THE UNIVERSITY OF CALGARY

THE EFFECTS OF BIOTIC AND ABIOTIC FACTORS ON THE FORAGING SUCCESS OF A LOTIC MINNOW,

Rhinichthys cataractae

ΒY

NANCY ELIZABETH GLOZIER

A THESIS

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DEPARTMENT OF BIOLOGICAL SCIENCES

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THE UNIVERSITY OF CALGARY FACULTY OF GRADUATE STUDIES

The undersigned certify that they have read and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled, THE EFFECTS OF BIOTIC AND ABIOTIC FACTORS ON FORAGING SUCCESS OF A LOTIC MINNOW, <u>Rhinichthys cataractae</u>, submitted by Nancy Elizabeth Glozier in partial fulfillment of the requirements for the degree of Masters of Science.

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ABSTRACT

The diet of the stream-dwelling longnose dace, Rhinichthys cataractae (Valenciennes), consists mainly of two benthic prey types, the larvae of mayflies and chironomids. These prey types differ in several behavioural characteristics which affect dace foraging success. More mayflies are active on upper substrate surfaces than chironomids and dace encounter these active prey more often. However, dace are less successful at capturing active mayflies since this prey drifts in the water column to escape from dace and because chironomids show no escape response. The total number of each prey type captured depends on the interaction of encounter rate and capture efficiency (capture/attack) for these prey. Although dace consumed more chironomids than mayflies in the field, mayflies contributed more to the net rate of energy intake (E/T)of dace than chironomids because they provide a larger energy package. Similarly, the E/T of dace in the laboratory was positively related to mayfly density. Further laboratory and field tests revealed that substrate complexity and prey density also affect the foraging success and E/T of dace.

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A test of the two-prey optimal foraging model indicated that mayflies are the most profitable. (energy/handling time) prey type and dace should consume them whenever encountered. Dace should also eat chironomids when encountered since handling time for either prey type is short. In the field and in laboratory experiments dace foraged on both prey types, but consumption of chironomids did not significantly add to the E/T of dace.

The classical two-prey optimal foraging model overestimated the E/T of dace by 7 - 10 X. Modification of this model to include the different capture efficiencies of dace foraging on mayflies or chironomids yielded rates which were not different from observed E/T values. Thus, predator capture efficiencies should be included in foraging models especially for predators like dace which have capture efficiencies below 1.0 and that have values specific for a prey type.

In summary, dace encountered more mayflies than chironomids but were more successful at capturing chironomids. The tradeoff between encounter rate and capture efficiency resulted in dace capturing more chironomids. Mayfly density but not chironomid density positively affected dace E/T, while substrate complexity was inversely related to the E/T of dace.

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CHAPTER 1

INTRODUCTION

1.1 Introduction to Foraging Theory

A basic assumption of most foraging theory is that each individual's primary goal is fitness maximization (Krebs and McCleery 1984). For example, optimal foraging models assume that natural selection favours individuals possessing foraging behaviours which maximize fitness (Calow and Townsend 1981; Sih 1982; Krebs and McCleery 1984; Pyke 1984). The merit to the individual of any particular set of foraging behaviours should be evaluated by determining the direct effect of these behaviours on individual fitness. However, this direct effect on fitness is generally difficult to assess. Instead, maximization of the long-term rate of net energy intake has commonly been used as an indirect indicator of fitness maximization (Hughes 1979; Mittelbach 1981; Werner et al. 1983a, 1983b; Stephens and Krebs 1986) because this proxy for fitness allows the generation of testable predictions (Krebs and McCleery 1984).

Maximization of fitness can be achieved through the optimal allocation of a limited supply of energy to behaviours which will maximize survival and fecundity, but minimize developmental time (Sih 1982; Calow 1985). Therefore, using net energy intake as a correlate of fitness assumes that individuals with higher rates of net energy intake (E/T) enhance fitness by increasing the contribution of energy to all three aspects of fitness. Conflicts may occur when, for example, a behaviour maximizes energy return and contributes positively to fecundity and development, but adversely affects the survival component of fitness.

Fish predator-prey systems are especially suited to examine predictions from optimal foraging models. Fish diet directly influences growth rate while fecundity is related to body size (Nikolskii 1969; Hall et al. 1970; Werner and Hall 1976, 1977; Sih 1982; Dill 1987). Thus, a fish with a higher energy intake will simultaneously decrease developmental time and increase fecundity. However, the effect of the survival component on fish foraging behaviour may conflict with energy maximization unless the organism forages under low predation risk.

Longnose dace, <u>Rhinichthys</u> <u>cataractae</u> (Valenciennes), are fish predators which forage within the stone

substrate of streams on a wide range of macroinvertebrates (Bartnik 1970; Gibbons and Gee 1972). During the day dace remain concealed and inactive under stones with active foraging occurring at night as light intensity drops below 10 lux (Culp 1989). During this nocturnal foraging period, risk from visual piscivorous birds and fish is thought to be lowest (Eggers 1978; Bohl 1980) and the conflict between maximizing energy intake and survival should be at a minimum. A central theme of the thesis is to determine whether dace attempt to maximize their net rate of energy intake (E/T) at night. To address this objective, I first conducted laboratory experiments that examined the behavioural patterns of dace and their common prey types during the predator-prey interaction. I then investigated the effects that several environmental factors have on the E/T of dace in laboratory experiments and in the field.

1.2 Factors Affecting Foraging Success of Fish

Predator-prey interactions are often described by the sequence of events involved in predation, namely, search, encounter, attack and capture of the prey item by the predator (Pastorok 1981; Sih 1984). Failure by the

predator at any stage during the interaction can set this predation cycle back to search and will reduce the predator's net rate of energy intake (Healey 1984).

Mobile predators encounter various habitats which differ in prey abundance, type and/or availability and they must make decisions about where and on what to forage (Townsend and Winfield 1985). If the forager attempts to maximize its net rate of energy intake (i.e., an optimal forager), it should forage in a habitat where maximum E/T can be achieved. Recently, several investigators (Hall et al. 1970; Werner and Hall 1976, 1977, 1979; Hall and Werner 1977; Werner et al. 1983a, 1983b) have compared interhabitat choices by lentic fish to predictions from optimal habitat models. These investigations reveal that overall habitat profitability to a fish depends on prey type and density (Mittelbach 1981; Werner and Hall 1979), structural complexity of the habitat (Ware 1972; Fraser and Cerri 1982; Townsend and Winfield 1985) and interactions between these factors (Cooper and Crowder 1979; Mittelbach 1981; Crowder and Magnusson 1982). Although these studies have tested predictions of optimal habitats in lentic environments, this approach has not been utilized in streams. Since lotic habitats also vary in substrate complexity, prey

type and abundance, dace must also be faced with interhabitat foraging choices.

1.2.1 The Effects of Prey Behaviour

Prey behaviour can influence the success of the predator by either reducing encounter rates or capture efficiences (i.e., captures/attack) of the predator (Pastorok 1981; Healey 1984; Sih 1984). Two behavioural mechanisms by which prey may reduce encounters with predators are a reduction of activity (Ware 1973; Kislalioghi and Gibson 1976; Zaret 1980; Kerfoot 1982; Pienkowski 1983; Sih 1984) or the occupation of refugia (Sih 1984). Effective prey escape behaviour also can reduce captures after an attack has been initiated (Sih 1984; Drenner et al. 1978; Vinyard 1980; Fulton 1982). Thus, prey behaviour prior to encounter and after an attack could affect the net E/T obtained by the predator by reducing encounter rates and/or capture efficiencies. In fact, it has been suggested that predator diet may not result from an active choice by the predator, but that it may simply be the result of differential prey vulnerability arising from prey specific behaviour

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patterns (Ivlev 1961; Menge 1972; Ware 1972, 1973; Pastorok 1981; Peckarsky 1984).

The majority of work on predator prey interactions between fish and their invertebrate prey has occurred in lentic ecosystems and has focused on the effects that size and visibility of prey types have on fish diet (Werner and Hall 1974; Confer and Blades 1975; O'Brien et al. 1976; Eggers 1977). Despite this emphasis, several investigations have indicated that prey behaviour is also important (Vinyard 1982; Winfield et al. 1983). For example, the well documented upward vertical migrations by zooplankton at night may act to decrease encounter rates with visually foraging fish (Zaret and Suffern 1976; Wright et al. 1980; Iwasa 1982). These vertical migrations could be viewed as the zooplankton occupying a refuge of low light intensity which expands to include upper water levels at night. In addition to the behaviour of zooplankton before encounter, some species possess evasive behaviour once attacked (Kerfoot et al. 1980). Planktivorous fish experienced lower capture efficiences on prey which exhibit a better escape response than on prey which have poor evasive capabilities (Winfield et al. 1983; Vinyard 1982). These studies indicate that

zooplankton behaviour can decrease the E/T obtained by fish by decreasing encounter rates or attack efficiences.

In lotic ecosystems, the emphasis has again been directed at visually foraging fish which take most of their prey items from the water column (Ware 1973). Although physical characteristics of prey like size and contrast with the background, influence encounter rates with trout, prey behaviour also can affect predator-prey encounter rates if prey activity or exposure levels change (Ware 1972, 1973; Irvine and Northcote 1983). Prey of lotic fish may reduce encounters with visual predators by occupying refugia in the substrate during the day (Ware 1972, Glozier and Culp 1989) and/or drifting more frequently at night (Allan 1978).

For benthic, nocturnal predators like dace, behavioural characteristics of prey probably also play, an important role in predator diet. Although little information is available on the behaviour of nocturnal stream fish, the foraging behaviour of stoneflies, which also forage nocturnally in the benthos (Molles and Pietruszka 1983) is better known. Allan et al. (1987) examined the effects of a range of prey behavioural types on the capture rates of stoneflies. They found that encounter rates were greatest for the most active prey

type (large <u>Baetis</u> mayflies), while capture efficiencies were greatest for the least mobile prey which did not have an escape response (small blackfly larvae). Because of the tradeoff between encounters and capture efficiency it was suggested that it would be more advantageous for the stoneflies to consume blackflies since the increased capture efficiencies more than compensated for the reduced encounter rates. As in the water column of both lakes and streams, prey behaviour before and after an attack by a benthic predator can influence: (1) predator encounters and capture efficiences; and (2) which prey may potentially yield a higher E/T for a predator like dace.

1.2.2 The Effects of Prey Density

The effect of prey density on the capture rates of predators was initially described by Solomon (1949), then expanded upon by Holling (1959, 1965, 1966) in a series of papers which describe three types of functional responses of predators to prey density. For each functional response, predator capture rates increase with prey density until an asymptote is reached. The effect of increasing prey density theoretically increases predator

capture rates by increasing the predator's encounter rate with the prey. Asymptotic capture rates are reached by all predators when prey encounter rates are high enough that the predator spends the majority of its time handling prey items, rather than searching for prey.

1.2.3 The Effects of Habitat Complexity

Investigations into the effects of substrate complexity on foraging efficiency of fish indicate that an increase in substrate complexity tends to decrease overall E/T by increasing search time for prey and, thus, decreasing encounter rates (Huffaker 1958; Glass 1971; Stein and Magnuson 1976; Charnov et al. 1976; Crowder and Cooper 1982; Cook and Streams 1984; Fraser and Emmons 1984). This suggests that in the field, optimally foraging fish would feed in areas with minimal structure. However, as prey density is often correlated with structural complexity (Macan 1949; Gerking 1957; Crowder and Cooper 1982), an interaction between complexity and prey density may occur and fish may actually maximize E/T at some intermediate level of structural complexity. Furthermore, prey types with different levels of mobility or escape capabilities may utilize an increase in

structural complexity to a different degree. For example, a mobile prey type may enter refugia in a complex environment while immobile prey may remain in place. Therefore, an increase in complexity could increase search time for mobile prey to a different degree than for immobile prey, and the effects of substrate complexity may be dependent on prey behavioural type.

1.3 Research Objectives

The overall objective of my research was to determine if type and density of prey and substrate complexity affect the net rate of energy intake of dace (<u>R</u>. <u>cataractae</u>). First, the effect of these three factors on the E/T of dace was established in laboratory experiments. Second, a comparison was made between the laboratory results and the trends in E/T observed for dace in the field relative to prey type, prey density and substrate complexity. The specific objectives of each of the following chapters are listed in Table 1.1.

TABLE 1.1. : The general objectives of Chapters 2 - 5.

Chapter	Objectives .
2	 to determine general laboratory methods, including acclimation periods and substrate configurations, through preliminary experiments.
	 to document behavioural characteristics of prey, including behaviours which may affect encounter rates or capture efficiences of dace.
3	 to determine if foraging success of dace is affected by prey with different behavioural characteristics.
4	 to rank prey types in order of profitability, and to test these rankings in the two-prey, optimal foraging model.
	 to determine if substrate complexity, prey behaviour and prey density affect the E/T of dace, and to make qualitative predictions of distributions of dace in the field from these results.
5	 to test the qualitative predictions of dace distribution in terms of substrate complexity, prey behaviour and prey density.

1.4 Study Area

Jumpingpound Creek is a 4th order foothills stream located 30 km west of Calgary, Alberta (latitude 510 09' 16'' N, longitude 114° 31' 42'' W). The stream drains a 571 km^2 area of foothills, is ice covered during the winter months (November - April) and exhibits an annual peak in discharge during mountain runoff in June. The study area is located in open meadow with occasional aspen (Populus tremuloides) and willow bushes (Salix sp.) on the banks. The substrate is composed of sand, gravel and large cobbles and water velocities at the substrate-water interface range from 10 to 30 cm/s. In addition to dace, several other species inhabit the stream including rainbow trout (Salmo gairdneri Richardson), spoonhead sculpin (Cottus ricei (Nelson)), trout-perch (Percopsis omiscomaycus (Walbaum)), longnose sucker (Catostomus catostomus (Forster)), white sucker (Catostomus commersoni (Lacepede)) and brook stickleback (Culaea inconstans (Kirtland)). Invertebrate fauna include members of the Chironomidae, Simuliidae, Ephemeroptera, Plecoptera and Trichoptera.

CHAPTER 2

BEHAVIOURAL CHARACTERISTICS OF PREY

2.1 Introduction

Prey behaviour can alter the number and type of prey items in a predator's diet principally by affecting capture rates of a predator during either the encounter or capture phase of the predation cycle (Pastorok 1981; Allan et al. 1987). The behavioural responses of the dace prey (mayflies and chironomids), may differ because mayflies are more mobile than relatively immobile chironomids. To determine if dace foraging success is potentially affected by prey behaviour, I documented the behavioural responses of these two prey types in the presence of foraging dace. I then develop predictions on whether encounter rates or capture efficiencies of dace are likely to be affected by these antipredator responses.

Whether prey behaviour affects encounter rates will depend in part on the type of sensory system used by dace to detect prey. The sensory systems used by fish for prey detection include vision (Zaret 1980; Guthrie 1986),

olfaction (Bardach et al. 1965, 1967; Todd et al. 1967; Hara 1986), lateral line (Bleckmann 1980; Bleckmann et al. 1981; Bleckmann and Schwartz 1982) and hearing (Hawkins 1986). Nocturnal dace probably rely the least on vision for prey detection since light levels are below the intensity required for vision in minnows (Harden Jones 1956). Nocturnal fish do use olfaction for prey detection (Hare 1986). If this is the case for dace, the proximity of prey to water currents which carry chemicals towards the substrate surface would affect prey detection. More exposed prey (i.e., those occupying upper substrate surfaces) would likely be detected more frequently than prey buried in the gravel.

The lateral line of fishes is sensitive to distortions of laminar water flow (Vogel 1982) and fish can use it to determine the distance and direction of a surface wave source like that produced by a moving prey item (Schwartz 1967; Bleckamnn 1980; Elepfandt 1982; Muller and Schwartz 1982). Other benthic fish of streams detect prey items with the lateral line when the prey is positioned above, laterally or to the front of the fish (Hoekstra and Janssen 1985). If the lateral line of dace is used in prey detection, the location and activity of prey will affect dace encounter rates. Prey types moving

on the substrate surface may create disturbances of the water current, and should be more detectable by the lateral line than prey which are either on the surface but non-moving, or buried beneath the surface. Hearing in fish is also sensitive to the movement of prey items (Hawkins 1986). Prey movement likely enhances prey detection by dace through either the lateral line or hearing sensory systems.

The number of prey consumed by a predator of differing prey behavioural types is probably a result of tradeoffs between prey detection and capture efficiency (Allan et al. 1987). Although movement of prey on upper substrate surfaces may increase encounters, mobile prey often have an effective escape response which reduces predator capture efficiency. For example, entry into the drift by prey may be an effective escape mechanism used to avoid dace predators since reactive distances of dace are < 1 cm at night (Beers and Culp, submitted MS). At field current velocities of 8 - 20 cm/s, drifting prey would escape from the reactive field of dace in less than 0.2 sec. Thus, drifting by prey potentially reduces the capture efficiency and overall capture rates of dace.

I determined the behavioural characteristics of three common prey types of dace, the mayflies <u>Paraleptophlebia</u>

heteronea and Ephemerella (Ephemerella) aurivilli, and larvae of the Chironomidae. First, the behaviours which may affect dace encounter rates were examined in clear plexiglas streams. These behaviours include prey exposure measured as the proportion of prey on upper substrate surfaces and the frequency of movement. Second, drifting behaviour was compared between the prey types as it could potentially influence dace capture efficiency. Before these prey behaviour experiments were started, preliminary experiments were conducted to determine the acclimation period required for dace and to test the validity of using artificial substrates in the laboratory streams.

2.2 Preliminary Experiments and General Laboratory Methods

2.2.1 General Laboratory Methods

Circular, artificial streams (volume = 6 L, planar area = 471 cm², Fig. 2.1A) were used in all laboratory experiments that examined the foraging behaviour of dace. This stream design was successfully used to examine the behaviour of other aquatic organisms (Walde and Davies



А



Fig. 2.1. Design of the (A) circular artificial streams, (B) the medium and (C) small substrate blocks. 1984; Glozier and Culp 1989), and it allows both the fish predator and the invertebrate prey unrestricted movement up or downstream.

Habitat complexity was manipulated by changing the total amount of planar area of artificial substrates which were secured to the stream bottom. In order to reproduce precisely the desired substrate complexity in each replicate stream, substrates consisting of cubes and slates of ABS plastic were fastened together with non-toxic silicon to simulate medium (surface area = 24 cm^2) and small (surface area = 3.8 cm^2) stones and their associated medium and small crevices (Fig 2.1B and C). Two medium sized substrates and 8, 16 or 24 small substrates were attached with silicon to the bottom of each stream to create low, medium and high substrate complexities with 178, 255 and 331 cm^2 of substrate surface area $/ 0.1 \text{ m}^2$ area, respectively. In addition, an 8 mm layer of gravel (2-5 mm) covered the stream bottom between the substrates to simulate the gravel bed in riffles of Jumpingpound Creek. Since dace could enter and search the medium crevices but not small ones (pers. obs.), the high complexity streams had more substrate surface area and absolute prey refugia than the low complexity streams.

Water in the artificial streams was continuously circulated through a Frigid Units water management system where the water was saturated with oxygen and filtered. A natural photoperiod and temperature regime (Fig. 2.2) was maintained for all experiments and current velocity ranged from 20.2 cm/s in the water column to 13.4 cm/s at the substrate/water interface and 7.7 cm/s between the substrates.

Dace (mean total length = 64.1 ± 1.1 mm) were collected from Jumpingpound Creek by electrofishing, placed in holding tanks under the natural photoperiod and temperature regime for at least one week prior to the experiments, and maintained on commercial trout food. Prey types were collected from the Bow River near Calgary, and held for a maximum of one week at 10° C with algae or detritus supplied as food. To ensure adequate acclimation of prey, they were introduced to the streams 24 h prior to the foraging experiment (Elliott 1968; Glozier and Culp 1989). During this acclimation period < 5 % of the prey died.

During the foraging bout, low intensity red light was used to aid visual observations of the active foraging time of dace. Red light did not noticably affect the behaviour of the predator or prey. After the foraging



Fig. 2.2. : Diel changes in light intensity (□--□) and water temperature (●----●) during the laboratory experiments.

experiment, dace gut contents were collected by anal backflushing (Culp et al. 1988) and examined under a 25 X dissecting microscope to determine the type, number and width of head capsules of consumed prey.

For all statistical analyses in the thesis, null hypotheses were rejected at p < 0.05. Before applying parametric statistical analyses, equality of variances was confirmed with Bartlett's test for homogeneity of variances. If parametric assumptions were not met, in most cases the data were appropriately transformed (Zar 1984) and then analyzed with parametric tests. If transformation was not possible, an equivalent nonparametric statistical procedure was applied. Unless otherwise noted, the measure of variability reported with the means is ± 1 standard error.

2.2.2 Acclimation Experiments

2.2.2.1 Methods

The experiments to determine the required acclimation period for dace were performed in the artificial stream system (Section 2.2.1). For these experiments, dace were collected from Jumpingpound Creek and held at the
experimental photoperiod and temperature regime for one week.

An organism's rate of acclimation to new foraging conditions is correlated to its learning rate (Alcock 1979). Since learning is slower when learning opportunities (e.g., feeding events) are rare, the maximum acclimation period required for dace should be determined under conditions with few prey capture opportunities. Theoretically, capture opportunities should be lowest in high complexity (Charnov et al. 1976, low prey density (Holling 1959) habitats with a prey type which has a successful escape response (Allan et al. 1987). Therefore, the acclimation period for dace was determined in high complexity streams with a low density of mobile prey (mayflies).

Dace capture rates for different acclimation periods were compared in treatments where dace had 2, 3, and 4 foraging bout experiences. Three dace were randomly assigned to each treatment and were placed in the high complexity streams without food to allow 24 h of acclimation to the artificial stream conditions. On the second day, approximately 2-3 hours after the simulated sunset, dace were transferred from these starvation streams to similar streams (i.e., acclimation streams)

which had a prey density of 30 P. heteronea larvae. Dace were allowed to forage for one hour and were subsequently returned to the starvation streams. Thus, each night the dace experienced one foraging bout followed by a 24 h period without access to prey so that the meal was digested before the next foraging bout. This feeding regime is similar to their foraging pattern in Jumpingpound Creek (Culp 1989) except that the foraging bout in the laboratory had only a 1 h duration. The shorter laboratory feeding regime was necessary to ensure that < 20% prey depletion occurred (Mittelbach 1981; Persson 1985; Bence and Murdoch 1986). The pattern was repeated on consecutive days and the gut contents of three replicate dace from each treatment level collected. Capture rates were calculated by dividing the number of mayflies found in the gut by the time the fish were actively foraging in the stream. The results were analyzed with a single factor, Model 1 ANOVA to determine if the capture rates differed with number of foraging bouts.

2.2.2.2 Results and Discussion

Dace capture rates of <u>P</u>. <u>heteronea</u> larvae were higher after three and four foraging bout experiences compared with the rates after only two experiences (Fig. 2.3). The number of foraging bouts significantly influenced dace capture rates (F = 9.95, p < 0.025). Furthermore, Newman-Keuls multiple range tests showed that the capture rates after three and four foraging bouts were similar (q = 0.535, p > 0.50) and significantly higher than the capture rates after 2 foraging bouts (3 vs 2 bouts, q = 5.88, p < 0.005; 4 vs 2 bouts, q = 5.35 p < 0.005).

Since dace capture rates increased with number of foraging bouts to an asymptote at the third foraging bout experience, dace foraging behaviour should not be examined prior to the foraging bout of day three. In all subsequent experiments, dace were acclimated for at least 4 days and during this time experienced a minimum of three foraging bout experiences.

This acclimation period is shorter than the 6-9 day acclimation period determined by Werner et al. (1981) for bluegill sunfish. However, the bluegills were only exposed to their prey items for 15 min or less each day. Allowing dace to remain in the acclimation streams for 1



Fig. 2.3. : Capture rates of dace (n=3) after 2, 3 and and 4 foraging bout-experiences. Non significance (p>0.05) is indicated between treatments with a bar (-----).

h each day increased the chance of successful captures and, hence, learning during this period. It would appear that the acclimation period required by fish depends on the number of learning or capture opportunites allowed, as well as the number of consecutive days of acclimation.

2.2.3 Comparison of Capture Rates in Artificial and Natural Substrates

2.2.3.1 Methods

To determine if trends in capture rates are similar in different substrate types, the effect of increasing substrate complexity on dace capture rates was examined in natural and artificial substrates. Natural substrates consisted of pebbles and stones arranged in the same configurations as described for the low and high complexity artificial substrates (Section 2.2.1). Because natural stones are variable in size, the total substrate area of the low and high complexity natural substrate configurations (low: 228.3 \pm 9.9 cm² / 0.1 m², high: 444.2 \pm 17.1 cm² / 0.1 m²) was greater, and more variable, than the corresponding artificial substrates (low: 178 cm² / 0.1 m², high: 331 cm² / 0.1 m²).

The procedures outlined in Section 2.2.1 were followed and the acclimation period of 3 foraging bouts determined in Section 2.2.2 was used. Five dace were randomly assigned to each treatment and dace capture rates at a prey density of 70 <u>P</u>. <u>heteronea</u> larvae/stream were determined by examination of gut contents.

Although total substrate area differed between artificial and natural substrates, capture rates in both substrate types were expected to be inversely related to substrate complexity. For each substrate type, one-tailed Student t-tests were used to compare the capture rates in low and high complexity.

2.2.3.2 Results and Discussion

Both the natural and artificial substrate types yielded the predicted trend in capture rates (Fig. 2.4 and 2.5). A significantly greater capture rate occurred in substrates with less surface area (i.e., lower complexity) in both substrate types (natural, t = 3.49, p < 0.005; artificial, t = 4.90, p < 0.001). Although, capture rates were higher in artificial substrates, this substrate type had less surface area than the corresponding natural substrates and, therefore, this







Fig. 2.5. : Capture rates of dace (n=5) in artificial substrates of low (📉) and high (🧮) complexity.

trend is consistent with the prediction of higher capture rates in lower complexities. Thus, in the artificial and natural substrates, capture rates of dace increased with reductions in substrate complexity.

2.3 Prey Behaviour Experiments

2.3.1 Introduction

After determining the appropriate methods with preliminary experiments, I examined the behavioural characteristics of three common prey types of dace. In particular, I documented prey behaviour which may influence encounter rates with dace and escape behaviours of <u>P. heteronea, E. aurivilli</u> and Chironomidae larvae which could reduce the capture efficiencies of dace.

2.3.2 Methods

The artificial streams with medium complexity substrate and the methodology described in Section 2.2 were used in these experiments. To allow observation of prey behaviour, the streams and substrates were made of

plexiglas and an 8 mm layer of glass beads replaced the layer of gravel used in earlier experiments.

Eighty individuals of each prey type tested (P. heteronea, E. aurivilli and Chironomidae), were randomly assigned to the replicate streams and acclimated to the experimental conditions for 24 h. Prey behaviour was recorded under red light (Elliott 1968; Glozier and Culp 1989), in six control streams without dace and in six experimental streams to which dace had been randomly assigned. Dace were introduced into the experimental streams 1 h after the simulated sunset and allowed to forage for 15 min. The prey behaviours recorded were (1) the proportion of prey occupying positions exposed to dace predators (i.e., tops and sides of substrates), (2) the proportion of prey moving in these exposed positions, and (3) the number of prey drifting per minute in the water column. Movement of prey was defined as a change in position of the head or posterior abdominal segment in any 3-dimensional direction.

To determine if the behaviour of the prey types differed between the controls and experimental streams and between prey types, prey exposure and activity (1 and 2 above) were analyzed with 2-way, model I ANOVA after square-root arcsine transformation. The two factors were

predator presence (levels of control and experimental) and prey type (levels of <u>P</u>. <u>heteronea</u>, <u>E</u>. <u>aurivilli</u> and Chironomidae). Drift rates (3 above) were compared in a similar manner but because of unequal variances ($B_c =$ 14.1, p < 0.03), I used the non-parametric Friedman's two-factor test (Zar 1984). Additionally, if no significant interaction was found between the factors but there were significant effects of prey type, parametric or non-parametric multiple sample comparisons (Zar 1984) were performed to determine which prey types differed.

2.3.3 Results

The proportion of prey occupying upper substrate surfaces was significantly different between prey types and between the control and experimental streams (Table 2.1). <u>E. aurivilli</u> were more exposed than <u>P. heteronea</u> and Chironomidae larvae were exposed the least (Table 2.2, Fig. 2.6). For all prey types, there were fewer exposed individuals after dace had been foraging for 15 min.

In contrast, the proportion of prey moving on upper surfaces was greater for <u>P</u>. <u>heteronea</u> than for <u>E</u>. <u>aurivilli</u> (Fig. 2.7). Chironomid larvae were never

TABLE 2.1 : Two-factor analysis of variance of the effect of prey type and treatment (with or without dace) on the proportion of prey exposed. NS = not significant and * = significant difference at p < 0.05.</pre>

SOURCE OF VARIATION	F-STATISTIC	p

prey type	111.67	<0.001 *
treatment	39.62	<0.001 *
prey type x treatment	1.31	<0.290 NS

TABLE 2.2 : Newman-Keuls multiple range test on the differences between the proportion of individuals exposed for <u>P</u>. <u>heteronea</u>, <u>E</u>. <u>aurivilli</u> and Chironomidae larvae. NS = not significant and * = significant difference at p < 0.05.</pre>

COMPARISON	q-STATISTIC	p
<u>E. aurivilli</u> vs Chironomidae	20.96	<0.001 *
<u>E. aurivilli</u> vs <u>P. heteronea</u>	8.13	<0.001 *
<u>P. heteronea</u> vs Chironomidae	12.83	<0.001 *



Fig. 2.6. : Proportion of prey exposed (n=6) for P. <u>heteronea</u> (P.), E. <u>aurivilli</u> (E.) and Chironomidae (C) in the control (C,) and experimental streams (E,).





observed in an active state and, therefore, were not included in the analysis of activity. The proportion of active <u>P</u>. <u>heteronea</u> was significantly different from the proportion of active <u>E</u>. <u>aurivilli</u> (Table 2.3). Furthermore, the proportion of prey active in the control and experimental streams was significantly different (Table 2.3) with a reduction in activity occurring after the introduction of a foraging dace.

Prey drift rates in streams with foraging dace were significantly different from prey drift rates in control streams (Table 2.4). Furthermore, more prey drifted after the onset of dace foraging (Fig. 2.8). Multiple comparisons (Table 2.5) indicated that drift rates for the two mayfly species were similar but higher than Chironomidae drift rates.

2.3.4 Discussion

The prey behaviours which would potentially affect dace encounter rates are prey exposure and activity. These behaviours were different for all three prey types, although mayflies were more similar to one another than to chironomids. More <u>E</u>. <u>aurivilli</u> were exposed on upper substrate surfaces than <u>P</u>. <u>heteronea</u>, which were more

TABLE 2.3. : Two-factor analysis of variance of the effects of prey type and treatment (with or without dace) on the proportion of prey active on the upper substrate surfaces. NS = not significant and * = significant difference at p < 0.05.

SOURCE OF VARIATION	F-STATISTIC	p
prey type	 13.74 _	<0.003 *
treatment	4.45	<0.050 *
prey type x treatment	0.53	<0.250 NS

TABLE 2.4. : Nonparametric, Friedman's two-way test of the effects of prey type and treatment (with and without dace) on the drift rates of prey. NS = not significant and * = significant difference at p < 0.05.

SOURCE OF VARIATION	H-STATISTIC	p
,		
prey type	6.38	<0.050 *
treatment	. 13.18	<0.001 *
prey type x treatment	4.89	<0.100 NS

TABLE 2.5 : Nonparametric multiple range test on the differences between the drift rates of the three prey types. NS = not significant and * = significant difference with p < 0.05.

COMPARISON	q-STATISTIC	р.
<u>E. aurivilli</u> vs Chironomidae	3.44	<0.050 *
<u>E. aurivilli</u> vs <u>P. heteronea</u>	1.61	<0.500 NS
<u>P. heteronea</u> vs Chironomidae	3.51	<0.025 *



Fig. 2.8. : Drift rates of <u>P. heteronea</u> (P.), <u>E.</u> <u>aurivilli</u> (E.) and Chironomidae (C) in the control (C, _____) and experimental streams (E, ______).

exposed than Chironomidae larvae. However, the order of greatest activity for these prey types was <u>P. heteronea</u> > <u>E. aurivilli</u> > Chironomidae. Note that <u>E. aurivilli</u> mayflies were more exposed but less active than <u>P. heteronea</u> mayflies which likely results in similar dace encounter rates for these two mayflies. Encounter rates of dace with both types of mayflies would be expected to be higher compared to those with less exposed and inactive Chironomidae larvae.

For both <u>P</u>. <u>heteronea</u> and <u>E</u>. <u>aurivilli</u> an increase in drift occurred in streams with foraging dace, while Chironomidae drift changed little. Increased mayfly drift resulted from mayflies releasing from upper substrate surfaces with or without direct contact with a foraging dace. Capture efficiencies of dace are probably similar for the two mayflies but lower than for Chironomidae larvae which did not drift when attacked.

Compared to chironomids, the higher exposure and activity levels of both mayfly species should produce a higher number of encounters between dace and mayflies. Once encountered, however, chironomids probably escape less frequently than mayflies. Whether dace consume mayflies or chironomids more frequently will depend on the tradeoffs between encounter and capture efficiency. A

similar tradeoff was noted for stoneflies foraging on mayflies and blackflies (Allan et al. 1987) where it was more profitable for stoneflies to forage on inactive blackflies. To determine if dace encounter rates and capture efficiencies follow these predictions based on prey behaviour, further experiments documenting dace behaviour were conducted (Chapter 3). Since the behavioural chacteristics of both mayflies were similar, the two mayfly species were considered as a single prey behaviour class (mayflies) for comparison to a second prey class (chironomids).

CHAPTER 3

ENCOUNTER RATES, CAPTURE EFFICIENCIES AND HANDLING TIMES OF DACE

3.1 Introduction

The composition of a predator's diet often represents the result of the non-selective process of consuming vulnerable prey items, rather than the active process of rejecting potential prey items (Ivlev 1961; Menge 1972; Ware 1972, 1973; Pastorok 1981; Peckarsky 1984). Predators may fail to include a prey item in the diet which is present in the environment because: (1) the prey item is not encountered; or (2) the predator fails to capture the prey item once it is encountered (Pastorok 1981; Allan et al. 1987). The number and type of prey items consumed by a predator are likely an outcome of the encounter rates and capture efficiencies (capture/attack) experienced by the predator during its foraging bout.

Factors which potentially affect encounter rates of dace with prey include prey density (Section 1.2.2),

prey behavioural characteristics (Section 1.2.1), habitat complexity (Section 1.2.3) and the time spent handling a prey item (Pyke 1984). The probability of an encounter between dace and a prey item is expected to rise with increases in either prey density or frequency of prey behaviours which tend to increase detectability by a predator. Conversely, encounters between dace and prey should decline as habitat complexity increases. Since searching and handling of prey items are assumed to be mutually exclusive predator behaviours (Krebs and McCleery 1984), an increase in handling time should decrease total search time and, thus, encounter rates.

The proportion of predator attacks which result in successful prey capture may also change with prey behaviour and substrate complexity. For example, lower capture efficiences are expected for dace foraging on mayflies which escape in the drift than for more sedentary chironomids (Chapter 2). Additionally, if prey escape responses are more effective in more complex environments, capture efficiencies may be inversely related to habitat complexity.

Therefore, my objectives were to examine how dace encounter rates and capture efficiencies are altered by prey density, prey behavioural type and habitat

complexity. Additionally, since an increase in total handling time can reduce encounter rates, I determined whether the proportion of foraging time dace spent handling prey items changed with prey type, prey density or habitat complexity.

3.2 Methods

Encounter rates, capture efficiences and handling times were observed for dace foraging in oval plexiglas streams (Brusven 1973; Frutiger 1984). Width, depth and water velocities of these streams were similar to the circular streams (Section 2.2), and all other experimental conditions (i.e., natural light and temperature regime, predator and prey acclimation and artificial plexiglas substrates) were the same as previously described (Section 2.2).

The foraging behaviour of three dace/treatment was recorded with a Panasonic WV-1800 infrared sensitive video camera. The eight treatments included all the possible combinations of two densities of prey (ambient $(1500 / 0.1 \text{ m}^2)$ and 0.5 ambient $(750 / 0.1 \text{ m}^2)$), two substrate complexities (low and high, section 2.2) and two prey types (i.e., mayflies and chironomids). Dace

behaviour was classified according to an ethogram described by Beers and Culp (submitted MS, Table 3.1). To simplify the analysis and interpretation of results, behaviours were treated as either searching (i.e., swimming, rooting or sit and wait) or handling (i.e., attack, capture, mastication and swallow).

Encounter rates of dace were calculated as:

$$S = At / T_{st}$$
(3.1)

where S = encounter rate, At = no. of attacks and $T_{st} =$ total search time (h). Search time was defined as the time period between the onset of any searching behaviour (Table 3.1) and the initiation of an attack. Since the reactive distance of dace at night is short (< 1 cm, Beers and Culp, submitted MS), it was not possible to distingish between an encounter and an attack. Thus, calculation of encounter rate with the number of attacks in the numerator of equation 3.1 assumes that the ratio of attacks/encounter is similar across all treatments.

Handling time was defined as the time between the initiation of an attack and the return to any of the searching behaviours. The proportion of the foraging bout spent handling prey items (HTP) was calculated as;

TABLE 3.1. : Ethogram of the searching and handling behaviours of foraging dace. A = active foraging, R = resting (modified from Beers and Culp, submitted MS).

SEARCHING BEHAVIOURS :

- Swimming (A) movement of dace near the substrate or in the water column without repeated touching of the substrate.
- Rooting (A) repeated probing of the substrate with snout.
- Sit and Wait (R) body stationary and supported by the substrate.

HANDLING BEHAVIOURS :

Attack (A) - quick burst of movement oriented towards a prey item.

Capture (A) - intake of prey item into the mouth.

Mastication (A) - upward movement of head in vertical arc with distinct opercular motion indicating chewing.

Swallow (A) - distinct head and opercular movements as in Mastication but ceasing with no re-emergence of prey item.

$$HTP = T_{ht} / T_T$$
(3.2)

where ${\rm T}_{\rm T}$ = total foraging time and ${\rm T}_{\rm ht}$ = total handling time.

To determine how many prey items were captured during the 20-30 min foraging bout, gut contents of dace were collected with the anal backflushing technique (Culp et al. 1988). Capture efficiencies (CE) were then calculated as follows:

$$CE = C / At$$
(3.3)

where C = number of prey items in the gut.

The effects of prey density, prey type and substrate complexity on dace encounter rates, capture efficiencies and proportion of time handling prey items were examined with 3-factor, model 1 ANOVA. A square-root arcsine transformation was applied to the capture efficiencies and handling time data before this analysis

3.3 Results

Encounter rates of dace ranged from approximately 45 chironomids/h in the treatment with high complexity and 0.5 ambient density, to 125 mayflies/h under conditions of high complexity and ambient density (Fig. 3.1). There were no significant interactions between the effects of prey type, prey density or habitat complexity on dace encounter rates. Although there was a general reduction of encounter rates between low and high complexities, these trends were not significant (Table 3.2). In fact, the only factor which significantly influenced dace encounter rates was prey type. Across all treatments dace-mayfly encounter rates averaged 98 ± 18 mayflies/h, while dace-chironomid encounter rates averaged 51 ± 11 chironomids/h.

The analysis of dace capture efficiencies was similar in that there were no significant interactions between the effects of prey type, prey density or habitat complexity. The only factor which significantly influenced capture efficiencies was prey type (Table 3.3, Fig. 3.2). Mean capture efficiencies of dace foraging on chironomids was 0.55 ± 0.10 and was nearly double the capture efficiency for mayflies, 0.29 ± 0.05 .



Fig. 3.1. : Encounter rates of dace (n=3) foraging on mayflies (M,) or chironomids (C,) in two substrate complexities (low or high) at ambient or 0.5 ambient densities.

TABLE 3.2. :

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Three-factor analysis of variance of the effects of prey type, prey density and substrate complexity on dace encounter rates. NS = not significant and * = significant difference at p < 0.05.

SOURCE OF VARIATION	F-STATISTIC	p
prey type	4.83	0.04 *
prey density	1.17	0.30 NS
substrate complexity	2.20	0.16 NS
prey type x prey density	0.31	0.59 NS
prey type x substrate complexity	0.10	0.76 NS
prey density x substrate complexity	3.28	0.09 NS
prey type x prey density x substrate complexity	1.65	0.22 NS

TABLE 3.3. :

Three-factor analysis of variance of the effects of prey type, prey density and substrate complexity on dace capture efficiencies. NS = not significant and * = significant difference at p < 0.05.

SOURCE OF VARIATION	F-STATISTIC	р р
prey type	5.07	0.04 *
prey density	1.36	0.26 NS
substrate complexity	0.68	0.42 NS
prey type x prey density	0.36	0.56 NS
prey type x substrate complexity	0.45	0.51 NS
prey density x substrate complexity	0.001	0.98 NS
prey type x prey density x substrate complexity	0.38	0.55 NS



The proportion of time spent handling mayflies or chironomids under the conditions of high or low complexity, or ambient or 0.5 ambient density, did not differ (Fig. 3.3, Table 3.4). The proportion of foraging time dace spent handling prey items was low, averaging 0.008 \pm 0.002 across all treatments, because the handling time per prey item is very short (4.5 \pm 0.5 s/prey item).

3.4 Discussion

As hypothesized in Chapter 2, the prey type which was more exposed and active was encountered more frequently by dace. In fact, dace encountered mayflies twice as often as chironomids in all treatments. From these experiments, it is not possible to determine the exact mechanism that produces the higher encounter rate of dace with mayflies. However, it may be related to dace being able to use a greater range of sensory systems to detect mayflies (i.e., lateral line, hearing, and olfaction), while chironomids concealed in the gravel are detected primarily through olfaction.

Dace capture efficiencies for chironomids were nearly double that of mayflies which were observed to



Fig. 3.3. : Proportion of time spent handling prey items for dace (n=3) foraging on mayflies (M,) or chironomids (C,) in two substrate complexities (low or high), at ambient or 0.5 ambient densities.

TABLE 3.4. : Three-factor analysis of variance of the effects of prey type, prey density and substrate complexity on the proportion of time spent handling prey items. NS = not significant.

SOURCE OF VARIATION	F-STATISTIC	p
prey type	0.16	0.70 NS
prey density	0.38	0.55 NS
substrate complexity	0.93	0.35 NS
prey type x prey density	4.49	0.05 NS
prey type x substrate complexity	0.04	0.85 NS
prey density x substrate complexity	3.72	0.07 NS
prey type x prey density x substrate complexity	0.82	0.38 NS

use a drift escape response to avoid dace predators (Chapter 2). These results are similar to that of Allan et al. (1987) where active mayflies were encountered more frequently by stonefly predators but were captured with less efficiency than blackfly larvae. In fact, for the stoneflies, it was more profitable to forage on the less active blackfies since the increased capture efficiencies more than compensated for the lower encounter rates. In comparison, dace were more efficient at capturing active mayflies than the slower moving stonefly predator. The dietary importance of these prey types to dace will depend on how the higher encounter rates and lower capture efficiencies for mayfly prey tradeoff against the lower encounter rates and higher capture efficiencies for chironomids.

As prey density increases, predator capture rates and presumably encounter rates, are expected to increase to an asymptote (Holling 1959). This asymptote is common to all functional response curves and results from the predator spending the majority of its foraging time on the activity of handling prey items. Because encounter rates did not significantly increase for dace foraging on either prey type even with a doubling in prey density, both experimental densities were probably

located towards the lower end of a functional response curve. This conclusion is also supported by the low proportion (< 0.02) of foraging time spent handling prey items by dace regardless of prey density. Although encounter rates may increase more rapidly at some prey density > 1500 / 0.1 m², these experimental prey levels are the average level found across the streambed in Jumpingpound Creek (Chapter 5).

Although more prey refugia were present in high complexity substrate, dace capture efficiences and encounter rates were unaltered by substrate treatment. This statistical result for encounter rates may be an artifact of the large variability in this variable since encounter rates generally decreased with habitat complexity. However, the capture efficiency data indicate that prey escape behaviours are equally effective in all substrates. The primary escape mechanism of mayflies is entry into the water column (Chapter 2), and the effectiveness of this escape behaviour probably is not changed by substrate complexity. Furthermore, chironomids did not exhibit a strong escape response to dace in any substrate.

In summary, dace spent very little time handling mayflies or chironomids in any treatment likely because
both prey types were within the gape size of dace. On the other hand, prey behaviour did appear to have an important effect on the rates of prey encounter and capture by dace.

CHAPTER 4

OPTIMAL FORAGING MODELS AND THE NET RATE OF ENERGY INTAKE OF DACE

4.1 General Introduction

In the field longnose dace are faced with a choice between two distinct prey types, mayflies and chironomids (pers. obs.). The specific behavioural patterns of mayflies and chironomids (Chapter 2) result in differences in dace encounter rates and capture efficiencies (Chapter 3). Dace encounter rates with the more active and exposed mayflies are higher, and their capture efficiencies are lower, than with sedentary chironomids. These two prey types probably also differ in energetic content since mayflies are generally larger. Whether dace should consume both prey types, if both are available, will depend on how the encounter rates, capture efficiencies and energetic contents of prey balance with the metabolic costs of foraging.

Optimal foraging models are based on the assumption that foragers are designed to maximize their long term rate of net energy intake (E/T) (Stephens and Krebs

1986, see Table 4.1 for additional assumptions). Net E/T is calculated in classical optimal foraging models with encounter rates, energetic costs and benefits, and handling time but not capture efficiency. The model has the implied assumption that the forager captures: (1) 100% of all encounters; or (2) an equal proportion of all encounters, regardless of prey type. It is apparent from the capture efficiencies of dace foraging on mayflies (CE = 0.29 ± 0.05) and chironomids (CE = $0.55 \pm$ 0.10) that neither of these underlying assumptions hold for dace.

The objectives of this chapter were to compare the observed net rate of energy intake for dace foraging in circular streams (E(obs)/T) to predicted net rates of energy intake calculated from two models: (1) the classical two-prey optimal foraging model (E(opt)/T); and (2) a modified optimal foraging model which incorporates differential capture efficiences between prey types (E(ce)/T). Additionally, the models will be used: (1) to predict whether optimally foraging dace should consume both prey types, or ignore the less profitable prey type; and (2) to determine if these predictions are altered by substrate complexity.

TABLE 4.1. : Assumptions of optimal foraging models (modified from Krebs and McCleery 1984).

- 1) Prey value is measurable as net energy or some other comparable single dimension.
- 2) Handling time is a fixed constraint.
- 3) Handling and searching cannot be done at the same time.
- 4) Prey are recognized instantaneously, without error.
- 5) Prey are encountered sequentially and randomly.
- 6) Energetic costs per second of handling are similar for different prey types.
- 7) Predators are designed to maximize rate of net energy inake.

4.1.1 Two-prey Optimal Foraging Models

Classical optimal foraging models have concentrated on predicting which prey types the forager should consume in order to maximize net energy intake (Calow and Townsend 1981). The most common model incorporates a choice between two prey types, each encountered by the predator at encounter rates S_1 and S_2 during the time the predator spends searching for prey (T_s). The net energy obtained from each prey type is E_1 and E_2 , obtained in T_{h1} and T_{h2} units of handling time. The overall net rate of energy intake has been described as:

(Krebs and McCleery 1984). From this equation, predictions can be made as to whether the predator should consume both prey types. For example, if prey type 1 has a higher profitability than prey type 2 (i.e., $E_1/T_{h1} > E_2/T_{h2}$), the predator should always take prey type 1. The predator should only exclude prey type 2 when the net rate of energy intake from foraging on

prey type 1 alone is greater than foraging on both prey types, that is:

$$s_1E_1$$
 $s_1E_1 + s_2E_2$
----- > ------ (4.2)
 $1 + s_1T_{h1}$ $1 + s_1T_{h1} + s_2T_{h2}$

Thus, to determine if prey specialization is optimal for dace, prey profitability rankings for mayflies and chironomids must initially be established (section 4.3). Encounter rates, handling times and net energetic content of prey items can then be used in the models to determine net energy intake rates for dace consuming only prey type 1 (i.e., left side of equation 4.2) and for dace consuming both prey types (i.e., right side of equation 4.2).

4.2 Prey Profitability

4.2.1 Introduction

Prey profitablity (P_i) , in optimal foraging models is defined as the ratio between the net energy content (E_{ni}) and the handling time (T_{hi}) of a particular prey type (i) :

$$P_i = E_{ni} / T_{hi}$$
(4.3)

(Calow and Townsend 1981; Krebs and McCleery 1981). Since handling time of dace foraging on mayflies or chironomids is similar (Chapter 3) the difference in profitability should be determined largely by the difference in net energy content of the prey types. Mayflies are larger than chironomids and likely have a higher energy content. Thus, mayflies should be the more profitable prey type. My objective was to determine whether mayfly profitability was greater than that of chironomids, and if this was the case, to determine if this trend was consistent in conditions of different substrate complexity and prey density.

4.2.2 Methods

4.2.2.1 Prey Energy Content

To determine the relationship between prey size and energy content, benthic samples of chironomids and mayflies were collected from Jumpingpound Creek and preserved with 10% formalin. Since prey head capsules are the most recognizable and intact portion of prey items found in dace gut contents (Culp et al. 1988), head capsule width was used as a measure of prey size. In order to predict the dry weight of a prey item from a given head capsule width, linear regressions between the log transformed prey dry weights (dependent variable) and head capsule widths (independent variable) were performed. Head capsule widths and dry weights of approximately 60 P. heteronea, E. aurivilli and Chironomidae larvae were measured for each regression. Dry weights were measured with a Cahn 25 automatic electrobalance after prey samples had been dried in individual weighing boats at 60 °C for 48 h. Head capsule widths were measured to the nearest 0.04 mm with a dissecting microscope at 25 X power. Conversions from dry weight to energy content for Ephemeroptera and

Diptera were 22.88 and 17.89 J/mg dry weight respectively (Cummins and Wuycheck 1971).

The regressions and the biomass to energy conversion factors were used to estimate the energy content of all prey items found in dace gut contents and the average energy content of prey items (E_i) offered to dace during each experimental treatment. Average energy content of prey for each experimental treatment was determined by selecting 10 individuals at random from the pool of prey items used in a particular experiment. To ensure that average energy content of the prey items did not change over the course of the laboratory experiments (Oct-Dec 1987), energy content of prey was compared across all experimental treatments throughout the experimental period with a model 1 one-way ANOVA for each prey type.

4.2.2.2 Prey Profitablity

I calculated the net energy obtained by dace (E_{ni}) per unit of handling time (T_{hi}) for a single prey item, to determine profitability (E_{ni}/T_{hi}) of chironomids and mayflies. Handling time for each prey item consumed was recorded from the video tapes (as in Section 3.2) and, since each replicate dace consumed more than one prey item, mean handling time per prey item was used as an estimate of T_{hi} for each fish. The net energy of a given prey type (E_{ni}) was calculated for fish as follows:

$$E_{ni} = E_i - E_{da}(T_{hi} + T_{si})Wgt$$
 (4.4)

where
$$E_i$$
 = average energy content of prey
type i (J),
 T_{hi} = mean handling time / prey item i (h),
 T_{si} = search time / prey item i (h),
Wgt = wet weight of dace (g),
Eda = active metabolic rate of longnose

dace $(Jg^{-1}h^{-1})$.

The active metabolic rate of longnose dace (E_{da}) at 15° C was estimated as follows after modification from Facey and Grossman (submitted MS)

$$E_{da} = 13.6Y$$
 (4.5)

where 13.6 is the conversion factor for mg O_2 expired during fish respiration to standard energy units (J) (Elliott and Davison 1975) and

$$Y = 0.22 + 0.03X$$
 (4.6)

X is the swimming velocity in standard body lengths per second and was calculated by

$$X = (V+DV)/SL$$
(4.7)

The average water velocity (V) was measured with a micro velocity meter, while the average swimming velocity of each dace (DV) was determined by recording the time necessary for the dace to swim known distances during the video tape analysis (Section 3.2). The standard length (SL) of each dace was estimated from a measurement of total length (TL, cm) and the regression equation:

$$TL = 1.155(SL) + 0.312.$$
 (4.8)

The relationship between total length and standard length had a significantly positive slope (t = 59.77, p < 0.001) and yielded a coefficient of determination (r^2) of 0.99 (Fig. 4.1).

The profitablity of mayflies and chironomids was determined for both high and low complexity streams at 0.5 ambient and ambient density. To determine if profitability differed between prey types, substrate complexities or prey densities, a model 1, 3-way ANOVA was performed.



Fig. 4.1. : Plot of standard length (x) versus total length (y) of dace (n=48).

4.2.3 Results

4.2.3.1 Prey Energy Content

Simple linear regressions between log of dry weight (DWi) and head capsule width (HWi) for Chironomidae, <u>P</u>. <u>heteronea</u> and <u>E</u>. <u>aurivilli</u> all yielded slopes significantly different from zero (Table 4.2, Fig. 4.2 -4.4). The coefficients of determination (r^2) were greater for mayflies than for Chironomidae (Table 4.2). Dry weights of the two mayfly species had a similar range (0.05 - 1.30 mg) which was greater than that for Chironomidae larvae (0.002 - 0.28 mg).

Total energy content of prey types did not change over the course of the experiments (Table 4.3). Consequently, the energy contents from each date were pooled and the average energy content of <u>P. heteronea</u>, <u>E. aurivilli</u> and Chironomidae larvae were compared with an ANOVA. Energy content of prey types differed (F = 133.84, p < 0.001), and Newman-Keuls multiple range tests indicated that energy contents of the two mayfly species were similar and significantly different from the lower energy contents of chironomids (Table 4.4, Fig. 4.5).

TABLE 4.2. : Linear regression analysis of log [dry weight (DW)] (y) and prey head capsule width (HW, x). * = slopes significantly different from 0 at p < 0.05.

REGRESSION EQUATIO	N 	r ²	t	p		
Chironomdae (c):	Chironomdae (c):					
log(DWc) = 3.67(HW	c)-2.21	0.54	8.40	<0.001 *	ŀ	
<u>P. heteronea</u> (p):						
log(DWp) = 1.52(HW)	p)-1.80	0.83	16.81	<0.001 🗧	ł	
<u>E. aurivilli</u> (e):						
log(DWe) = 1.76(HW)	e)-2.11	0.79	14.72	<0.001	ł	



Fig. 4.2. : Plot of head capsule width (x) versus log [dry weight] (y) for <u>P. heteronea</u> (n = 58).









TABLE 4.3. : One-factor analyses of variance of the effects of experimental date on the energy content per prey item for <u>P. heteronea</u>, <u>E. aurivilli</u> and Chironomidae. NS = not significant.

PREY TYPE	F-STAI	ristic p	
	ین هو این هو که هو هو وی چه بره بره بره بره بخا خد انتا اند ندا نده هد	، دینے کی سے جے جے بیے ہیں ہیں اس کی کی کی ہیں ہے جے جے جے ان کا ان اور	
P. <u>hetero</u>	<u>nea</u> 2.0	0.08	NS
<u>E. aurivi</u>	<u>11i</u> 1.8	.5 0.10	NS
Chironomi	dae 1.0	0 0.43	NS

TABLE 4.4. : Nonparametric multiple range test on the differences between energy contents of the three prey types. NS = not significant and * = significant difference at p < 0.05.

COMPARISON	q-STATISTIC	p
<u>P. heteronea</u> vs Chironomidae	20.59	<0.001 *
<u>P. heteronea</u> vs <u>E. aurivilli</u>	1.42	<0.10 NS
<u>E. aurivilli</u> vs Chironomidae	19.17	<0.001 *



Fig. 4.5. : Average energy content/prey item (n=10)
for <u>P. heteronea</u> (P.,), <u>E. aurivilli</u>
(E.,), and Chironomidae (C,).

- -

4.2.3.2 Prey Profitability

Prey profitability (E_{ni}/T_{hi}) from all treatments had unequal variances $(B_c = 23.02, p < 0.005)$. Therefore prey profitabilities were log (x) transformed before a parametric ANOVA was applied. There were no significant interactions between the effects of prey type, prey density or substrate complexity on the profitability of prey to longnose dace (Table 4.5). Additionally, neither substrate complexity nor prey density affected prey profitability. Prey profitability was, however, significantly affected by prey type with mayflies 6 - 9X more profitable than Chironomidae larvae in all treatments (Fig. 4.6).

4.2.4 Discussion

The significant relationships between log [dry weight] and head capsule for all prey types allows energy content for each prey item found in the gut of dace to be estimated from a measure of head capsule width. Additionally, total energy content of the prey items remained similar over the course of the

TABLE 4.5. : Three-factor analysis of variance of the effects of prey type, prey density and substrate complexity on prey profitability to dace. NS = not significant and * = significant difference at p < 0.05.

SOURCE OF VARIATION	F-STATISTIC	р
prey type	99.64	<0.001 *
prey density	0.01	0.92 NS
substrate complexity	2.08	0.17 NS
prey type x prey density	0.17	0.69 NS
prey type x substrate complexity	0.08	0.78 NS
prey density x substrate complexity	0.001	0.98 NS
prey type x prey density x substrate complexity	0.97	0.34 NS



Fig. 4.6. : Prey profitability for dace (n=3) foraging on mayflies (M,) or chironomids (C,), in two_substrate complexities (low and high), at ambient and 0.5 ambient densities. experiments. This ensures that comparisons of total energy consumed by dace between treatments were not affected by changing prey sizes.

The energy content/prey item of both mayflies was similar and approximately 7X that for chironomids. As handling time was similar regardless of prey type (Chapter 3), mayfly profitability was also approximately 7X that of chironomids. Furthermore, the ranking of prey types by profitability was not changed by substrate complexity or prey density (Chapter 3). Therefore, the factor which apparently is most important for determining prey profitability for dace is prey energy content. Townsend and Winfield (1985) have previously suggested that if attacks on different prey items are similar in handling time or energy expended per prey item, the energy content of prey items will be a good estimate of profitability.

4.3 Predicted and Observed Net Rates of Energy Intake

4.3.1 Introduction

For the two-prey, classical optimal foraging model (equation 4.1, section 4.1.1), prey must be ranked in order of profitability. Mayflies are more profitable than chironomids (section 4.2) and are ranked as prey type one, meaning that dace should always consume mayflies when encountered. It would be profitable for dace to specialize on mayflies if the net energy obtained by foraging exclusively on mayflies is greater than that gained by including both mayflies and chironomids in the diet. Comparisons were made between the net rate of energy intake obtained by dace foraging in treatments that included: (1) only mayflies; or (2) both mayflies and chironomids. Since the predator's decision to specialize depends largely on encounter rate with the most profitable prey type (Krebs and McCleery 1984), encounter rate with mayflies was kept constant in both treatments and encounters with chironomids were simply added in the second treatment. Thus, the values for S, E, and T_h for mayflies (prey type m) in equation 4.9 (modified from equation 4.1) are the same on both

sides of the inequality and the values for S, E, and T_h for chironomids (prey type c) are added only on the right side of the inequality. Dace should specialize on mayflies when the following conditions are met,

s _m e _{nm}		$s_m E_{nm} + s_c E_{nc}$	
	>		(4.9)
1 + S _m T _{hm}		$1 + S_m T_{hm} + S_c T_{hc}$	·

For dace to obtain a lower net rate of energy intake from foraging on both prey types, the addition of energy from chironomids ($S_c E_{nc}$) must be small, while the addition to total foraging time by the extra time spent handling chironomids ($S_c T_{hc}$) must be large in comparison. The energy gain obtained from chironomids by dace will be minimal since both encounter rate (S_c) and, especially, net energy per chironomid larva (E_{nc}) are small compared to values of these parameters for mayflies (Chapter 3). However, the addition to total foraging time by time spent handling chironomids ($S_c T_{hc}$) will also be minimal since handling time for all prey items is short (< 5 s). Therefore, specialization will depend on how the energy gain from chironomids (the

numerator) balances with the time required for that energy gain (the denominator).

The net energy gain from foraging solely on mayflies, or on both mayflies and chironomids, was calculated for the classical optimal foraging model and a modification of this model which incorporates the different capture efficiencies (CE) of the prey types. Predictions of E/T for both models were based on encounter rates and handling times determined from the video analysis (Chapter 3) and were compared to the E/T observed for dace foraging in low and high complexity substrate.

4.3.2 Methods

4.3.2.1 Predicted Net Energy Intake

The net rate of energy intake was calculated using encounter rates (S) and handling times (T_h) recorded with the infrared sensitive video camera (Section 3.3). The predicted net rate of energy intake using the classical optimal foraging model (opt) for dace consuming only the most profitable prey type (mayflies) (E(opt,m)/T) was calculated as follows:

E(opt,m)/T =		(4.10)
	1 + S _m T _{hm}	
		•

SmEnm

For dace consuming both prey types (mc) the predicted net rate of energy intake (E(opt,mc)/T) was calculated as follows:

$$S_{m}E_{nm} + S_{c}E_{nc}$$

$$E(opt,mc)/T = ------ (4.11)$$

$$1 + S_{m}T_{hm} + S_{c}T_{hc}$$

where	S_m = encounter rate for mayflies,
	S_{C} = encounter rate for chironomids,
	$T_{hm} = handling time for mayflies,$
	T_{hc} = handling time for chironomids,
	$E_{nm} = net energy for mayflies,$
	E_{nc} = net energy for chironomids.

Since dace have differential capture efficiencies with these two prey types, I modified the equations above to incorporate the capture efficiencies (CE) of dace reported in section 3.3. Therefore, the predicted net rate of energy intake accounting for capture

efficiency (E(ce)/T) for dace consuming only mayflies was

$$S_{m}E_{nm}(CE_{m})$$

 $E(cem)/T = ------ (4.12)$
 $1 + S_{m}T_{hm}$

and for dace consuming both prey types was

$$(S_m E_{nm}) (CE_m) + (S_c E_{nc}) (CE_c)$$

E(cemc)/T = ----- (4.13)
1 + $S_m T_{hm} + S_c T_{hc}$

where $CE_m = capture$ efficiency for mayflies, and $CE_c = capture$ efficiency for chironomids.

4.3.2.2 Observed Net Energy Intake

To test the accuracy of the predictions from the two models, comparisons were made of the E/T predicted by the models to the observed net energy intake of dace foraging in the circular artificial streams. To calculate the observed net energy intake of dace it was necessary to obtain estimates of the energy consumed

(i.e., type and number of prey items in the gut), the energy expended during active or resting search modes (Section 3.2) and foraging time.

The general methods outlined in Chapter 2 were used for these experimental treatments. Dace were acclimated to either low or high complexity at two prey densities: 0.5 of the ambient mayfly density or 0.5 of the ambient mayfly density plus 0.5 of the ambient chironomid density. After an acclimation period dace were allowed to forage under the experimental conditions for 1 h period, 2-3 h after the simulated sunset. During this foraging bout dace were continuously observed under low intensity red light and the total foraging time and the proportion of time spent actively foraging or resting on the substrate was recorded. Dace gut contents were sampled after the foraging bout with the anal backflushing technique (Culp et al. 1988). Gut contents were examined under a 25X power dissecting scope and each prey item was identified and the head capsule width measured. From the head capsule width, the energy content of that particular prey item (E_{ii}) was estimated using the dry weight/head capsule regression and the biomass to energy conversion factor (section 4.2). The

observed net rate of energy intake (E(obs)/T) was calculated as follows;

where $E_{ij} = energy value of ith prey item of$

prey type j (J),

 $E_{da} = active metabolic rate of dace (Jg^{-1}h^{-1}),$ $T_{a} = time spent actively foraging (h),$ $E_{dr} = resting metabolic rate of dace (Jg^{-1}h^{-1}),$ $T_{r} = time spent resting (h),$ $T_{t} = total foraging time (T_{a}+T_{r}) (h),$ A = assimilation efficiency (1.0), Wgt = wet weight of dace (g).

As the assimilation efficiency is simply a constant by which prey energy is reduced and this factor was not included in the predictive models, a value of 1.0 was used to allow direct comparisons of predicted and observed net rates of energy intake. The active metabolic rate of dace (E_{da}) was calculated as in

Section 4.2.2 while the dace resting metabolic rate (E_{dr}) was calculated as follows:

$$E_{dr} = 0.22 \times 13.6 = 2.99 Jg^{-1}h^{-1}$$
 (4.15)

(from equations 4.5 and 4.6, with swimming velocity (x) = 0 cm/s). Thus, for each fish the net energy obtained was calculated through direct measurements of energy consumed and estimates of the energy used.

4.3.2.3 Statistical Analysis

A three-factor, model 1 ANOVA, with replication (n = 3) was applied after the E/T values were log (x + 10) transformed. This transformation was required since heterogeneous variances were found (Bc = 63.4, p < 0.001) and several negative values existed. The three factors were diet (mayflies (m) or mayflies and chironomids (mc)), model (optimal foraging model (E(opt)/T), optimal foraging model with capture efficiency (E(ce)/T)) and observed energy intake rate (E(obs)/T), and substrate complexity (low and high). If no interactions occurred between these factors and if the model factor was significant, the predicted and

observed net rates of energy intake were compared with Newman-Keuls multiple range tests.

4.3.3 Results

No significant interactions occurred between the effects of diet, model or substrate complexity on net rate of energy intake of dace (Table 4.6). In general the rate of net energy intake was slightly higher for dace which included both prey types in their diet than for those that foraged exclusively on mayflies. However, the inclusion or exclusion of the second ranked prey in the diet did not significantly affect the net rate of energy intake (Fig. 4.7 and 4.8, Table 4.6). Substrate complexity did have a significant effect on the net rate of energy intake. Net rates of energy intake in low complexities were significantly higher than in the high complexity treatment (Fig. 4.7 and 4.8).

The predictions of E/T using the classical optimal foraging model (E(opt)/T) were much higher than the results from either the modified model, which included capture efficiencies (E(ce)/T) or the observed E/T (E(obs)/T). In fact, these differences were significant for the effect of model on net energy intake (Table

TABLE 4.6. : Three-factor analysis of variance of the effects of prey diet (no. of prey types), model (2 predictive and 1 observed) and substrate complexity on dace net rate of energy intake. NS = not significant and * = significant difference at p < 0.05.</pre>

SOURCE OF	VARIATION	F-STATISTIC	p
prey diet	· ,	0.14	0.71 NS
model		34.20	<0.001 *
substrate	complexity	15.36	0.001 *
prey diet model	x	0.22	0.80 NS
prey diet substrate	x complexity	0.25	0.62 NS
model x substrate	complexity	1.14	0.34 NS
prey diet	x		
substrate	complexity	0.26	0.77 NS



Fig. 4.7. : The observed net rate of energy intake
 (E(obs)/T) for dace (n=3) foraging on
 mayflies or mayflies & chironomids in low
 substrate complexity, and the net rate of
 energy intake predicted from the optimal
 foraging models without (E(opt)/T) and with
 (E(ce)/T) capture efficiency.
 Non significance between treatments is
 indicated by a bar (-----)



Fig. 4.8. : The observed net rate of energy intake (E(obs)/T) for dace (n=3) foraging on mayflies or mayflies & chironomids in high substrate complexity, and the net rate of energy intake predicted from the optimal foraging models without (E(opt)/T) and with (E(ce)/T) capture efficiency. Non significance between treatments is indicated by a bar (-**___**)
4.6). Furthermore, Newman-Keuls multiple range tests indicated that the net energy intake rates using E(opt)/T were significantly different from either the E(ce)/T or the E(obs)/T values (Table 4.7). Finally, The net rate of energy intake predicted from the model which incorporates capture efficiencies was not significantly different from the observed net rate of energy intake obtained by dace foraging in the circular streams.

4.3.4 Discussion

In both substrate complexities the classical optimal foraging model (E(opt)/T) overestimated the observed rate of net energy intake, while the predictions from the model incorporating dace capture efficiency (E(ce)/T) were the same as the observed values (E(obs)/T). Nevertheless, both models accurately predicted the qualitative trends in net energy intake. For example, the conclusion that dace should not specialize on mayflies would be the same regardless of the model used. Similarly, both models predicted that the rates of net energy intake would be reduced in substrates with higher complexity.

TABLE 4.7. : Newman-Keuls multiple range test of the differences in net rate of energy intake between the predictions from the two models, E(opt)/T and E(ce)/T and observe, (E(obs)/T), intakes of energy. NS = not significant and * = significant difference at p < 0.05.</pre>

COMPARISON			q-STATISTIC		р	
E(opt)/T	vs	E(obs)/T	10.37	<0.001	*	
E(opt)/T	vs	E(ce)/T	9.89	<0.001	*	
E(ce)/T	vs	E(obs)/T	0.48	>0.500	NS	

The advantage of the capture efficiency model is that it also predicted the rates accurately. Accuracy in predicting these quantitative rates would be important if capture efficiencies for different prey items varied between habitats. Furthermore, the importance of a prey type to the predator may be overestimated if capture efficiency is not included in the model.

At mayfly densities similar to those in these experiments (750 / 0.1 m^2), dace should always attack chironomids when encountered. Even though mayflies were 7X more profitable than chironomids, including chironomids in the diet slightly increased the net rate of energy intake for dace. The incorporation of this lower profit prey into the diet conforms with the expectations for an optimal forager since search time. for a prey item is high compared to handling time, (Chapter 3) and the probability of missing a mayfly encounter while handling a chironomid is low. However, dace may specialize on mayflies if encounter rates with mayflies increased to the point where the handling of less profitable prey results in lost opportunities to encounter mayflies. To determine the conditions under which dace should specialize on mayflies, I modified inequality 4.9 to include capture efficiency and an

encounter rate/prey density ratio. These further calculations indicated that mayfly densities would have to exceed 50,000 / 0.1 m² before dace would obtain a 5% increase in E/T by specializing on mayflies. Prey densities of this magnitude were never observed in the field (Chapter 5) and I would not expect dace to specialize on mayflies in most field situations.

In other tests of optimal foraging models, although fish were expected to specialize on the most profitable prey type, fish were found to include some of the lower ranked prey items (Werner and Hall 1974; Ringler 1979). In these tests, capture efficiencies were assumed equal and handling time was short (<1 - 2 s). The disagreement between predicted and observed diets is universal across all optimal foraging tests regardless of predator type (Townsend and Winfield 1985). Because specialization is based largely on encounter rates with the most profitable prey, including the capture efficiencies for this prey type may be critical to obtain accurate predictions. Furthermore, it may be that handling time per prey item has to be close to the inter-encounter interval before the handling of less profitable prey types interferes with the maximimum E/T obtainable by a predator. Instead of invoking factors such as predator

sampling or misidentification of prey by the forager to explain the presence of lower ranked prey in a predator diet (Krebs and McCleery 1984), my results suggest that these incorrect predictions could result from insufficient knowledge of the behavioural characteristics of both the predator and the prey.

In my laboratory experiments, when predator and prey behaviour are included in the classical optimal foraging model, the revised model accurately predicts both the trend and the energy intake rates of dace. Additionally, from these experiments it appears that E/T of dace is inversely related to substrate complexity but remains unchanged by the addition of a second prey type when mayfly density is constant. Therefore, further experiments were performed to determine if these trends held across a wider range of mayfly and chironomid densities and substrate complexities (Section 4.4) 4.4 Effects of Prey Density and Substrate Complexity on Dace E/T

4.4.1 Introduction

The net rate of energy intake of foraging dace may vary among habitat patches in streams. Factors which affect net energy intake rates of dace include prey type, prey density and substrate complexity. Indeed, an increase in substrate complexity lowered the net rate of energy intake of dace (Section 5.3). However, when mayfly density was held constant, the net rate of energy intake of dace was unaffected by the presence or absence of chironomids. I predicted that, if the density of mayflies and chironomids and substrate complexity were simultaneously changed, the rates of net energy intake of dace would be: (1) positively related to mayfly density; (2) unaffected by chironomid density; and (3) negatively related to substrate complexity. Therefore, the objectives of this section were to determine the relationship between dace E/T as mayfly and chironomid density and substrate complexity were varied in the experimental streams.

4.4.2 Methods

The methods used to determine E(obs)/T for the experimental treatments were the same as for the observed net rates of energy intake which were calculated in Section 4.3.2.2. Three factors were varied including mayfly density, chiromomid density and substrate complexity. Thirty different combinations of these factors were examined such that mayfly and chironomid density ranged from 0 to 80/stream (i.e., 0-1500 / 0.1 m^2) and three substrate complexities were used (low, medium and high; Section 2.2). To determine if any of these factors accounted for a majority of the variance associated with the net rate of energy intake of dace, a multiple regression (Damon and Harvey 1987) was performed on the log (x + 10) transformed data (section 4.3.2.3). In this analysis the log [net rate of energy intake + 10] was the dependent variable (y) and mayfly density, chironomid density and substrate complexity were the independent variables $(x_1, x_2, and$ x₃).

4.4.3 Results

The average rate of net energy intake across all experimental treatments was 55.4 ± 7.1 J/h. The multiple regression was significant (F = 25.43, p < 0.001) and the multiple correlation coefficient (r^2) was 0.47. Additionally, the partial regression coefficients for mayfly density and substrate complexity were significant (Table 4.8). The partial regression coefficient for chironomid density was not significantly different from zero and although a stepwise multiple regression indicated that chironomid density could be removed from the analysis, this removal did not change the original coefficients or significance values. Mayfly density was positively related to E/T and accounted for 65% of the variability (standard regression coefficient, STD COEF, Table 4.8, Figs. 4.9 - 4.11). Substrate complexity was negatively related to E/T and explained 25% of the variability (Table 4.8). The multiple regression is therefore explained by an equation relating mayfly density (MD) and substrate complexity (SC) to net energy intake rates (E/T) where

$$\log (E/T+10) = 0.011MD - 0.003SC + 1.674$$
 (4.16)

TABLE 4.8. : Multiple regression parameters for the effects of mayfly density, chironomid density and substrate complexity on the net rate of energy intake for dace foraging in the laboratory. NS = no significant effect and * = significant effect at p < 0.05.</pre>

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VARIABLE	COEFFICIENT	STD COEF	tt	p
constant	1.69	0.00	9.54	<0.001 *
mayfly density	0.011	0.64	6.05	<0.001 *
chironomid density	-0.0001	-0.01	-0.12	0.90 NS
substrate complexity	-0.003	-0.23	2.93	0.004 *



Fig. 4.9. : Rates of net energy intake for dace foraging in low substrate complexity at two total prey densities (TD), ambient and 0.5 ambient and with various mayfly (MD) and chironomid (CD) densities (individuals per stream).



Fig. 4.10. : Rates of net energy intake for dace foraging in medium substrate complexity at two total prey densities (TD), ambient and 0.5 ambient, and with various mayfly (MD) and chironomid (CD) densities (individuals per stream).



Fig. 4.11. : Rates of net energy intake for dace foraging in high substrate complexity at two total prey densities (TD), ambient and 0.5 ambient, and with various mayfly (MD) and chironomid (CD) densities (individuals per stream).

4.4.4 Discussion

As I hypothesized, net energy intake rate of dace in the laboratory streams was positively related to mayfly density but unaffected by chironomid density. Since handling times for the two prey types are similar, and mayflies are a larger energy package compared to chironomids (Section 4.2), mayfly density contributed more to the energy intake rates of dace even when chironimid density was high. Optimally foraging dace in the field should forage in areas where mayfly densities are high, regardless of chironomid density. Nevertheless, chironomids should be included in the diet of dace if they are encountered.

Increasing substrate complexity affects the foraging success of fish by decreasing encounter rates and E/T (Glass 1971; Stein and Magnuson 1976; Charnov et al. 1976; Crowder and Cooper 1982; Cook and Streams 1984; Fraser and Emmons 1984). Encounter rates for dace tended to decrease with increasing substrate complexity although the trend was not significant (Chapter 3). Importantly, however, the trend between encounter rates and substrate complexity translated into a significant, inverse relationship between substrate complexity and

the rates of net energy intake of dace. In the field, optimally foraging dace should foraging in areas with minimal structure. However, as prey density and diversity are correlated to structural complexity in natural habitats (Crowder and Cooper 1982), and mayfly density significantly affects dace E/T, dace may actually maximize E/T at some intermediate level of structural complexity where mayfly density is high.

CHAPTER 5

HABITAT DISTRIBUTION OF DACE IN THE FIELD

5.1 Introduction

Longnose dace live in close proximity to the substrate in fast flowing riffles (Bartnik 1970; Gibbons and Gee 1972; Scott and Crossman 1973; Facey and Grossman submitted MS) and are abundant in Alberta foothills streams. Their diet varies but it usually includes common benthic aquatic insects such as mayflies, chironomids, simuliids, stoneflies and caddisflies (Gee and Northcote 1963; Gerald 1966; Gibbons and Gee 1972; Brazo et al. 1978; Pappantonious and Dale 1982). Similarly, at the study site in Jumpingpound Creek, approximately 30 km west of Calgary, dace forage on benthic macroinvertebrates within the stone substrate. Their foraging is restricted to nocturnal periods when the light intensity is less than 10 lux (Culp 1989); they remain concealed beneath stones during the day.

In the laboratory, mayfly density and substrate complexity were found to affect the net rate of energy intake of dace (Chapter 4). Mayfly density and substrate complexity vary across the streambed (pers obs.) in the field and dace can presumably move from one area of the streambed to another. If dace attempt to maximize net energy intake as would be predicted from optimal foraging theory, they should forage in areas with the potential for high energy return. From the results of the laboratory experiments, I predicted that areas with potentially high energy returns for dace would have high mayfly density and low substrate complexity.

In a field situation factors which were held constant in the laboratory, such as current velocity, and density of other macroinvertebrates, vary across the streambed along with substrate complexity and mayfly density. Thus, the first objective of the field study was to locate areas of the riffle where dace forage at night, and to compare the biotic and abiotic conditions at these locations to the average conditions across the streambed.

Even if dace foraging locations are similar to the available habitat conditions, individual dace may forage in areas which allow them to achieve a higher net rate of energy intake than individuals foraging in other areas. Therefore, the second field objective was to

determine if the net rate of energy intake obtained by individual dace is related to biotic and abiotic conditions found in the foraging locations. For example, do dace which forage in areas of high mayfly density or low substrate complexity achieve higher rates of net energy intake than dace which forage in areas which are predicted to be less profitable? Additionally, the relationships among mayfly density, chironomid density, substrate complexity and net rate of energy intake of dace in both the field and laboratory are compared.

5.2 Methods

Dace were collected in April 1987 by electrofishing within the study area (described in Section 1.4), approximately 2-3 h after sunset (2330-030 h). Water temperatures at this time of year ranged from 8.5 to 12 O C during the night. The location at which each dace (n = 11) was collected was marked with a numbered, coloured stone and the time of collection noted. Within one hour of collection, fish guts were sampled with the anal backflushing technique (Culp et al. 1988) and the contents preserved in 95% ethanol.

Benthic invertebrate densities at each point of dace collection (i.e., dace locations) and at locations systematically positioned across the entire riffle habitat (i.e., habitat locations) were collected and a stone sampling technique was used for estimating abundance of stone-dwelling organisms (Wrona et al. 1986). This procedure consisted of locating the nearest small (4-16 cm²), medium (16-64 cm²) and large (64-256 cm²) stone, collecting the macroinvertebrates on these stones with an appropriately sized net (Fig. 5.1) and preserving the samples in 10% formalin. In the laboratory, samples were sorted, the macroinvertebrates identified at least to order and counted under a 25 X power dissecting microscope.

Average benthic density for each macroinvertebrate order identified was calculated by:

$$d_{i} = n_{s} x_{si} + n_{m} x_{mi} + n_{l} x_{li}$$
(5.1)

where $d_i = mean$ number of macroinvertebrates of type i in 0.1 m² area,

> n_s = average number of small stones / 0.1 m², n_m = average number of medium stones / 0.1 m², n_1 = average number of large stones / 0.1 m²,



Fig. 5.1. : Schematic representation of a stone net sampler used to collect the macroinvertebrates from the benthos.

•

and x_{si} , x_{mi} , x_{li} = the average number of macroinvertebrates of type i on small, medium and large stones, respectively

(modified from Wrona et al. 1986). The average number of small, medium and large stones / 0.1 m^2 was determined by counting the number of stones in each size class in 30 replicate 0.1 m^2 quadrats taken systematically throughout the riffle. The standard error reported with the density estimates includes both the variation associated with the spatial dispersion of the macroinvertebrates and the variation associated with the heterogeneous nature of stones across the streambed (Wrona et al. 1986). Note that since this error term incorporates two sources of variation, parametric statistical procedures are not applicable and therefore nonparametric procedures were applied (Wrona 1988 pers. comm.).

Total wet biomass of macroinvertebrates / 0.1 m². was measured by filtering the sorted samples on Whatman number 1 filter paper for 7-8 minutes, and weighing the sample to the nearest 0.01 mg on a Sartorius electronic analytical balance. Total macroinvertebrate biomass per 0.1 m² was calculated using equation 5.1 but x_{si} , x_{mi} ,

and x_{1i} were replaced with x_s , x_m , x_1 , the average total macroinvertebrate biomass for small medium and large stones, respectively.

In addition to macroinvertebrate density and biomass, current velocity at the substrate water interface and substrate complexity were measured at each sample location. Water velocity was measured with a Scientific Instruments current meter while substrate complexity was estimated by measuring the total upper stone surface area in a 0.1 m^2 guadrat. For circular stones within the quadrat the maximum diameter was measured and the surface area of each stone calculated as the circle area. For rectangular or oblong stones, length and width were taken and the area of the rectangle used as the estimate of the stone surface area. The total surface area of stones within the 0.1 m^2 quadrat was calculated by summing all individual stone areas. This measure of substrate complexity (i.e., total upper stone surface area) is the same measure in the laboratory experiments (Chapter 4).

Comparisons between the mean values of macroinvertebrate densities and biomass, substrate complexity and current velocity at the habitat locations to the mean values at the dace locations were made with

either a t-test, where parametric testing was appropriate, or a Mann-Whitney test when nonparametric testing was more appropriate.

The second field objective was examined by determining the relationship among the net rate of energy intake obtained by individual dace and the mayfly density, chironomid density and substrate complexity conditions found at the point of collection (dace locations). The gut contents of dace were sorted under a 25 X power dissecting scope and all mayflies identified at least to genus. Other prey items were identified at least to order. Since > 95% of all prey items consumed were either mayflies or chironomids, the rare occurrence of other prey items such as simuliids, trichopterans or plecopterans was not included in the net energy calculations. For each prey item found in the qut, head capsule widths were measured and the total biomass and energy estimated as in Section 4.2. Dace consumed Baetis tricaudatus and Cinygmula sp. mayflies as well as P. heteronea and E. aurivilli in the field. Linear regressions of the log [dry weight] and head capsule width for these additional mayflies were performed as in section 4.2. Both regressions yielded a significant, positive slope and the coefficients of determination

 (r^2) were greater than 0.85 (Table 5.1, Fig. 5.2 and 5.3).

The observed rate of net energy intake was calculated as in Section 4.3.2.2, equation 5.14. The metabolic rate of dace (Y) was estimated for a temperature of 10 $^{\circ}$ C where,

Y = 0.09 + 0.07X(5.2)

and X = the swimming velocity in standard body lengths per second (equation 4.7) (Facey and Grossmann, submitted MS). To determine if mayfly density, chironomid density or substrate complexity influenced the net rate of energy intake of dace foraging in the field, a multiple regression analysis (Damon and Harvey 1987) was performed with the log (x) transformed energy intake rates (Damon and Harvey 1987).

 REGRESSION EQUATION
 r^2 t
 p

 B. tricaudatus (b):
 10g (DWb) = 2.06 (HWb) - 2.207
 0.90
 23.57
 <0.001 *</td>

 Cinygmula sp. (ci):
 10g (DWci) = 1.43 (HWci) - 2.18
 0.87
 19.41
 <0.001 *</td>









5.3 Results

5.3.1 Habitat and Dace Site Comparisons

Dace occupied streambed locations which generally had lower water velocities than the habitat locations (Fig 5.4), although this difference was not significant (U = 63.5, p > 0.20). However, the variance associated with the water velocity at dace locations was significantly lower than the variance over the entire streambed (F = 3.98, p < 0.05). Similarly, total surface area of stones within the 0.1 m² quadrat ranged from 258 to 567 cm², and while the average substrate surface area was lower at dace locations compared to the habitat locations (Fig 5.5), the difference was not significant (t = 0.41, p > 0.50).

Mayflies and chironomids were the most abundant macroinvertebrates and comprised over 90% of the benthos (Fig. 5.6). Other macroinvertebrates which were occasionally found in the benthic samples but were never found in dace gut contents include Hydracarina, Oligochaetae, Nematoda, Ostracoda, Coleoptera and Copepoda. Although macroinvertebrate densities and total biomass tended to be higher in dace locations, these







Fig. 5.5. : Substrate surface area of stones per sample quadrat in dace and habitat locations (n=11).



Fig. 5.6. : Density of mayflies (MAY), chironomids (CHIR), trichopterans (TRI), plecopterans (PLEC), and simuliids (SIMU) in habitat and dace locations (n=11). values were not significantly different from those at the habitat locations (Table 5.2, Fig. 5.7).

Since habitat samples were located systematically over the entire riffle it is possible that dace were also foraging in many of the habitat locations. There were regions of the streambed where dace were never collected or observed (Culp, unpubl. data). Therefore, after comparing the biotic and abiotic factors at habitat and dace locations, I identified four habitat locations within regions where dace were absent. The average chironomid density (807.2 \pm 133.6 / 0.1 m²), mayfly density (791.6 \pm 206.2 / 0.1 m²) and total macroinvertebrate biomass (660.0 \pm 329.1 mg/0.1 m²) in these four samples were approximately half the average density and biomass estimates found in dace locations. Additionally, the total substrate surface area and current velocity were 15% and 35% higher in these regions without dace than in the locations with dace.

Comparisons between habitat and dace locations suggest that dace were foraging in areas of the streambed which were similar to the average streambed conditions. Dace tended to be located in areas with high invertebrate biomass and chironomid density, low substrate complexity, and low velocity. Furthermore, it

TABLE 5.2. : Mann-Whitney U values for comparisons between prey density and biomass at the habitat and dace locations. NS = not significant.

FACTOR	U	p
Mayfly density	68.0	> 0.20 NS
Chironomid density	72.0	> 0.20 NS
Trichopteran density	69.0	> 0.20 NS
Plecopteran density	64.0	> 0.20 NS
Simuliid density	63.5	> 0.20 NS
Total biomass	65.0	> 0.20 NS





appears that if more samples had been taken from areas where dace were absent, I may have detected an avoidance by dace of areas with low mayfly and chironomid density and high substrate complexity.

5.3.2 Net Rates of Energy Intake of Dace

Of all prey items consumed by dace, > 95% were mayflies or chironomids, and these were taken in a ratio of 0.29 : 0.71 (mayfly : chironomid). Conversely, mayflies contributed more to the total energy intake of dace than did chironomids as the ratio of the gross energy consumed by dace was 0.62 : 0.38 (mayflies : chironomids). The average net rate of energy intake of dace at Jumpingpound Creek was 66.2 \pm 6.6 J/h. Note that this rate was not significantly different from the average rate found in the laboratory experiments (mean = 55.4 \pm 7.1, t=0.52, p > 0.50).

Partial regression coefficients from the multiple regression among mayfly density, chironomid density, substrate complexity and net energy intake of dace were not significantly different from zero. Nevertheless the signs of these regression coefficients were the same as the coefficients for these factors in the laboratory

experiments (Table 5.3, Figs. 5.8 - 5.10). The mayfly density coefficient was positive while both substrate complexity and chironomid density had negative coefficients. Although the multiple regression was not significant (F = 0.56, p = 0.66), the standard regression coefficients indicated that substrate complexity explained the most variance, while chironomid and mayfly density explained approximately an equal amount of the variance associated with the E/T of dace foraging in Jumpingpound Creek.

5.4 Discussion

Dace foraged in areas of the streambed with conditions similar to the average biotic and abiotic conditions found throughout the riffle. These foraging areas tended to have high chironomid density, low current velocity and low substrate complexity. Fish were absent from areas of low mayfly and chironomid density, high current velocity and complex substrate. It was expected that in order to maximize net rate of energy intake, dace should forage in areas of high mayfly density and low substrate complexity (Chapter 4). Although the distribution of foraging dace was not

TABLE 5.3. :

Multiple regression parameters for the effects of mayfly density, chironomid density and substrate complexity on the net rate of energy intake (y) for dace foraging in the field. NS = no significant effect and * = significant effect at p < 0.05.

VARIABLE	COEFFICIENT	STD COEF	t	p
constant	2.08	0.00	8.82	0.00 *
mayfly density	0.0001	0.19	0.42	0.69 NS
chironomid density	-0.0001	-0.22	-0.49	0.64 NS
substrate complexity	-0.001	-0.43	-1.25	0.25 NS


Fig. 5.8. : Relationship between the rate of energy intake of dace in the field (y) and mayfly density (x) (n=11).







Fig. 5.10. : Relationship between the rate of energy intake of dace in the field (y) and substrate area (x) (n=11).

statistically different from the average habitat conditions, the field trends followed the expected pattern from the laboratory results.

Antipredator behaviour of prey may have confounded my ability to detect the relationship of foraging dace to the distribution of their prey. During the prey behaviour experiments, (Chapter 2) mayflies were observed to disperse by either drifting or moving into substrate refugia immediately after a dace began foraging. Since the benthic samples in the field were taken after dace had been foraging for 4 h, prey dispersal behaviour may have altered the prey distribution at dace foraging locations. Therefore, as an alternative to the method I used to determine if dace distribution was related to macroinvertebrate density, future studies could map out prey density across the streambed prior to the foraging period of dace, and the sites of highest dace foraging activity related to these prey distributions.

An increase in substrate complexity or substrate surface area $/ 0.1 \text{ m}^2$ at a constant prey density should increase predator search time, thereby decreasing encounter rates and net rates of energy intake (Fraser and Emmons 1984). An increase of substrate surface area

from 178 to 331 ${\rm cm}^2$ / 0.1 m² did decrease net energy intake rates for dace in the laboratory experiments (Chapter 4). In the field, dace foraged in low complexity areas and were absent from high complexity areas, although substrate complexity in the dace foraging and habitat locations were not significantly different. Since the lowest substrate complexity at dace locations was 258 cm² / 0.1 m², future investigations could include systematic collection of dace from a wider range of habitats to ensure the entire range of dace foraging locations is sampled.

A factor kept constant in the laboratory but that changed across the streambed is current velocity. For stream fish a higher current velocity increases the metabolic costs associated with swimming or holding position (Facey and Grossman, submitted MS). Therefore, to reduce metabolic costs dace should avoid high velocity areas. Even though dace foraged in current velocities that were lower than the average for the riffle this difference was not significant. As metabolic rates of dace increase slowly with increasing current velocity (Facey and Grossman, submitted MS), metabolic costs to dace over the range of velocities found across the stream bed may be similar. If this is the case, the

distribution of dace in proportion to the available current velocities across the streambed is not surprising. In fact, Facey and Grossman (submitted MS), found a similar distribution for longnose dace in a stream in Georgia, USA.

Dace gut content samples revealed that all dace were eating mayflies and chironomids, the most abundant of prey types. From the laboratory results, I predicted that for prey densities of 750 / 0.1 m², dace should not exclude the less profitable prey (i.e., chironomids, Chapter 4). Further calculations indicated that it would be unprofitable for dace to specialize on mayflies even at mayfly densities exceeding 50,000 / 0.1 m². Since the maximum mayfly density recorded in the field was 4000 / 0.1 m², it is unlikely that conditions would ever warrent that dace exclude chironomids from their diet.

I expected that dace would obtain higher rates of net energy intake at higher mayfly densities. In the laboratory experiments, mayfly density and substrate complexity were positively and negatively related to net energy intake rates, respectively, while chironomid density had little effect (Chapter 4). However, mayfly density, chironomid density, and substrate complexity in the field did not significantly influence net energy

intake rates. Despite this result, the partial regression coefficients indicated that the direction of the trends was similar in both the field and the laboratory experiments.

Dace density was held constant in the laboratory but it was not measured in the field. If the per capita energy gain of dace decreases with increasing dace density, the potential net energy return of a particular location on the streambed may be quantitatively different from my laboratory predictions which do not consider dace density. For example, areas of high mayfly density may be equivalent to the areas with low mayfly density if the density of dace is positively correlated with prey abundance. Although the variable nature of streambeds and the addition other factors, such as dace density, may have masked the trends in net energy intake of dace in the field, the field results were qualitatively consistent with those of the laboratory experiments.

CHAPTER 6

SUMMARY AND CONCLUSIONS

A basic assumption of optimal foraging theory is that foragers are designed to maximize fitness or a proxy of fitness, the net rate of energy intake (E/T). Fish are particularly suited to studies of optimal foraging since their size is directly related to fecundity. Therefore, I investigated optimal foraging theory using a common Alberta stream minnow, the longnose dace (<u>R</u>. <u>cataractae</u>). My objectives were to examine the effect of several biotic and abiotic factors, including prey behavioural type, prey density and substrate complexity, on the E/T of dace.

In the field, dace forage on two distinct prey types, mayfly and chironomid larvae. In a series of laboratory experiments, I examined the behaviour of these prey to determine how prey behaviour affects dace foraging success. Mayflies were found to occupy more exposed upper substrate surfaces and to be more active in these exposed areas than chironomid larvae. Additionally, mayflies responded to foraging dace by

drifting while chironomids lacked any observable escape response.

These distinct prey behaviours lead to differing foraging success by dace. More mayflies than chironomids were encountered by dace. However, since mayflies could escape in the drift, once prey were encountered fewer mayflies were captured than chironimids. Although chironomids were encountered less frequently, dace were more successful at capturing them. The total number of prey captured of each type depended on the tradeoff between the encounter rate and capture efficiency (captures/attack) of dace with their prey.

The profitability (energy/unit handling time) of a prey type to dace depended largely on the energy content of the prey item since handling time for both prey types was similar (< 4.5 sec). Therefore, the larger mayflies were significantly more profitable than chironomids and, in my tests of optimal foraging models, mayflies were ranked first.

My tests of the classical, two-prey optimal foraging model indicated that dace should consume both prey types when encountered, and never exclude the less profitable chironomids from their diet if encountered. This is largely because of the short handling times for these

prey. Therefore, probability of a dace missing a mayfly while handling a chironomid is low. Furthermore, the classical optimal foraging model, which incorporates predator encounter rates but not capture efficiencies, predicted the correct trends in foraging success but always overestimated E/T. By adding capture efficiencies of dace foraging on mayflies or chironomids into the model, I was able to correctly predict the trends and accurately estimate the net rates of energy intake. Modification of the optimal foraging model to incorporate realistic foraging parameters, like capture efficiency, can be important particularly when the parameter values differ between prey types or habitats.

In the laboratory, the E/T of dace was positively related to mayfly density, negatively related to substrate complexity (i.e., total substrate area) and unaffected by chironomid density. In the field, dace tended to avoid areas of high substrate complexity and low mayfly density. As predicted from the optimal foraging models, dace consumed mayflies and chironomids in both the laboratory and field. In fact, in the field > 95% of the prey items found in dace gut contents were either mayflies or chironomids. As in the laboratory,

however, mayflies contributed the majority of the energy to the net rates of energy intake of dace.

In conclusion, documentation of both the prey behaviour and predator behaviour allows for a more complete understanding of predator-prey interactions. In particular, knowledge of prey behavioural characteristics allowed the generation of predictions regarding predator foraging behaviour and success on different prey types. Furthermore, knowledge of predator behaviour confirmed these predictions and allowed modification of the optimal foraging model to create a more accurate and realistic model of dace foraging behaviour.

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