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DIGESTION RATES AND GASTRIC EVACUATION TIMES IN RELATION TO TEMPERATURE OF THE SACRAMENTO SQUAWFISH, *PTYCHOCHEILUS GRANDIS*

Squawfish, *Ptychochilus* sp., are large piscivorous cyprinids which have a reputation of being major predators on salmon and trout, although documentation for this is poor. Brown and Moyle's (1982) review on squawfish concluded that squawfish are not likely to affect salmonid populations in free flowing streams (Falter 1969; Ebel 1970; Buchanan et al. 1980, 1981), but that significant predation could occur in areas where streams are altered (dams, diversions) and in relation to fish releases.

Sacramento squawfish, *Ptychocheilus grandis*, have been reported to prey heavily on juvenile salmonids in the Sacramento River, CA, especially below Red Bluff Diversion Dam (RBDD) (Hall 1977), and have been implicated in the continuous decline of chinook salmon, *Oncorhynchus tshawytscha*, in recent decades (U.S. Bureau of Reclamation 1983, 1985). Currently governmental agencies charged with the management of anadromous fishes in California are attempting to decrease the number of squawfish in the Sacramento River, especially near RBDD. The justification for Sacramento squawfish removal is based on a report by Hall (1977). Unfortunately, the estimate of squawfish predation rates by Hall (1977) were made without knowledge of the digestion rates or gastric evacuation times of Sacramento squawfish in relation to temperature and is likely an overestimate.

Bentley and Dawley (1981) found that northern squawfish, *P. oregonensis*, consumed 14.3 g of fish per day at 10°C. Based on this estimate Sacramento squawfish below RBDD would consume only 3 or 4 salmon/day (mean size of hatchery salmon released into the Sacramento River is 4.0 to 5.0 g). This estimate is lower than the 20 salmon/day calculated by Hall (1977) for Sacramento squawfish below RBDD. The ability of predatory fish to consume prey is mediated, at least in part, by the digestion rate and the extent of gastric evacuation (Grove and Crawford 1980; Jobling and Wandsvik 1983). Several workers (Falter 1969; Steigenberger and Larkin 1974; Persson 1979, 1981, 1982; Jobling 1980; Smith 1980; Hofer et al. 1982) have shown that digestion rates in fishes increases with increasing temperature.

The purpose of this study was to determine digestive rates and time for gastric evacuation of the Sacramento squawfish in relation to temperature. Sacramento squawfish digestion rates increased with increasing temperature, while evacuation times decreased with increasing temperature.

Methods

Sacramento squawfish (\bar{x} = 370 mm standard length [SL], range = 300-456 mm SL) were captured, using hook and line or a boat electrofisher, immediately below Red Bluff Diversion Dam (RBDD). The length-weight relationship for Sacramento squawfish was $Y = 4.03 + 2.66X$. Fish were transported to University of California, Davis, and treated immediately with nitrofurazone or potassium permanganate. The fish were held for several days at their capture temperature before the tem-

perature was adjusted to the experimental temperatures. The temperature was adjusted upward 1.0°C or downward 0.5°C per day until the experimental temperature was reached. Temperatures were maintained using an immersion heater and thermostat. Fish were then held for 14 d at the experimental temperature. Sacramento squawfish were fed mosquitofish, *Gambusia affinis*; golden shiner, *Notemigonus crysoleucas*; or threespine stickleback, *Gasterosteus aculeatus*, in excess during the holding period.

Sacramento squawfish were starved 72 h at 5° and 10°C and 48 h at 15° and 20°C prior to the digestive trials. Digestive trials were 4, 16, 32, and 48 h at 5°C; 2, 4, 8, 16, and 32 h at 10°C; 1, 2, 4, 8, and 16 h at 15°C; and 2, 6, and 10 h at 20°C.

Sacramento squawfish were force-fed juvenile chinook salmon obtained from the Coleman National Fish Hatchery (mean wet weight = 3.7 g). Each squawfish was fed four salmon because squawfish captured below RBDD in 1982 averaged approximately four salmon ($x = 3.9$, Vondracek et al.¹) in their foreguts. The weight of each squawfish was estimated before a digestive trial. Each juvenile chinook salmon was weighed before the feeding trials. The salmon were selected by size to insure that each squawfish received an equivalent size adjusted ration. I attempted to feed a ration of about 2.0% of the squawfish wet weight. The mean ration actually fed was 1.8%. Squawfish were selected by size for each digestive time period to ensure an even distribution of sizes.

During force feeding Sacramento squawfish were placed into a V-shaped trough lined with polyethylene foam. Once in the trough another piece of foam was placed over the fish to restrain it. No anesthetic was used. The chinook salmon were introduced into the anterior portion of the alimentary tract of the squawfish using a large syringe (Falter 1969). The syringe (18 mm diameter) was inserted into the esophagus and past the pharyngeal teeth with the plunger removed. Once in place the salmon were introduced into the syringe. The plunger was then replaced and depressed. Groups of three to five squawfish were placed into small circular tanks maintained at the desired temperature immediately after feeding. Individual fish were identified by

placing a numbered Floy² anchor tag between the rays of the dorsal fin.

After the prescribed digestion period Sacramento squawfish were netted from the small experimental tanks and placed into the foam-lined trough. A catheter connected to a small water pump was inserted into the anus. Digestion tract contents were flushed through the mouth and collected in a fine mesh net. The digestive tract contents were weighed (salmon were weighed individually if digested <30% and en masse if >30%) and placed in a drying oven in 60°C for 24 h. Dry weights did not change after 24 h. An initial dry weight of each ration was determined by sacrificing 5 to 10 salmon prior to the digestive trials. Mean percent dry weight of the salmon was 20.8 ± 2.0% for the 10° and 15°C trials and 21.9 ± 2.1% for the 5° and 20°C trials. If the dry weight of the digested ration exceeded the estimated initial dry weight, the percent of the ration was set to 100%. The dry weight of the digested ration exceeded the estimated initial dry weight during 17 trials with a mean of about 104%.

Digestive rates at each temperature were determined by linear regression of the percent of the ration remaining in the alimentary tract versus time after force feeding. The initial wet weights of the salmon fed to the squawfish were not used in the regression analysis. Time for alimentary tract evacuation for each temperature was assumed to be the point where the extrapolated regression for digestion intersected the x axis (time after force feeding).

Results

The digestive rates of Sacramento squawfish were directly related to temperature, while the gastric evacuation times were inversely related to temperature (Fig. 1). The digestive rates were 1.8%/h at 5°C, 2.6%/h at 10°C, 6.3%/h at 15°C, and 8.2%/h at 20°C. Gastric evacuation times were 61 h at 5°C, 38 h at 10°C, 17 h at 15°C, and 14 h at 20°C.

The digestive process appeared to involve at least two phases. During the initial phase, the wet weight of the ingested salmon increased. The duration of the initial phase was inversely related to the experimental temperature. At 5°C the initial phase was at least 16 h, 4 h in duration at 10°C, 2 h at 15°C, and approximately 2 h at 20°C. During the second phase the percent dry weight of salmon remaining in the digestive tract decreased linearly with time.

¹Vondracek, G., S. R. Hanson, and P. B. Moyle. Sacramento squawfish, *Ptychocheilus grandis*, predation on juvenile chinook salmon, *Oncorhynchus tshawytscha*, below the Red Bluff Diversion Dam in the Sacramento River, California. Manuscr. in prep. Wildlife and Fisheries Biology, University of California, Davis, CA 95616.

²Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

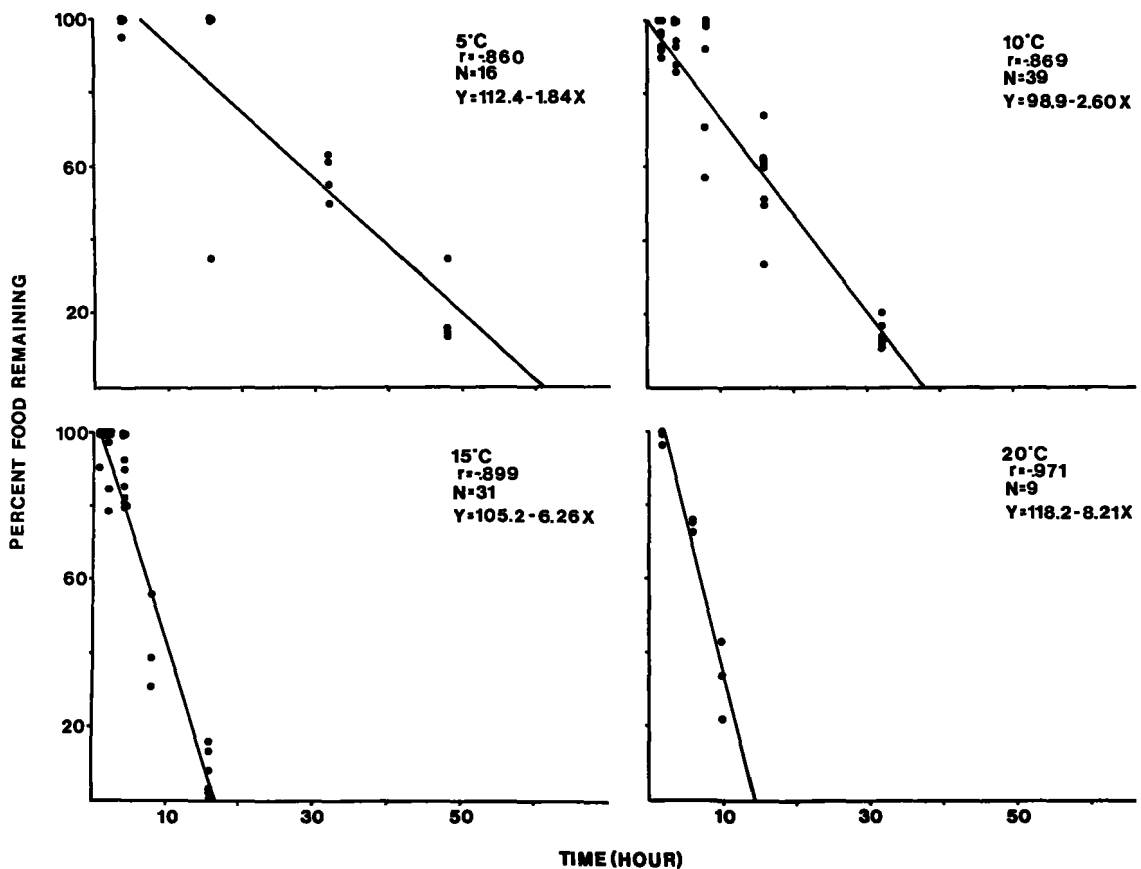


FIGURE 1.—The percent dry weight of juvenile chinook salmon remaining in the digestive tract of force-fed Sacramento squawfish after specified digestion periods at 5°, 10°, 15°, and 20°C. Each squawfish was fed four salmon.

The mean time for complete gastric evacuation over the temperature range examined can be calculated using a curvilinear equation in the form:

$$\log GE = 1.996 - 0.045T \quad (1)$$

where GE = gastric evacuation (h)
T = temperature (°C)

Although other equations may be equally applicable, Equation (1) fits the data well ($r^2 = 0.978$, Fig. 2).

Discussion

The digestion and gastric evacuation rates of Sacramento squawfish in relation to temperature differ in some respects than for the northern squawfish. The gastric evacuation times of the Sacramento squawfish in this study are different from the times calculated from equations presented in Falter (1969)

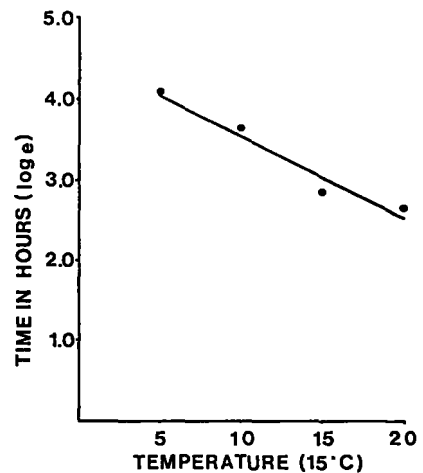


FIGURE 2.—Estimated time for complete gastric evacuation of Sacramento squawfish force-fed four juvenile chinook salmon at 5°, 10°, 15°, and 20°C.

and Steigenberger and Larkin (1974) (Table 1); however, the times noted in this study are bracketed by the other studies. Falter's equations predict that gastric evacuation would be complete in about 29 h at 6° and 10°C and about 10 h at 16.5° and 20°C. In contrast Steigenberger and Larkin's data predict that northern squawfish would complete gastric evacuation in 84, 51, 23, and 13 h at 6°, 10°, 15°, and 20°C, respectively.

TABLE 1.—Estimated time (hours) for total evacuation of stomach contents of Sacramento squawfish held at selected temperatures.

Source	Temperature (°C)			
	6	10	15	20
Falter 1969	30	29	9 (16.5°C)	11
Steigenberger and Larkin 1974				
small	84	51	23	13
large meal	163	141	28	18
Vondracek (this study)	61 (5°C)	38	17	14

There were several differences in the protocol between the studies of Falter (1969), Steigenberger and Larkin (1974), and the present investigation which may account for the differences noted in digestion and gastric evacuation. Differences in protocol included length of acclimation period, meal size, predator size, and number of prey per meal. Falter apparently acclimated the northern squawfish in his experiments for variable time period, but not <48 h. Falter fed only one prey item at a time then sacrificed the squawfish in his studies and dissected the alimentary tract. The squawfish in Falter's study ranged from 100 to 550 mm total length. Steigenberger and Larkin (1974) used northern squawfish between 150 and 400 mm fork length, only allowed an overnight acclimation period to each temperature and also sacrificed the squawfish. In this study Sacramento squawfish (size range 300-456 mm standard length) were acclimated for at least 14 d to each temperature, fed four prey items, and then had their alimentary tracts pumped. Jobling (1981) pointed out that gastric evacuation is volume-dependent and that as the number of prey per meal increases gastric evacuation time increases.

In the present experiment digestion was linear during the second phase of the digestive process. Jobling (1981) stated that the difference between the surface-to-volume ratio between large and small food particles is important in determining the pattern of digestion. Jobling further suggested that an exponential function describes the digestive

process of small, easily digested prey items, but a linear expression gave the best fit for large prey items.

The digestive rates and gastric evacuation times of the Sacramento squawfish in relation to temperature suggest that the consumption estimate of Hall (1977) of 20 juvenile salmon/day per squawfish was likely an overestimate. Water temperatures at RBDD are typically near 4.5°C in January and may increase to 10°C by late March (U.S. Bureau of Reclamation unpubl. data). Bentley and Dawley (1981) found that northern squawfish only consumed 14.3 g of fish per day at 10°C which would equal <10 fish per day even if the average size was 1.5 g. I suggest that squawfish would not consume 20 salmon/day between January and March during this period when approximately 80% of the juvenile salmon migrate downstream. As water temperatures continue to increase, predation by squawfish would likely also increase. However, juvenile salmon migrate primarily at night in the Sacramento River (Hallock and Van Woert 1954; Vondracek et al. fn. 1) which limits the predation by the visually oriented squawfish.

I suggest that the predation rate of Sacramento squawfish on juvenile salmon at RBDD is lower than previously believed because of the physiological effects of temperature on squawfish digestion during January to March.

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LABORATORY REARING OF THE SQUID *LOLIGO PEALEI* TO THE JUVENILE STAGE: GROWTH COMPARISONS WITH FISHERY DATA

The common squid of the Northwest Atlantic, *Loligo pealei* Lesueur, 1821, is a valuable species that is exploited not only as a food for human consumption, but as an important research model in biomedicine (especially for the giant axon). Summers (1983) reviewed much of the ecological and fisheries literature in his description of the life cycle of *L. pealei*. There is an important gap in our knowledge of feeding, growth, and behavior during the early phases of the life cycle. In 1980, we reported the first data from young *L. pealei* reared to 40 d posthatching (Yang et al. 1980). We now present additional data on squid reared from hatching to 6 mo and compare existing laboratory growth data with estimates from fisheries data.

Materials and Methods

The squid were reared in closed system aquaria in artificial seawater (Instant Ocean¹). All details of system design and rearing techniques can be found in Yang et al. (1983, 1986). Wild-collected egg strands and laboratory-spawned eggs were obtained from the Marine Biological Laboratory in Woods Hole, MA and air shipped to Galveston, TX on 27 August 1985. Transit time was 30 h and the eggs were shipped in natural seawater (33 ppt). Upon arrival the water temperature was 16°C, pH 7.5, and NH₄-N 1.52 mg/L. The eggs were acclimated immediately and placed in a 1,600 L circular culture tank (CT) for incubation and early rearing. The major hatch occurred on 9 September 1985, and on 11 September (day 1 of the experiment) the spent egg capsules were removed. During this 14-d incubation

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