

MECHANISMS OF PREY SELECTIVITY IN THE PIUTE SCULPIN, COTTUS BELDINGI

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ABSTRACT.

The mechanics of the predation of the sculpin, *Cottus beldingi*, was examined in artificial laboratory stream conditions using three different prey types; *Gammarus lacustris*, *Arcynopteryx californicus*, and *Ephemerella (drunella)*. It was found that encounter probability and capture success were most important in determining the observed prey selectivity. In feeding trials in which all three prey species were present selectivity was highest for *Gammarus* and lowest for *Ephemerella*. This reflects the observed differences in the activity levels of these species.

INTRODUCTION

Sculpins often comprise a large percentage of the fish biomass of communities in which they occur. The Piute sculpin (*Cottus beldingi*) is the most abundant fish in Lake Tahoe, comprising from 7 percent of the total littoral species abundance (Baker 1967) to 43 percent of the total species abundance at the 150 meter depth (Baker and Cordone 1969). It has been determined that the pelagic sculpin, (*C. aleuticus*) is the most abundant fish in Lake Washington (Ikusema 1974). Jones (1972) found densities of 6 piute sculpin per square meter in Sagehen Creek, California. Consequently, sculpins might be expected to have a substantial impact upon the food base of communities in which they are found. Early studies on sculpin feeding behavior have centered on the potential impacts of sculpin on growth and production of the more economically important salmonids.

Sculpins are opportunistic feeders and known to attack prey from ambush (Miller 1951; Daniels and Moyle 1978), feeding primarily on benthic insects and crustaceans and occasionally on fish larvae (Dineen 1951; Bailey 1952; Novak and Estes 1974). Although the prey types potentially eaten by sculpin have been studied, few attempts have been made to determine the mechanisms of prey selectivity. Li and Moyle (1976) attempted to determine some of the properties of selection in the pit sculpin (*Cottus pitensis*) in a field situation but were unable to arrive at conclusive selective mechanisms. Our attempt has been to determine in laboratory studies, some of the factors which operate to influence selectivity in the piute sculpin (*C. beldingi*).

METHODS AND MATERIALS

Aspects of the mechanics of prey selection in the piute sculpin (*Cottus beldingi*) were examined using two different laboratory channels. Ten sculpins were used in all experiments, ranging in length from 51 mm to 97 mm (Avg. TL = 73.8 mm, SD = 15.5). Between tests they were maintained separately in aquaria at 18°C. They were collected by electrofishing from Sagehen Creek and Prosser Creek, Nevada County California.

Feeding trials were performed in an artificial stream channel. The channel consisted of two sections of epoxy painted plywood trough each 2.5 m long by 0.65 m wide and 0.2 m deep. Flow in the channel was due to gravity, maintained by pumping. Pumped water entered the first channel where it flowed through the channel, out and down into the second channel, and then from the second channel into a drop-box from which it was withdrawn by the pump. The water was pumped through a constant temperature bath before entering the first section to control heating from the pump. Total drop through the channels was 15 cm and flow in both channels was continuous. The pump had a rated output of 125 liters/minute. Depth in the channels ranged from 5 to 15 cm, and the temperature ranged from 16°C to 18°C. Light was supplied by banks of fluorescent light on a 12 hr. light/dark cycle. A natural gravel/cobble rock substrate covered the bottom of the channels. Substrate diameter ranged from 10 mm to 110 mm, most commonly about 60 mm. Fish and invertebrates were restricted to a 2 m section of each channel by screening, and independent trails were run in each section. Each feeding trial lasted 24 hr., during which one fish was exposed to 30 potential prey. Trials involved either all prey of a single species, or 10 of each of three invertebrate species. A total of 40 trials were performed, 10 for each prey species, and series of 10 with all three species present.

Prey species considered were; *Arcynopteryx californicus* (Perlodidae, Plecoptera), *Ephemeroptera drunella* (Ephemerellidae, Ephemeroptera), and *Gammarus lactris* (Gammaridae, Amphipoda). Prey used in these experiments were maintained in the laboratory in aerated tanks for no more than two days prior to use. They were collected from Sagehen Creek (Nevada County, California) and from the Truckee River, Washoe County, Nevada. Prey species used were selected on the basis of behavioral diversity and relative abundance. Fish were not fed for 24 hours prior to feeding trials to standardize hunger levels. Length of all invertebrates used in each trial was measured to the nearest mm. *Arcynopteryx* and *Ephemereilla* were measured from the anterior end of the labrum to the base of the caudal cerci. *Gammarus* were measured from the base of the antennae to the end of the telson. Invertebrates ranged from 7 to 24 mm in length. Prior to placing fish in the experimental channels for each trial, the invertebrates were allowed to habituate to the conditions in the channel for at least 1 hour. Fish were maintained in the ends of the channels, isolated from the invertebrates during the same time interval.

At the conclusion of each feeding trial the fish was removed from the channel, and the substrate was then carefully removed and unconsumed prey collected and measured. Occasional prey found dead in the channel were deleted from the subsequent data analysis. Electivity index values (D) were computed for prey of different size and type using the formula of Ivlev (1961) as modified by Jacobs (1974). $D = \frac{r_i - p_i}{r_i + p_i - 2 r_i p_i}$ where r_i is the proportion of prey type i consumed by the fish and p_i is the proportion of the same type prey present in the potential prey array.

A second series of observations was made in another experimental channel. The second channel was constructed of plexiglass, 2.4 m long by 0.2 m wide and 0.2 m deep. This channel had a pumped flow maintained by a submersible pump, and was kept at a temperature of between 16°C and 18°C by diverting a portion of the flow through a cooling bath. Flow velocity in this observation tank approximated that found in the feeding channels.

In 50 cm subdivisions of this channel observations were made on the various prey types of the percentage of time spent active, distance traveled, and the capture success of sculpins. Prey were considered active if they moved about the chamber, or if they visibly moved their gills or other appendages. Four series of 10 minute observations were made on groups of 3 individual large and small *Gammarus* and *Arcynopteryx*, and on small *Ephemereilla*. Large prey measured 18 mm - 20 mm, and small prey were 9 mm to 12 mm. (There were insufficient numbers of large *Ephemereilla* available for their inclusion in these tests).

Capture success for sculpins on various prey groups was determined by placing 10 prey of a particular type in one of the 50 cm subdivisions of the observation channel containing substrate similar to that in the feeding channels and monitoring the number of capture attempts and number of prey consumed by single fish over 10 minute intervals. Prey were habituated to the channel for 15 minutes prior to the introduction of the fish. Additional prey were added as others were consumed by the fish. The observation interval began as soon as the fish initiated attacks. A total of 390 minutes of observation were made including 118 attacks by sculpins.

The relationship between prey activity and frequency of attack by scuplins was determined by observing activity of *Arcynopteryx* in the presence of a fish for 10 minute intervals or until an attack occurred. Three prey were placed in the channel and the activity of each closely monitored. Prey were habituated in the channel for 15 minutes prior to beginning observations. Fish were starved for 24 hours prior to use. Distances moved were estimated with reference to cm scales inside and outside the observation chamber.

RESULTS

Results from the feeding trials indicate that size is strongly negatively correlated with electivity for *Gammarus*, but uncorrelated for *Arcynopteryx* (Figure 1a, b). A comparison of the plots proportion of prey of particular sizes eaten by the fish (r_i) versus the proportion of that prey size present at the beginning of the feeding trial (p_i) is also informative (Figures 2a, b). They are strongly correlated for *Arcynopteryx*, while *Gammarus* show no correlation. In conjunction with the electivity values these data indicate that there are distinctly different processes affecting the predation of scuplins on these two different prey types. These data indicate that various sizes of *Arcynopteryx* are eaten in proportion to their densities in the channel, while in contrast there is a higher proportion of smaller *Gammarus* eaten.

In the feeding trials using all three prey types simultaneously, electivity values were high for *Gammarus*, near zero for *Arcynopteryx*, and very low negative for *Ephemereilla* (Figure 3). The mechanism causing more *Gammarus* to be eaten than either of the other prey in relation to their abundance, and relatively few of the *Ephemereilla* to be eaten relative to their to their abundance is not defined by these feeding trials alone.

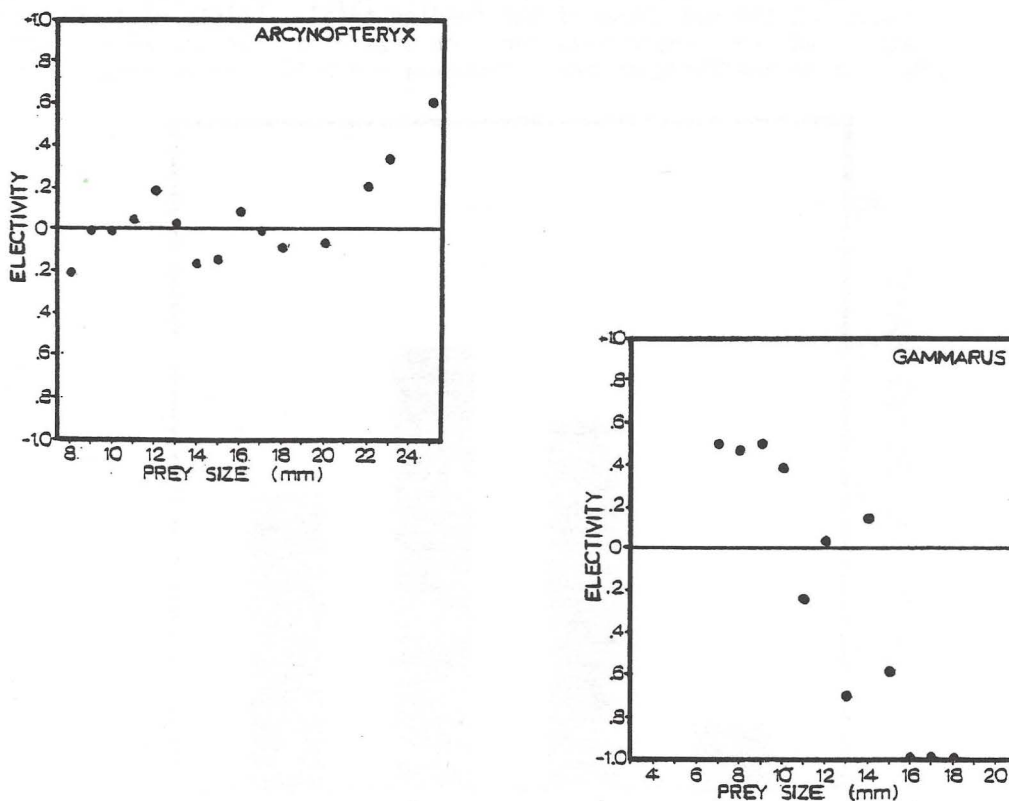


Figure 1a, b. Electivity versus prey size for *Gammarus* and *Arcynopteryx* alone in the large artificial stream channel. Points plotted are lumped data for each size class for ten 24 hour observations. Regression coefficients are; *Gammarus* $r = -.90$, *Arcynopteryx* $r = 0.19$.

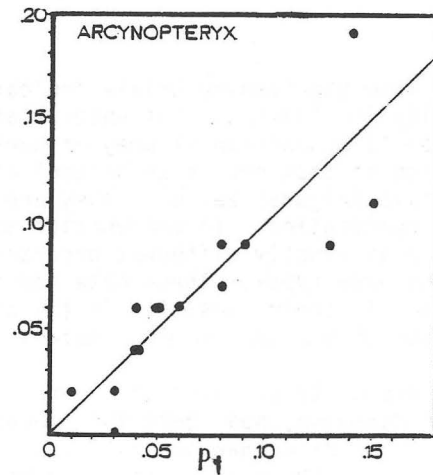
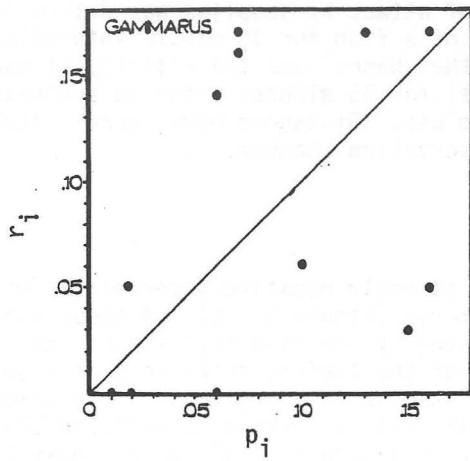


Figure 2a, b. Proportion of prey type i eaten by the sculpin (r_i) versus proportion of prey type i in the potential prey array (p_i) in the large artificial stream channel at the beginning of the feeding trial. Points plotted are values determined from lumped data for each size class for ten 24 hour observations. Regression coefficients are: *Gammarus* $r = 0.37$, *Arcynopteryx* $r = 0.87$.

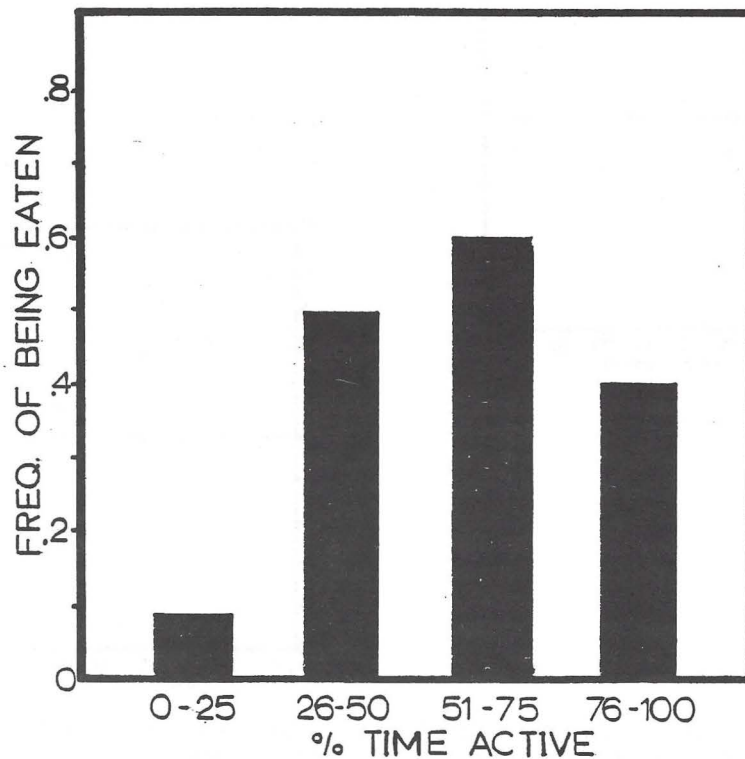


Figure 3. Frequency of *Arcynopteryx* being eaten by sculpins as a function of their activity levels. These represent grouped data from seventy 10 minute observation periods.

The behavioral observations of the activity of the different prey types indicate that there are substantial differences in the measured quantities dependent on prey size and species (Table 1). Small *Arcynopteryx* were active a significantly lower percentage of the time than any of the other prey examined, which did not differ significantly from each other. *Gammarus* were far more active in terms of distance covered in the observation period than the other prey, and within the group distance traveled increased with animal size. Observed capture success was highest for the small *Arcynopteryx*, and lowest for large *Gammarus* and large *Arcynopteryx*. These differences may reflect differences in the relative ease of handling the various prey. Qualitative observations of the captures does tend to support this contention, however there are also handling difficulties associated with the *Ephemereilla*, due to their tendency to resist ingestion by clinging to the sides of the mouth of the fish. This was sometimes observed to result in their rejection.

Observation of the percentage of time active and frequency of being eaten for *Arcynopteryx* indicated that the fish are extremely reluctant to attack non-moving prey and were only rarely observed to do so (less than 1% of attacks occurred on previously inactive prey). There also is a dramatic increase in risk associated with increasing activity to levels greater than 25% (Figure 4). This suggests that these fish do generally require some movement in order to correctly locate or identify prey prior to attack.

Table 1. Behavioral observations of prey species.

	AVERAGE PERCENT TIME ACTIVE (Activity)	AVERAGE DISTANCE TRAVELED CM/MIN (Mobility)	AVERAGE PERCENT CAPTURE SUCCESS
<i>Arcynopteryx</i>			
18 mm - 20 mm	99.5	0.4	53.6
9 mm - 12 mm	51.1	2.9	95.8
<i>Gammarus</i>			
18 mm - 20 mm	87.8	76.8	51.7
9 mm - 12 mm	92.6	22.6	78.2
<i>Ephemereilla</i>			
9 mm - 12 mm	99.8	0.1	87.5

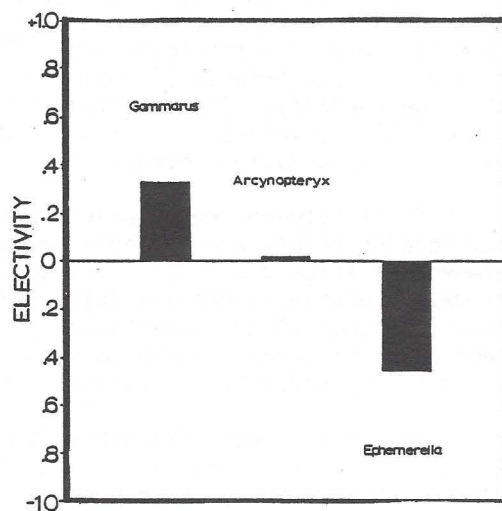


Figure 4. Average electivity of various prey types from ten 24 hour feeding trials in which all three prey types present.

DISCUSSION

The data presented here suggest a number of interesting characteristics of predation by sculpins on benthic invertebrates. Motion of the prey is apparently the most important factor determining the vulnerability of prey to predation by sculpins. Presumably prey which move less often or for short distances are detected much less frequently, and prey which are not seen to move are not attacked. There is literature documenting the importance of motion in fish predation. Lindstrom (1955) determined that the fry of char (*Salmo alpinus*) eat moving prey but do not initiate attack when the prey is motionless. Ware (1973) has shown that rainbow trout (*Salmo gairdneri*) are able to locate moving prey with greater ability than stationary prey. The combination of prey visibility and motion has been suggested to be of great importance in predator selectivity, particularly in instances where the prey array is composed of several different species (Zaret 1980). Therefore, it is probable that prey species which exercise the greatest mobility may suffer more intensive predation than more sedentary prey species.

Gammarus, *Arcynopteryx*, and *Ephemerebella*, are very similar in the total amount of time spent active, but *Gammarus* travel much greater distances (Table 1). From this standpoint, sculpin are far more likely to encounter *Gammarus* than the other prey. Higher mobility will result in higher contact rates and the opportunity for significantly more attacks on *Gammarus* (Gerritsen and Stricker 1977). This undoubtedly affected the observed predation rates in the three prey feeding trials, and may well explain most of the differences observed in these trials. This also suggests that on the basis of prey mobility alone, the large *Gammarus* would suffer heavier predation rates than small *Gammarus*. Several other factors may, however, combine to determine the final prey selectivity in sculpins. Qualitative observations indicate that pursuit distance in sculpin is relatively short. The lower average distance traveled by the small *Gammarus* would increase the probability of successful pursuit and capture by the sculpin once this prey is noticed. Percent capture success observations suggest higher rates of ingestion of small *Gammarus* than large ones (Table 1). This may be a function of prey escape ability and/or morphological limitations of the sculpins. Yoshiyama (1980) has determined that prey size consumed by three species of intertidal sculpins is correlated with mouth gape. The cumulative effects of lower mobility, and higher capture success presumably results in the observed higher electivities for the smaller individuals in *Gammarus*.

Arcynopteryx exhibit mobility levels intermediate between the *Gammarus* and *Ephemerebella*. Their intermediate electivity observations in the three prey feeding trials may result from this (Figure 4). Activity levels (as measured by percent time active) of the three prey species are not significantly different (Table 1), and this factor cannot explain the differential sculpin electivities observed in the three prey feeding trials. Activity without mobility was observed to be largely confined to the substrate where visibility to fish could be obscured by the surrounding cobble. This activity would not increase prey conspicuousness unless a sculpin is present in the immediate vicinity. *Arcynopteryx* and *Ephemerebella* are consumed less than *Gammarus* because of their lower mobility (Table 1), and are eaten in proportion to their own mobility. Size-related capture success seems to be of minor importance in determining electivity values for *Arcynopteryx* in the feeding trials, although differences were seen in the observation channel.

There does remain however some conflict between the observed lack of size related electivity for the *Arcynopteryx* feeding trials and the observed differences in the activity levels and capture success between the large and small individuals in the observation channel trials. At this point we are unable to resolve this difficulty and it seems in part due to the relatively greater amounts of time available to the fish in the feeding trials and to the lower prey encounter frequency likely to have been experienced during these trials. Experiments are currently underway to resolve this problem.

While we recognize that distance related encounter frequency is probably not the only factor which determines the selectivity of sculpins on all potential prey arrays, it does explain most of our observations. Sculpins seem not to exercise an active selectivity, but rather the observed selectivities seem to result primarily from the interplay of encounter probabilities and the capture success associated with particular prey types. It is also important to note that the infrequent attacks on non-moving dead prey suggest that there is some ability on the part of the fish to recognize the shape of potential prey in the absence of motion cues.

In contrast to what has been proposed by others (Gilson and Benson 1979) our data suggest that the selective impact of predation by sculpins on benthic communities will depend heavily on the relative activity levels of the prey species present rather than size alone and that the fish themselves exercise relatively little active selection.

In so far as ambush predators have been considered from a theoretical standpoint it seems that considerations of foraging tactics based on optimality considerations in the sense of Schoener (1971) are not particularly important. Sculpins do operate as selective predators, but the nature of the selectivity seems to be largely passive, and determined by the behavior of the prey.

ACKNOWLEDGEMENTS

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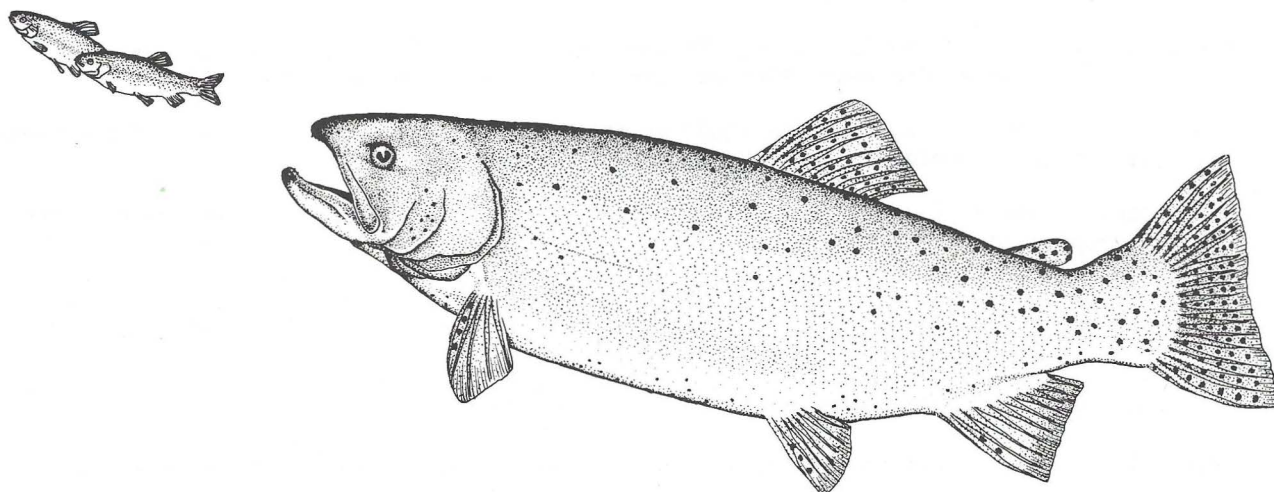
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