6
<u>Ulothrix</u> :	12-hr	53.0	44.4	40.2	-0.2	0.1	40.3
	±S.E.	±3.0	±2.6	±5.8	±1.9	±1.9	±3.0
	24-hr	30.2	33.0	27.9	-3.4	3.1	24.5
	±S.E.	±2.8	±2.7	±1.5	±3.4	±3.2	±1.1
Overall Avg. (All Trials, Both Algae)		43.9	37.1	39.0	-1.7	1.5	32.6

variation of ash content as their marker substance. Also, while no study has yet shown HRA to be assimilable, fiber, as mentioned earlier, has been shown to be assimilated by at least some fishes.

Feeding trials with the diatom food source generally showed little difference in assimilation within algal components between 12- and 24-hr trials (Table 3.2). There were, however, a few basic differences between algal components within trials. The first was the non-assimilability of fiber. Another, explained in part by the essentially unavailable energy tied up in fiber, was a pattern of significantly greater assimilation of the protein fraction than total caloric content. In 12- and 24-hr trials, protein was assimilated at 48.4 and 43.9% and energy at 35.4 and 30.2 % efficiency respectively ($P_{12\text{-hr}} < .01$, $P_{24\text{-hr}} < .05$). Lipid was also assimilated somewhat less efficiently than protein, though only significantly so in the 12-hr trial ($P < .05$).

For feeding trials with Ulothrix as the food source, protein, lipid, and energy were all assimilated significantly more efficiently ($P < .01$, $< .05$, $< .01$ respectively) in the lower ration 12-hr trial than in the higher ration 24-hr trial. Within-trial differences were less pronounced. With the exception again of cellulose, there were generally no significant differences in the efficiency at which algal components were assimilated in the 24-hr trial. In the 12-hr trial, assimilation was significantly greater for protein (53.0%) than energy (40.3%, $P < .05$).

Since the 24-hr consumption rate with Ulothrix (10%) was similar to the 12-hr consumption rate with diatoms (11%), these are perhaps the most appropriate trials to use for directly comparing the two algal food sources. Results of this comparison indicate that diatoms are

significantly more efficiently assimilated ($P < .01$) for all non-cellulosic components except lipids ($P = .31$). However, when the consumption of Ulothrix was lower (4% in the 12-hr trial), assimilation efficiencies were quite comparable to the results with diatom-fed fish.

DISCUSSION

Clearly, adult A. alutaceus are capable of digesting the algal food sources that form the bulk (Chapter 2) of their diet. In agreement with the suggestion of Moodie and Lindsey (1972), diatoms probably do "provide the principal nutrition." In contrast to Moodie and Lindsey (1972), however, it is apparent that filamentous algae are digested even though their fibrous cell walls are not.

The efficiency and mechanisms of digestion vary widely in herbivorous fishes. Assimilation efficiencies of 60-80%, for example, have been reported for both marine (Menzel 1959, Gerking 1984, Lassuy 1984) and freshwater species (DeSilva & Perera 1983). However, data presented by Prejs (1984) for two European cyprinids indicated only a 20-30% efficiency in the assimilation of plant material. The assimilation efficiency of adult A. alutaceus was similarly low at roughly 30-40% for most nonfibrous components.

The cessation of feeding in fishes is apparently controlled by dietary energy intake (Page & Andrews 1973). For this reason, it has been suggested that a major problem facing fishes that feed on relatively low protein plant matter is one of reaching satiation before sufficient protein is consumed (Bowen 1982, Millikin 1982). It is not surprising

therefore that many herbivorous fishes are more efficient in the extraction of protein than other algal components, particularly energy content (Montgomery & Gerking 1980, Klumpp & Nichols 1983, Lassuy 1984). This pattern was again observed in this study and proved a significant factor in the interpretation of algal food quality characteristics in a companion study (Chapter IV).

As its common name implies, the lower jaw of the chiselmouth bears a sharply edged cartilaginous plate, almost straight in adults, which is used for scraping algae-covered surfaces (Moodie & Lindsey 1972). A. alutaceus lacks a true stomach but has a well-developed pharyngeal mill (La Rivers 1962, Bond 1979). As is common for stomachless herbivorous fishes, A. alutaceus does have a coiled gut tract (Moodie 1966) but not the extraordinarily long gut tract of many other herbivorous fishes (Al-Hussaini 1949, Kapoor 1975). Mean relative gut length (length from esophagus to anus \div fork length) in adult A. alutaceus in this study was 2.7 ($n=120$, $sd=.35$). The pH of the chiselmouth digestive tract was nearly neutral to slightly basic with foregut pH averaging 7.6 ($n=15$, $sd=.5$) and midgut 6.8 ($n=15$, $sd=.5$). The slight reduction of pH along the digestive tract may be due to the addition of bile (Smith & Paulson 1974).

All of the traits outlined in the above paragraph are consistent with the "type III" categorizations of alimentation by Lobel (1981) and Horn (1989). Both authors suggested that such species are dependent upon trituration as a primary means of disrupting fibrous cell walls rather than hindgut fermentation or gastric acid lysis. A slightly basic pH may, however, aid in destruction of the toxins of cyanobacteria (Fogg 1962) or in the dissociation of protein-tannin complexes in certain dietary items

as in other taxa (Feeny 1970). Mosses, for example, are common in the winter diet of A. alutaceus (Chapter II) and are a known source of tannins (Howell & South 1981).

Fragmentation of algal strands was not investigated in this study. However, it is interesting in light of the dependence of A. alutaceus on pharyngeal mastication, that the assimilation of Ulothrix varied with feeding rate while the assimilation of diatoms did not. Diatoms have porous siliceous frustules while the cell walls of green algae are cellulosic. It is possible then that an increase in feeding rate may decrease mastecatory efficiency, and therefore assimilation, and that the importance of this effect varies with the nature of the algal cell wall.

Finally, the combination of relatively high ingestion rates, low assimilation efficiencies, and large population sizes suggests that A. alutaceus may play a significant role in the breakdown and transfer of autochthonous primary production to particulate-feeding members of the stream community. This same function has recently been ascribed to herbivorous cyprinids in European lake systems (Prejs 1984).

IV. FEEDING PREFERENCE OF A GRAZING CYPRINID IN RELATION TO THE NUTRIENT CONTENT OF ITS PLANT FOOD SOURCES

INTRODUCTION

The basis of dietary selection has been an area of longstanding interest in ecology, but its history is one of investigation primarily of carnivorous or nectar feeding species (Pyke 1978, Krebs et al. 1983). The initial success of foraging models for such species seems to have resulted from an early association of optimization with energy-based theory (Lotka 1922). A broad acceptance, or at least use, of energy as the currency of optimization allowed the field of optimal foraging theory to diversify into questions above the forager:food source interface and consider the context in which selection occurred (e.g., in the face of competition, Dill 1978; in the presence of predators, Townsend & Winfield 1985; among different habitats, Werner et al. 1983). Ware (1982) provides a concise review and cogent argument for the utility of energy-based optimality theory. The search for a single factor of similar explanatory power in the analysis of herbivore feeding patterns has been more elusive.

Within the fishes alone, the identified plant food sources and mechanisms for successfully foraging on them vary widely (Horn 1989) and the number of suggested bases for selection reflect this variation. Littler et al. (1983) suggested that the difficulty of harvest, or "toughness," was a factor in herbivore feeding pattern. The same factors that may account for algal toughness, e.g., fiber and calcification, may also represent nutritional constraints by reducing the actual amount or assimilability of the remaining organic fraction (Takeuchi et al. 1979, Montgomery & Gerking 1980). Lassuy (1984) suggested a similar negative

function for ash content in determining the algae included in the algal "crop" of a territorial damselfish. Horn and Neighbors (1984) observed a positive relationship between algal protein content and inclusion in the diet of a temperate intertidal blenny. Carbohydrate content has also been suggested to play an important role in the feeding preferences of herbivorous fishes (Montgomery & Gerking 1980, Horn et al. 1986).

Energy-maximization models have proven useful in understanding the diets of herbivorous homeotherms (Belovsky 1984), but may not be as suitable for herbivorous poikilotherms (Bowen 1987). Other studies have suggested that an energy-maximization approach was insufficient to explain herbivore feeding pattern (Westoby 1974, Jensen 1983, Horn et al. 1986). Energy intake, however, does seem to play an important role in controlling ingestion rate (Harper 1967, Adolph 1981) and therefore the rate of dietary intake of other nutrients. Expressions of nutrient or elemental ratios (Russell-Hunter 1970) may also provide suitable descriptions of food quality.

The publication by Bowen (1982) of his studies of the African cichlid Sarotherodon mossambicus seems in particular to have focussed attention on this approach. Bowen (1982) described a curvilinear relationship between the growth of S. mossambicus and the ratio of digestible protein to digestible energy (P/E ratio) in its diet. Because the curve approximates a second order polynomial, it implies optimality at some intermediate level of P/E ratio. Bowen suggested such an optimum at approximately 25 mgP/kJ. The concept has since proven valuable in the interpretation of the diets of other fishes (Horn et al. 1986) and holds

promise as a factor of broad explanatory power in the study of herbivore feeding patterns.

An understanding of the herbivorous feeding habits of the chiselmouth, Acrocheilus alutaceus, and its ability to assimilate algae (Chapters II & III) formed the basis for an investigation of feeding preference in a native stream fish and to address the utility of macromolecular component concentrations in explaining herbivore food choice. The use of a native species is important in that any interpretation of the basis of food choice decisions within the context of optimality theory implicitly assumes an evolutionary history between the consumer and its food source.

METHODS

In any investigation of feeding preference, there is a trade-off between the experimenter's ability to independently manipulate the various factors under consideration and the desire to use "realistic" food sources so that the decisions observed can be reasonably expected to represent those made in the natural habitat of the species. Food sources used in this study were composed of variously-dominated plant assemblages (Table 4.1) rather than individual species. This approach was taken primarily as a practical alternative to a massive culturing effort or the nearly impossible task of locating naturally occurring and abundant supplies of single-taxa food sources. However, as it is unlikely that a microphagous consumer such as A. alutaceus is able to discriminate individual algal species (Power 1983), assemblage-categorized food sources may also be more

Table 4.1. Composition of food sources used in preference experiment (% volume).

FOOD SOURCE	COMPONENT					
	Diatom	BGreen	Green (filmt)	Green (uni)	Moss	Organic Detritus
DIATOM	96.8	--	0.7	--	--	2.5
BLUEGREEN	35.5	63.3	1.2	--	--	--
GREEN	32.4	--	62.5	1.2	--	3.8
"MIX"	69.5	5.0	5.8	18.5	--	1.2
MOSS	0.2	--	11.2	0.0	87.5	1.1

representative of food patch types encountered in nature. Four of the five food sources used in this study were grown on 15 X 15 cm unglazed clay tiles in variously manipulated laboratory streams. Each variation produced a dense, even growth of a differently dominated algal assemblage - diatom, bluegreen (Cyanobacterial), green (Chlorophyte), and a "mixed" assemblage. A more detailed description of the laboratory streams is provided by Lamberti et al. (1987). The moss food source was collected from nearby streams, rinsed, and then attached to the tile with rubber bands. The biomass of each food source averaged between 30 and 40 g·m⁻² (dry wt).

The dominant taxa on diatom tiles were Synedra ulna and Achnanthes lanceolata; on bluegreen tiles, Nodularia sp.; on green tiles, Stigeoclonium tenue; and on "mix" tiles, these same species plus the unicellular green Scenedesmus. The moss used was Fontinalis with some epiphytic S. tenue. All of these taxa, except Nodularia, also occurred in the natural diet of adult A. alutaceus (Chapter II). Other bluegreens, such as Phormidium and Stichococcus, were common dietary items. Food sources used in this study were therefore representative of a cross-section of the natural diet of A. alutaceus while also of sufficient variety to allow the analysis of a diversity of patterns in nutritional content (Table 4.2).

Preference trials were run in a large (16'X32'X8') swimming pool which held 15 adult chiselmouths (\bar{x} = 203 mm FL). A. alutaceus of this size have assumed adult morphology but are still in a phase of relatively rapid growth (Chapter V). A series of nine trials, each separated by at least three hours, were run during daylight hours over a 3-day period.

Table 4.2. Summary of biochemical composition of food sources used in preference experiments (% dry wt, unless otherwise noted).

SOURCE	PROTEIN	LIPID	Non-fiber		ASH	ENERGY (kJ)
			CARBOHYDRATE	FIBER		
Diatom	12.8	6.6	6.0	6.5	64.9	7.8
Bluegreen	27.1	10.2	8.9	14.9	33.6	14.9
Green	13.7	9.6	13.9	20.9	40.9	13.3
Mix	12.4	16.4	7.7	17.8	42.4	13.6
Moss	7.0	8.4	18.0	50.2	7.8	17.6

In each trial, five food source tiles were arranged side-by-side in random sequence to avoid positional bias and placed at midpool. I then retreated to a raised platform at the edge of the pool and allowed the fish to feed until one plate was estimated to have lost over three-quarters of its original biomass. Trials were halted at this point in order to avoid preference choices biased by differential availability. Trials varied from 15 to 35 minutes in length.

Photographs were taken of each tile at trials end (except moss) and later analyzed with microcomputer and digitizer to estimate the biomass (area removed * \bar{x} biomass/area) of each food source consumed in that trial. Moss was simply reweighed and biomass loss calculated directly. A preference ranking for each trial was then assigned on the basis of biomass loss (most preferred = 5, least preferred = 1). Replicate samples of each food source were analyzed for protein, lipid, carbohydrate, fiber, ash, and energy content (as described in Chapter III).

RESULTS

Results of the preference experiments were very consistent (Table 4.3) and showed the following pattern in preference:

diatom > bluegreen > green > mix > moss,

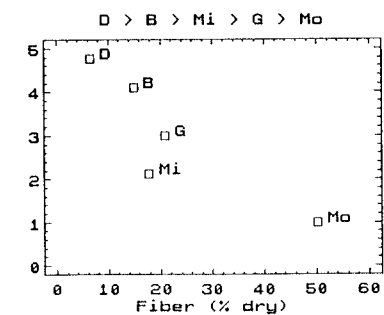
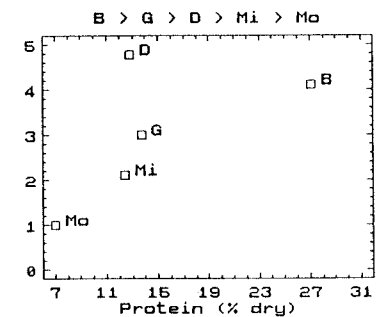
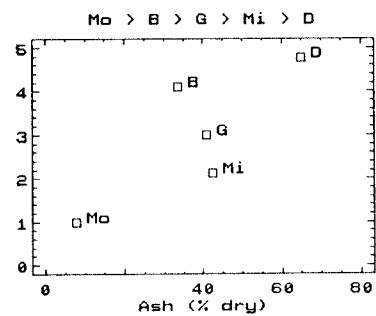
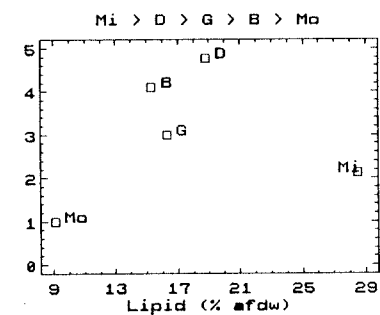
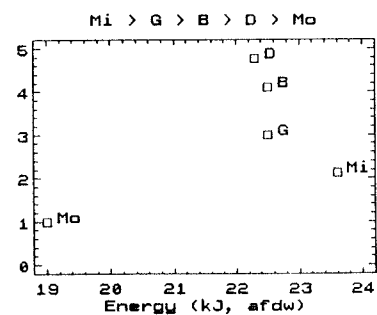
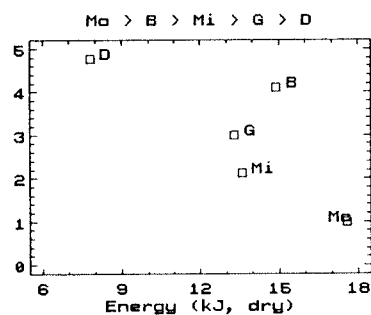
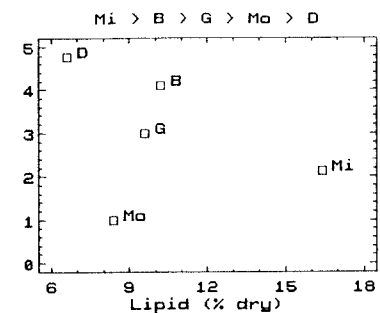
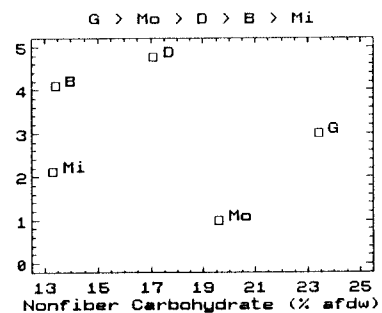
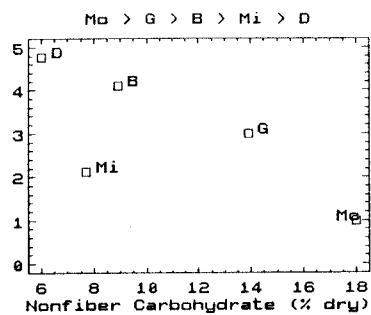
with mean rankings of 4.8, 4.1, 3.0, 2.1, and 1.0 respectively. A Tukey multiple range test indicated that mean ranks for diatom and bluegreen food sources were separable at the 95% confidence interval, and all others at 99%. This pattern was then used to compare the various algal components as descriptors of food choice.

Observed mean organic moiety concentrations, energy, and ash content are plotted against observed mean rank in Figure 4.1. Few of the measured

Table 4.3. Results of preference experiments with A. alutaceus
(Most preferred = 5, Least preferred = 1).

TRIAL NO.	(FOOD SOURCE, RANK)				
	Diatom	Bluegreen	Green	Mix	Moss
1	5	4	3	2	1
2	5	3	4	2	1
3	5	4	3	2	1
4	5	4	3	2	1
5	4	5	3	2	1
6	4	5	3	2	1
7	5	4	3	2	1
8	5	4	2	3	1
9	5	4	3	2	1
Average:	4.8	4.1	3.0	2.1	1.0

Figure 4.1. The relationships between observed mean organic moiety, ash, and energy content and observed mean preference rank (5 = most preferred, 1 = least preferred). Expected order of preference (see text) for each component is also noted (D=diatom, B=bluegreen, G=green, Mi=mix, Mo=moss).



algal components, whether expressed in terms of dry or ash-free dry weight (afdwt), showed a strong relationship to the observed pattern of preference. The "expected" order of preference, had the component expressed in that graph been the basis of selection (positive for nutrient or energy content, negative for fiber or ash content), is also shown. For example, if preference had been proportional to energy content (% dry wt, Fig. 4.1D), then the expected pattern of preference would have been: moss > bluegreen > mix > green > diatom. In this case, four of five food sources would have been switched from their observed ranking by one or more places. The sequence varied when energy was expressed as afdwt (Fig. 4.1E), but four of five sources would still have been ranked incorrectly. Clearly, energy content does not appear to have been the basis of selection. Lipid, carbohydrate, and ash contents also failed to correlate well with observed preference.

For those components illustrated in Figure 4.1, fiber content (Fig. 4.1I) most closely agreed with the observed choices of *A. alutaceus* with only the green and mix assemblages switched. A regression of fiber content (% afdwt) against mean preference rankings provided the best fit of any single component ($r^2 = 82.3\%$). The only other component for which r^2 exceeded 70% was a linear regression for protein content (% afdwt). In each case, however, if the pattern of preference had agreed with that suggested by the regression, the sequence of preference would again vary from observed by one switch in position.

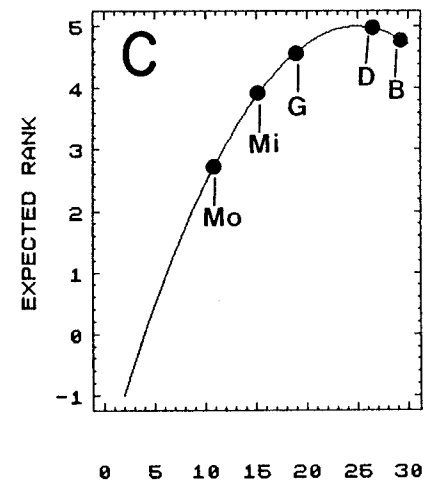
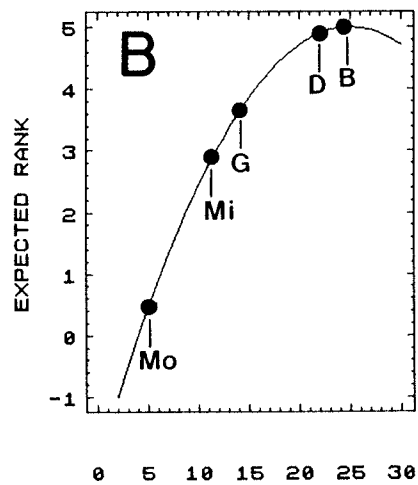
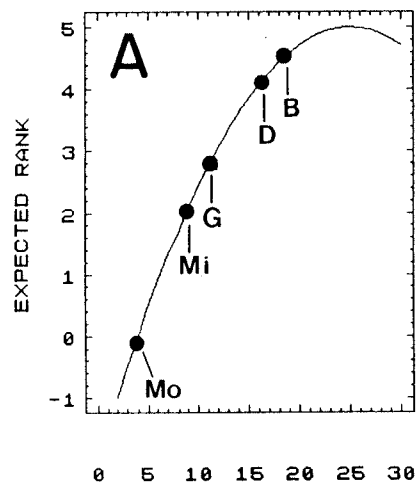
An interesting pattern emerges when the nutrient ratio approach of Bowen (1982) is employed. If the ratio of protein to energy is expressed in terms of the measured gross content, i.e., before any adjustment for

digestibility, and plotted along the curve presented by Bowen (Fig. 4.2A), the food sources fall into the same pattern expressed when simply plotted against protein content; bluegreen > diatom > green > mix > moss. However, because there are a number of ways to calculate, estimate, or express energy content, there is room for confusion in the interpretation of this ratio (Jobling 1983). This is particularly the case when assumptions are substituted for actual information on the energy value or digestibility of the food source. As Jobling (1983) pointed out, such nutrient ratios "to be strictly correct...should be expressed in terms of digestible nutrient per unit digestible energy with the digestible values being measured directly." Indeed, Bowen's curve was presented in terms of digestible protein to digestible energy.

Mean assimilation efficiencies determined in a companion study of *A. alutaceus* (Chapter III, Table 3.2) were applied directly to gross protein and energy values to estimate digestible protein to digestible energy ratios. Because of the disparity in protein and energy assimilation efficiencies, this conversion tends to increase the value of the ratio (Fig. 4.2B) but does not alter the previously observed pattern. Again, however, this is not an entirely correct interpretation of Bowen's suggested ratio.

Because it has been determined that *A. alutaceus* is not capable of digesting fiber (Chapter III), that fraction of the total energy tied up in fiber should not be included when computing digestible energy. Removal of this fraction of the energy content of each food source (assuming $4.1 \text{ kcal} \cdot \text{g}^{-1}$, Jobling 1983), should therefore produce a more accurate representation of the digestible protein to digestible energy ratio. When

Figure 4.2. Observed mean protein to energy (P/E) ratios versus expected preference rank had selection followed the curvilinear model of Bowen (1982). 2A = gross P/E; 2B = digestible P/digestible E, unadjusted for fiber; 2C = digestible P/digestible E, adjusted for fiber. D=diatom, B=bluegreen, G=green, Mi=mix, Mo=moss.



this value is then plotted along Bowen's suggested curvilinear relationship (Fig. 4.2C), the resultant pattern matches that observed in the preference experiments, i.e., diatom > bluegreen > green > mix > moss. Of those factors analyzed in this study, therefore, the ratio of digestible protein to digestible energy, when interpreted according to the model of Bowen (1982), provided the best descriptor of the observed feeding preferences of A. alutaceus.

DISCUSSION

Others (Horn et al. 1986) have assumed the validity of Bowen's optimality curve and used it to interpret their data, but this study is the first that I am aware of that set out to directly test its utility as a predictor of food choice. Bowen's model of food quality is based on the prediction of growth rather than preference. However, once the food source biochemical data were correctly translated to digestible protein and digestible energy, the model worked remarkably well. That the model worked so well may reflect its broader utility and the importance of optimal food choice during a relatively short growth season (Chapter V) in this species.

The results of this study are not, however, the first nor perhaps the most appropriate set of data available to test the model's utility. Takeuchi et al. (1979) fed a range of formulated diets to juvenile carp and observed growth over a 28-day period. A reinterpretation of their data, with the exception of one diet that was clearly inadequate (Takeuchi et al. 1979, Table 2, Diet no.1), is reproduced here in terms of P/E ratio

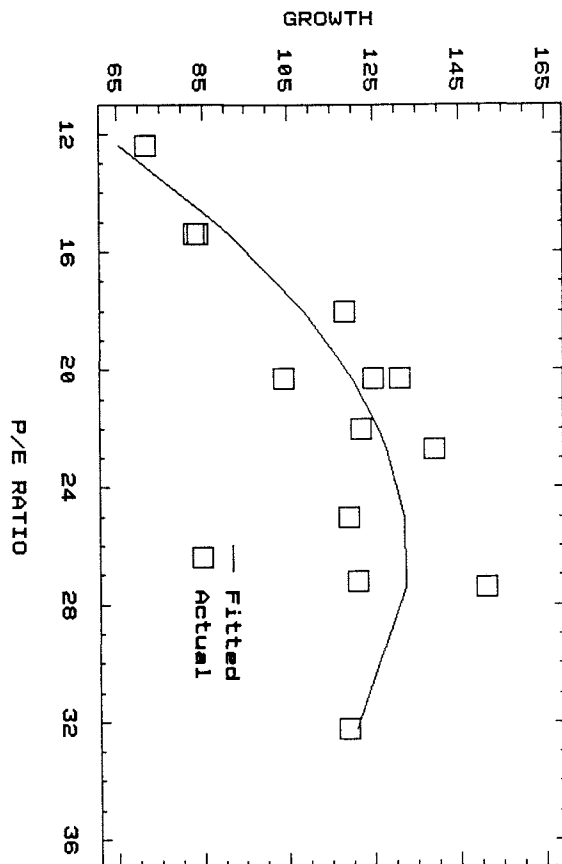
(Fig. 4.3). Though the data is expressed as crude protein (rather than digestible protein) to digestible energy, the pattern is similar to that of Bowen (1982). The data are best described ($r^2=77.1\%$, $P<.01$) by the second order polynomial equation:

$$Y = -.34X^2 + 18.1X - 105.6,$$

where Y is growth (% original weight) and X is P/E ratio (mgP/kJ). To maximize growth in this equation, the optimal value of P/E is 26.6 mgP/kJ, a value strikingly similar to the 25 mgP/kJ suggested by Bowen's model.

It is, of course, gratifying to see a model work so well in the interpretation of diverse data sets. However, while the model of Bowen (1982) is a simple projection of a curvilinear relationship, it is an information rich model that requires detailed, costly, and time-consuming analyses of the digestive capacity of the consumer as well as the biochemical composition of the food source. While such rigor is appropriate in testing the model, it should be noted that even in studies as extensive as these there is some level of assumption to be made. In my own investigations of A. alutaceus, for example, the algal species used in the preference study (other than the diatom food source) were not precisely the same as those used in the analysis of assimilation efficiency. Assimilation also varied, depending on food source, with the rate of ingestion. While I believe that the translations from one study to the other were reasonable, a certain arbitrariness is undeniable. A procedurally simpler, more parsimonious descriptor of food choice would be useful.

Figure 4.3. Relation of the crude protein to digestible energy ratio of formulated diets and the growth of juvenile carp (adapted from Takeuchi et al. 1979).



As an alternative approach, I ran a multiple regression analysis with an apparently beneficial factor (gross P/E) and an apparently negative factor (fiber, % dry wt). The resultant linear equation,

$$Y = .17X_1 - .80X_2 + 3.38,$$

where Y is expected preference ranking, X_1 is P/E, and X_2 is fiber, explained 91.3% of the variation between observed and expected rankings and correctly predicted the sequence of observed preference. Essentially the same results were therefore achieved, though admittedly with less understanding of the plant:herbivore system, with only three relatively simple analyses (protein, energy, and fiber) of the food source. While the equation will, of course, vary with other combinations of consumer and food source, this may be a promising and certainly simpler approach to the prediction of food choice in other herbivorous species.

V. NEW INFORMATION ON AGE AND GROWTH OF THE CHISELMOUTH,
Acrocheilus alutaceus (Agassiz and Pickering).

INTRODUCTION

The chiselmouth, Acrocheilus alutaceus, is a grazing cyprinid native to the Columbia and Fraser River drainages and the Harney Basin of southeastern Oregon. Although it is a major component of the fish community in large river systems within its range (Li et al. 1987), it has remained relatively unstudied. The Master's thesis of Moodie (1966) and subsequent publication (Moodie and Lindsey 1972) appear to be the only prior works that have concentrated on this species.

Moodie and Lindsey (1972) recorded a maximum age of six years at a fork length (FL) of about 230 mm. Otoliths were used for age determination. However, Moodie (1966) reported that 40% of the otoliths ground for use in the study were deemed unreadable. Wydoski and Whitney (1979) noted that A. alutaceus attain a length of 12 inches (305 mm) but cited no evidence of a greater longevity in such specimens. Understandably, Scott and Crossman (1973) concluded that age and growth information for this species is "not entirely satisfactory." New information is presented here on the longevity, growth, and timing of annulus formation in A. alutaceus.

METHODS

Fish used in this study were collected by electroshocking from the Willamette River near Corvallis, Oregon. Collections were made at monthly intervals, usually in the final week of the month. The fish were placed

immediately on ice and returned to the laboratory where they were weighed and measured, their sex determined, and scales and otoliths taken. Scales were removed from either side of the fish in an area just above the lateral line and just posterior to the dorsal fin. Although all three sets of otoliths could be taken from most specimens, the *lapillus* proved most useful for age analysis. Scales were taken from 169 fish, otoliths from 164. Both scale and otolith samples were stored in 80% ethanol.

Scales were read by projection on a microfiche reader. Otoliths were sectioned to a thickness of 0.45 to 0.55 mm and attached to glass slides with histological mounting medium. Sections were viewed with transmitted light at magnifications of 20-80X. Because it is known that this species in the Willamette River spawns in early summer, ages were assigned with an assumed birth date of June 1. This also coincides with the timing of annulus formation. The narrow, translucent hyaline zones were considered annuli. A subset of 20 otoliths were aged by a second reader. Neither reader was aware of the size of the fish from which the otoliths were taken.

Verification of the annular nature of the banding patterns was according to the "edge type" technique of Kimura et al. (1979). Edge types were classified as: 1) hyaline zone present; 2) narrow opaque zone present (less than 10% of the width of the prior opaque zone); or, 3) wide opaque zone present. Seasonal progression of edge type must indicate that only a single hyaline zone is formed per year to validate their use. An attempt was also made at verification using a $50 \text{ mg} \cdot \text{kg}^{-1}$ intraperitoneal injection of oxytetracycline. However, this failed to produce reliable results.

RESULTS AND DISCUSSION

Results of the edge analysis are presented in Table 5.1. Otoliths from many of the older fish (Fig. 5.1) were fairly easily aged, but determination of edge type was difficult. Only four of the 84 fish used for edge analysis were apparently over 13 years old. The opaque zone, generally recognized as being formed during periods of relatively good growth, began to appear in A. alutaceus in April and May but was not well established until June. It was not until July that edge type "3" was noted, afterwhich it predominated through the month of October. Interestingly, it is also the period between July and October that chiselmouths feed most heavily on diatoms (Chapter II), a preferred food source with an apparently high growth producing potential (Chapter IV). It is evident from edge analysis data then that there is only one cycle of opaque and hyaline zone formation per year.

Comparison of age determinations from otoliths recorded by the two readers (Fig. 5.2A) showed very strong agreement ($r^2 = 99.3\%$). In no case did age determinations vary more than one year between readers. Of the 164 otoliths viewed, 18 (11%) were deemed unreadable. Of the 169 sets of scales viewed, 34 (20%) were deemed unreadable. Age determinations from scales were not verified by a second reader but are clearly different from those recorded from otoliths (Fig. 5.2B). Scale and otolith ages agreed quite closely up to about the age of five but then began to depart sharply. This pattern is very similar to the findings of Barnes and Power (1984) who worked with the whitefish, Coregonus clupeiformis. Difficulty

Table 5.1. Seasonal pattern of edge type (1 = hyaline, 2 = narrow opaque zone, 3 = wide opaque zone) for A. alutaceus collected from the Willamette River, Oregon.

MONTH	EDGE TYPE		
	1	2	3
January	2		
February	8		
March	5		
April	6	1	
May	7	3	
June	3	9	1
July		5	8
August		1	7
September		1	5
October	2		7
November	1		
December	1		1

Figure 5.1. Detail of otolith from 19-yr old A. alutaceus.
Extension at lower left is edge of mounting medium, not
part of the actual otolith.

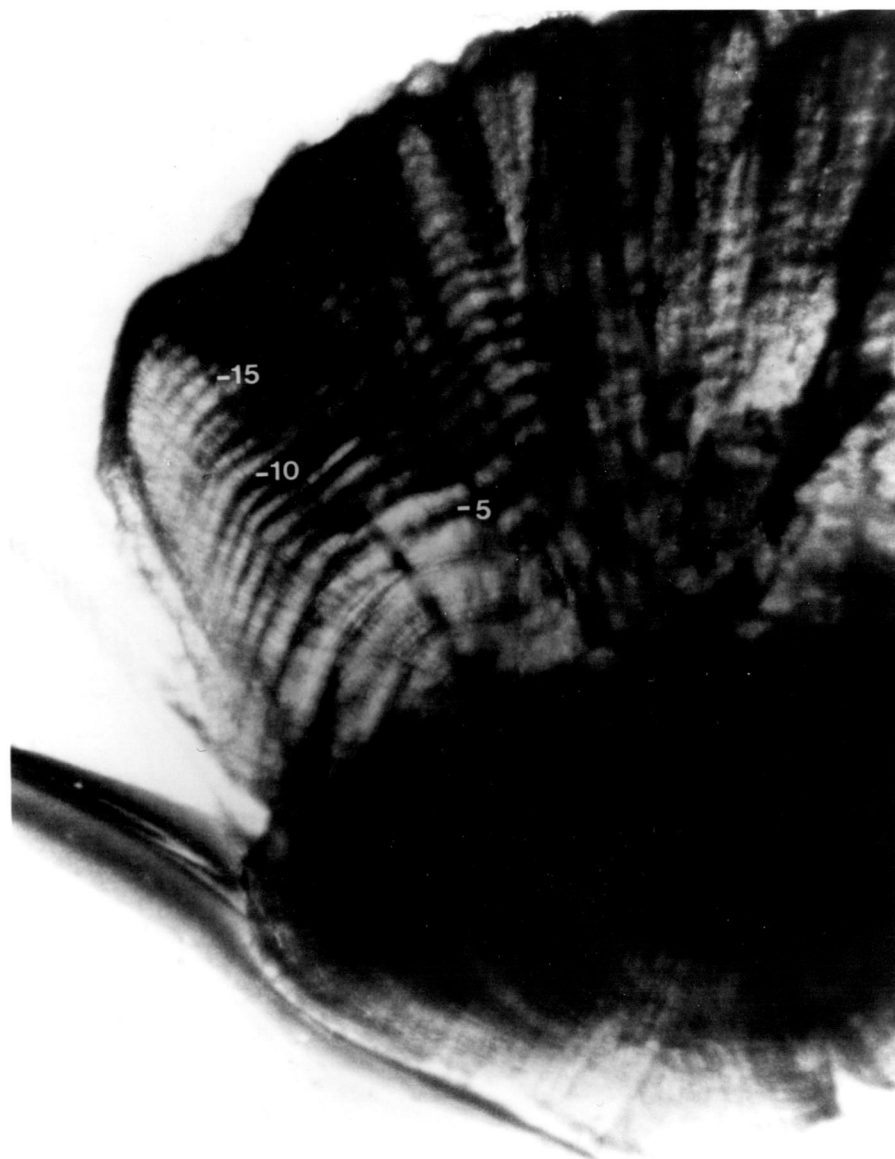
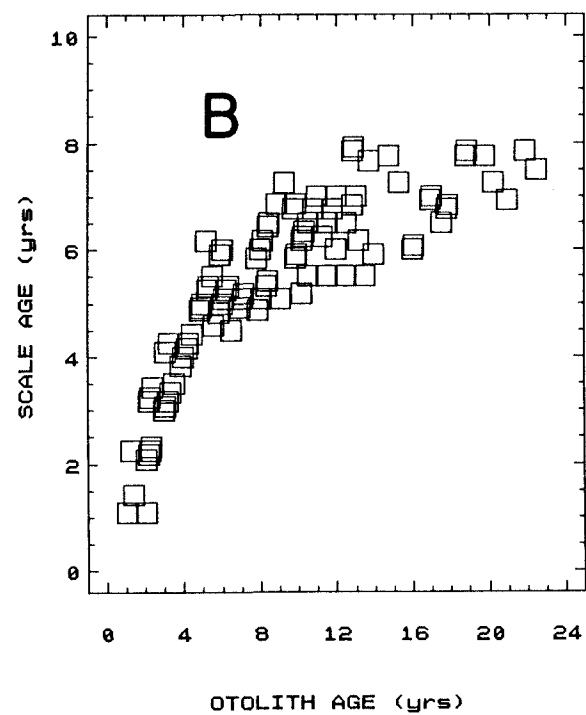
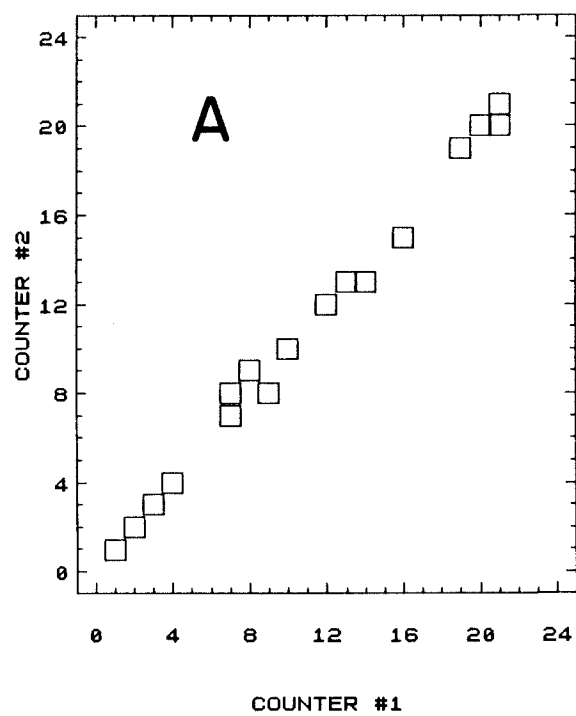


Figure 5.2. Comparisons of age determinations of two readers for 20 otoliths (2A) and of age determinations from the scales and otoliths of A. alutaceus.



has been encountered in the use of scales to age other cyprinid species as well (McConnell 1952, Carlander 1969).

The maximum age determined from scales was eight years. This same fish was assigned an age of 15+ yrs by otolith count. The maximum age recorded from otoliths in this study was 22+ years (a 304 mm FL, 378 g female) and maximum size was 321 mm FL (a 478 g, 18+ female). Recall that Moodie and Lindsey (1972) recorded a maximum age of only six years at a size of 230 mm FL. It is not clear, however, whether the discrepancies between their study and the present one are the result of differing techniques or simply that they failed to collect any fish above six years of age. While the latter may seem improbable, it is a possibility since A. alutaceus in this study averaged about 240 mm FL at six years of age.

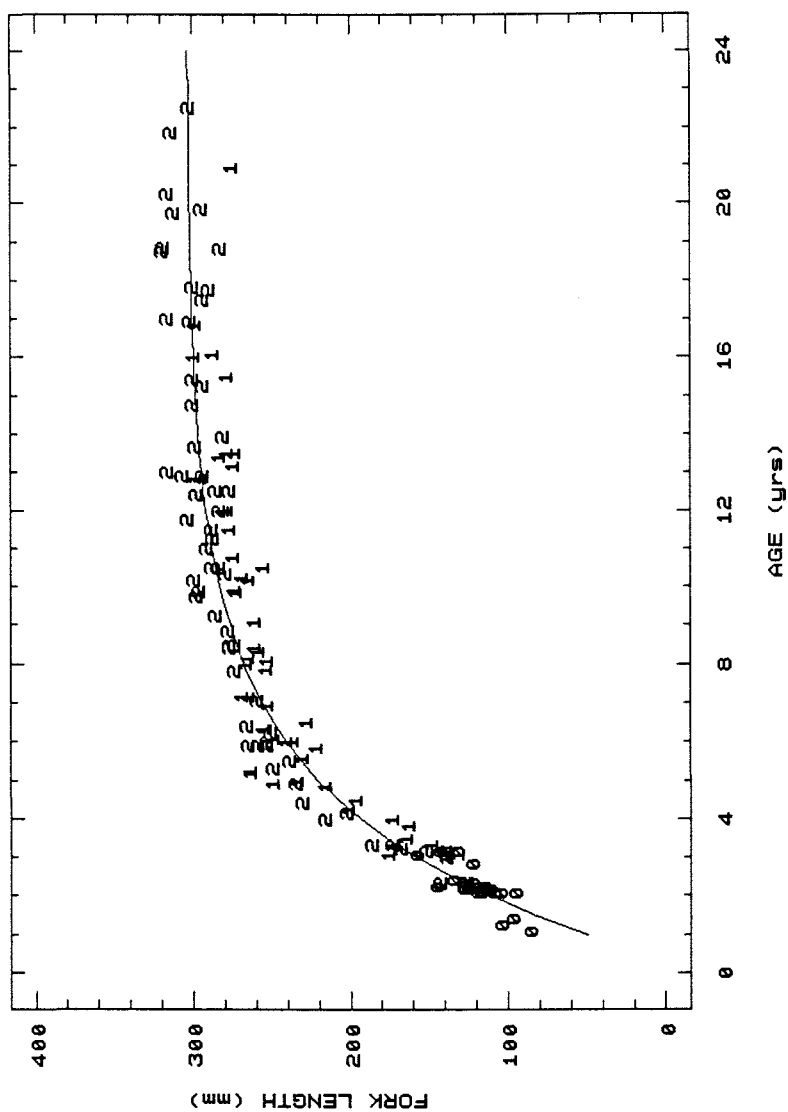
Length and otolith age data were fitted to a von Bertalanffy growth curve (Fig. 5.3) of the form:

$$L_t = L_{\infty}(1 - e^{-K(t-t_0)}),$$

where L_t = FL (mm) at time t , L_{∞} = asymptotic length, K = growth coefficient, t = age of the fish (yrs), t_0 = theoretical age at length 0. The best-fit parameter values (Statistical Graphics Corporation 1988) for L_{∞} , K , and t_0 were 303.3, 0.28, and 0.37, respectively ($r^2 = 95.3\%$). Length and weight data from 146 specimens from 86 to 321 mm FL provided the following relationship ($r^2 = 97.8\%$): $\text{Wet Wt.} = e^{(1.39 + .015*FL)}$. A mean fecundity of 18400 eggs was estimated (by volumetric displacement of subsamples of a known number of eggs) from four large females ($\bar{x} = 307$ mm FL, 446 g Wet Wt) collected just prior to the spawning season.

Though not statistically separable, it appears that females may grow somewhat faster and live somewhat longer than males. A similar finding

Figure 5.3. Age (yrs) and size (FL) data for 146 A. alutaceus from the Willamette River near Corvallis, Oregon. Data are fitted to a von Bertalanffy growth curve (see text).



has been reported for two species closely related to A. alutaceus, the peamouth chub, Mylocheilus caurinus, and the northern squawfish, Ptychocheilus oregonensis (Hill 1962, Rahrer 1963). Results of this study extend, without necessarily refuting, earlier findings and present a very different picture of the life history of the species than was previously known.

VI. GENERAL DISCUSSION AND CONCLUSIONS

In his extensive review of herbivory in marine fishes, Horn (1989) suggested that there were four levels of increasingly strong evidence of herbivory: 1) inclusion of a high percentage of plant material in the diet; 2) evidence of morphological adaptations; 3) demonstration of an ability to assimilate plant matter; and finally, 4) evidence of growth while feeding on plant matter. Mattson (1980) reviewed herbivory in a broader sense and suggested a range of evolutionary responses to the apparent nitrogen (or protein) limitations consequent to this feeding strategy. Among those responses were: an ability to select and use food sources of higher nutritional value; an increased consumption rate; prolonged periods of feeding; specialization of the digestive tract (though he related this to the presence of endosymbionts); occasional carnivory; a long lifespan; and relatively large body size. A review of the findings of my own studies reveals strong evidence of herbivory and demonstrates that the chiselmouth, Acrocheilus alutaceus, exhibits many of the expected evolutionary responses to such herbivory.

Nearly 90% of the annual diet of adult A. alutaceus in this study was plant matter, the bulk of it diatoms. Species of the genera Cymbella, Gomphoneis, Synedra, and Melosira were important contributors throughout the year. Green algae, particularly Ulothrix and Stigeoclonium, were also common contributors. Though at no time in this study could the feeding habits of A. alutaceus be called truly carnivorous, a significant portion of animal material was consumed during winter months. Adult A. alutaceus

feed both day and night and may in some seasons consume over one-quarter of their own body weight per day.

The conclusion of Moodie and Lindsey (1972) that diatoms "form the bulk of nutrition" in chiselmouths is probably correct. However, in contrast to the conclusions of Moodie and Lindsey (1972), both diatoms and filamentous green algae were assimilated. While the assimilation of diatoms did not vary significantly between feeding trials, the assimilation of Ulothrix varied inversely with ration size. This pattern may reflect both the differences in cell wall structure between these food sources and the dependence of A. alutaceus on a well-developed pharyngeal mill for the mechanical disruption of cell structure.

The ratio of digestible protein to digestible energy (P/E) of a food source has been suggested (Bowen 1982) to reflect its potential to support growth. Bowen (1982) suggested an optimal value of about 25 mgP/kJ. Adult A. alutaceus showed a consistent pattern of preference for diatoms (P/E ratio = 27 mgP/kJ) over other plant food sources. In fact, the observed pattern of preference (diatom > bluegreen > green > "mix" > moss) was well-described by Bowen's model. However, the linear combination of fiber (as a negative factor) and gross P/E (as a positive factor) provided an analytically simpler and similarly powerful descriptor.

The chiselmouth is one of the largest cyprinids native to the waters of the Pacific Northwest and apparently lives much longer (22+ yrs) than was previously known (6 yrs, Moodie & Lindsey 1972). Formation of the opaque zone, generally recognized as indicating a growth period, is most evident on A. alutaceus otoliths from July through October. This

coincides with the period of highest food intake and peak contribution of diatoms to the natural diet.

While direct evidence of growth when feeding on plant material has not been shown, i.e., the fourth level of evidence listed by Horn (1989), the strength of the other data is certainly convincing evidence of herbivory in A. alutaceus. It is also apparent that the species exhibits many of the adaptations suggested by Mattson (1980).

A couple of other interesting variations on suggested adaptations to herbivory might also be discussed in light of the findings with A. alutaceus. The first is that nutrient intake is proportional to the amount ingested as well as the efficiency with which it is assimilated. Sibly and Calow (1986) suggested, therefore, that the need to ingest larger amounts of poor quality food should lead to the evolution of relatively large gut capacity in herbivores. One implication of this proposal is that the juveniles of many species, because of their small body size, would be limited to carnivorous or omnivorous diets. Indeed, this is a commonly observed pattern in herbivores of many divergent taxa (Clark & Gibbons 1969, Pough 1973, Montgomery & Gerking 1980). However, because assimilation efficiency may be adversely effected by increased ingestion rate, as seen in this study with Ulothrix, some sort of balance must be struck between the capacity to ingest larger and larger amounts of food and the ability to absorb the nutrient content of the food source. Hofer and Shiemer (1981), who worked with a variety of cichlid and cyprinid fishes, noted that the optimum reabsorption of proteolytic enzymes occurred at relative gut lengths of 2.5 to 3.0. Recall that mean relative gut length for adult A. alutaceus was 2.7.

A second strategy would, of course, be to include higher quality food sources in the diet. While the tendency for plant matter to be regarded as relatively poor quality has certainly been challenged (Bowen 1987), others (Menzel 1959, Mattson 1980, Pandian & Vivekanandan 1985) suggest that the ingestion of at least some portion of higher quality food sources (usually in reference to animal material) is necessary. A. alutaceus does include a significant portion of animal material in its diet at certain times of year, but also apparently goes through extended periods (July through October) of nearly exclusive herbivory. Notably, it is the period of herbivory, not omnivory, which coincides with the clearest evidence of growth. This makes for a very interesting comparison of seasonal feeding habits with Bowen's P/E-based model of food quality.

Diatoms form 81% to 93% of the diet, by volume, during the period from July through October. Of the food sources used in the preference study, the diatom food source (with a P/E ratio of 27 mgP/kJ) most closely matched the predicted optimum value (25 mgP/kJ) of Bowen's model. The organic fraction of animal material consists primarily of protein and lipid, with little or no carbohydrate. If it is assumed that the protein and energy fractions of animal material are assimilated at 90% and 85% efficiency, respectively, and that protein and lipid fractions can be converted to energy by factors of 5.65 and 8.5 kcal·g⁻¹ (Jobling 1983), respectively, it would require a lipid content of over 30% before the P/E value approached the optimum suggested by Bowen (1982). For example, using these same conversion factors, animal material whose organic content was 90% protein and 10% lipid would have a P/E value of over 40 mgP/kJ, well beyond the proposed optimum. Animal tissue would, in fact, have to

be nearly 40% lipid before it would fall below 25 mgP/kJ. It is conceivable then that the inclusion of animal material may actually reduce the apparent quality of the diet when diatoms are available. This possibility, in turn, recalls the interpretation of previous energy-based optimal foraging theory. Could it be, in other words, that apparent energy-maximization in carnivores is simply acting to reduce the P/E ratio to a more acceptable level? Data presented by Jobling (1983, adapted from Watanabe et al. 1979) seems, in fact, to support this argument. Food sources with high P/E ratios (= relatively low energy content) supported less growth in rainbow trout than energy-rich food sources with P/E ratios nearer the 20 to 30 mgP/kJ range. The notion of a higher lipid content (and therefore energy content) preventing nutritional imbalance is certainly not new, but casts an interesting new light on the interpretation of prior investigations of optimal foraging theory.

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