Quantifying the Predation Rate of Planktivorous Fishes: Implications for Better Lake Management

プランクトン食性魚の捕食率の定量的評価

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Abstract : The nature of planktivorous fish feeding is analyzed using mathematical models. The reactive distance of a visual feeding fish is predicted by the model. Fish typically do not attack all the prey encountered. The fish may exercise active choice in prey selection and choose an optimal range of prey from encountered food to maximize benefits per unit foraging time. Therefore, to predict the range of prey sizes eaten and maximize energetic intake for a given fish, optimal foraging considerations are incorporated within the foraging model. Further, The feeding activity of planktivores is described in detail by a sequence of activities and their corresponding time intervals. The energetic costs involved and the time for each activity is necessary to determine the optimal choice of the prey and finally to predict the forging pattern of the predator. The effect of prey-size selectivity on overall lake ecosystem is further explored.

Keywords: Biomanipulation; Optimal Foraging; Planktivory Size; Selectivity; Visual Predation

1.0 Introduction

The water quality in lakes may be largely controlled by biotic factors. Constructing a quantitative description of the interaction between zooplankton and fish contributes to a better understanding of such an aquatic ecosystem. The ecosystems approach as a sustainable option for water quality management has gained wider acceptance in the recent past since eutrophication and the resulting phytoplankton blooms have become a worldwide problem (Scheffer, 1998). Biomanipulation and cascading trophic interaction theory (based on 'top down' effects) applied to freshwater pelagic ecosystems demands detailed analysis of prey-predator activity of zooplankton and fish. Intensive studies have been carried out in the recent past to model the aquatic food web from primary production to piscivory. (see Gulati *et al.* 1990 for a detailed review). Therefore, it is now required to separate these interactions and analyze in depth to gain insight as to how we could employ food web manipulation in effective management of water bodies. Simple, but a detailed foraging model that determines the feeding pattern of planktivores is thus formulated.

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It is clear that taxonomic and body size structure of zooplankton community are strongly influenced by planktivorous fish. Our study is designed to investigate quantitatively how fish predation would affect zooplankton community structure by analyzing the entire predation process through simple mathematical models. In addition, it is designed to investigate the cascading trophic interactions and to understand the mechanism of how the large bodied zooplankton are selectively eliminated by visually feeding planktivores. Selective predation of fish will favor phytoplankton growth because of the elimination of most efficient feeders on algae. The fish visual feeding is illustrated using a prey encounter model incorporating optimal foraging concept as the basis of prey selectivity. Encounter rates of prey depend on environmental parameters such as water turbidity and light climate. Fish feeding activity depends on water temperature apart from other considerations. Feeding rate for a fish considering its size and visual sensitivity is predicted based on these parameters. Prey, which are mainly cladocerans, are assumed to be patchily distributed, and are categorized according to their size class.

The reactive distances calculated from the model are validated for white crappie and for several prey size classes. The application of optimal foraging theory to fish-zooplankton interaction is too validated using field data. Finally, the predation pattern of white crappie is predicted under natural conditions. The implications of fish-zooplankton interaction on water quality management is further highlighted based on possible biological control techniques as applied to lakes and reservoirs.

2.0 Materials and Methods

Foraging behaviour of many fish species has been well studied, and consequently they are classified under three categories according to the search strategy employed in finding food. Ambush searchers are characterized by long saltatory periods, saltatory searchers by a stop-and-go pattern, and cruise searchers by continuous movements (O'Brien & Evans, 1991). This classification is necessary to determine the predation rate of zooplankton by planktivores because the feeding rate is directly dependent on the prey-predator encounter rate, which is determined by the search mode (see Fig. 2 for an illustration).

The sequential events of the predation cycle for a saltatory searcher is given in fig. 1. The feeding rate of the fish can be determined by following this sequence, which leads to either prey ingestion or escape. The number of prey encounters can be determined by evaluating the prey present within the visual field. The visual field is a function of the reactive distance, for both saltatory searching and cruise searching predators. Therefore, the determination of the reactive distance will be the first step in evaluating the feeding rate for a planktivores. The reactive distance can be calculated using fish visual sensitivity principles coupled with underwater light conditions.

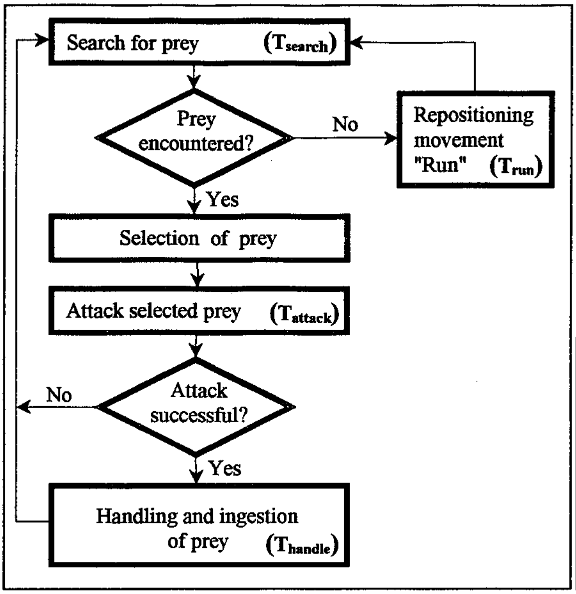
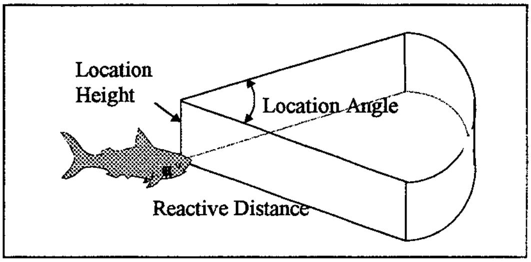


Fig.1. The sequence of a planktivore feeding cycle

Fig. 2. The prey search volume for a saltatory searching planktivore



The reactive distances are calculated for the fish following the principles presented by Aksnes & Giske (1993). The model for size selective predation on zooplankton by planktivorous fish is based on encounter principles and optimality theory. The model assumes that the fish decides to or not to pursue a prey at the time of prey encounter. Many authors have shown that the fish's foraging benefits may be optimized by selecting most profitable prey and ignoring sub-optimal prey at the time of encounter (Mittelbach, 1981; Townsend & Winfield, 1985 (for details of optimal foraging); Letcher *et al.*, 1996). The optimal strategy for the fish is specified as a range of prey lengths, so that only prey items contained in that range is pursued upon encounter. It assumes that the predator selects a prey item from among the optimal range by random choice.

3.0 Results

The predicted reactive distances are compared with experimental data in figs. 3(a) & (b) for white crappie. The energetic costs associated with fish foraging behaviour is calculated based on the sequence of events that takes place for each prey consumed. Comparisons of the relative abundance of prey species and size categories in the stomach to the lake environment (fig. 4) indicated white crappie (length > 100 mm) strongly select prey utilizing an energy optimization strategy. In most cases, the fish exclusively selected large *Daphnia* ignoring evasive prey types (Cyclops, Diaptomids) and small cladocera. This selectivity is the result of fish actively avoiding prey with high evasion capabilities even though they appear to be considerably high in energetic content and having translated this into optimal selectivity through capture success rates. The energy consideration and visual system, apart from the forager's ability to capture prey, are the major determinants of prey selectivity for white crappie still at planktivorous stages (up to about

150 mm in length). Figs. 5 & 6 present the environmental distribution of prey and the predicted pattern of foraging throughout a typical day.

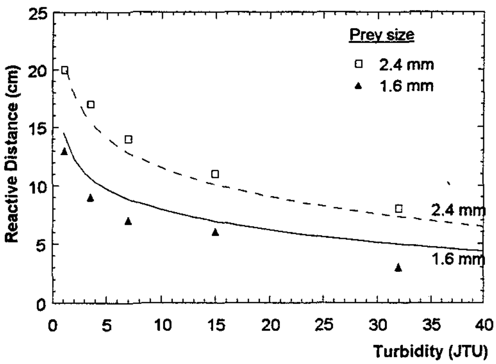


Fig.3(a). Relationship between reactive distance and turbidity of white crappie for two size-classes of *Daphnia magna* at 50 lx. Observed data based on Wright & O'Brien (1984).

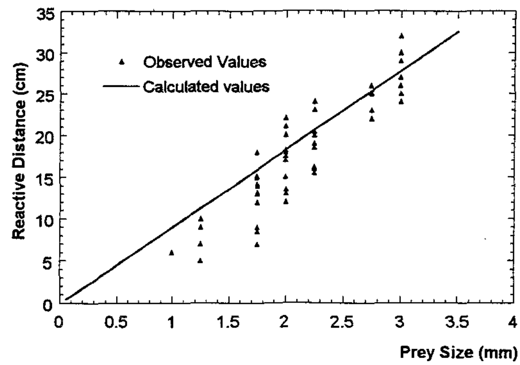


Fig.3(b). Comparison of observed and calculated reactive distances for white crappie (total length ~ 160 mm) preying on *Daphnia magna* at 50 lx and 1 NTU. Observed values based on Wright & O'Brien (1984).

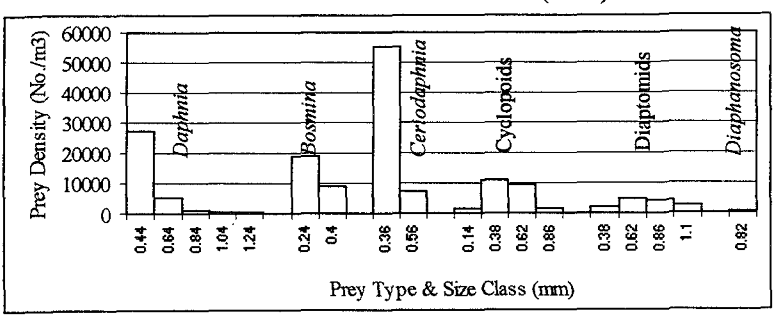


Fig. 4. Environmental distribution of zooplankton.

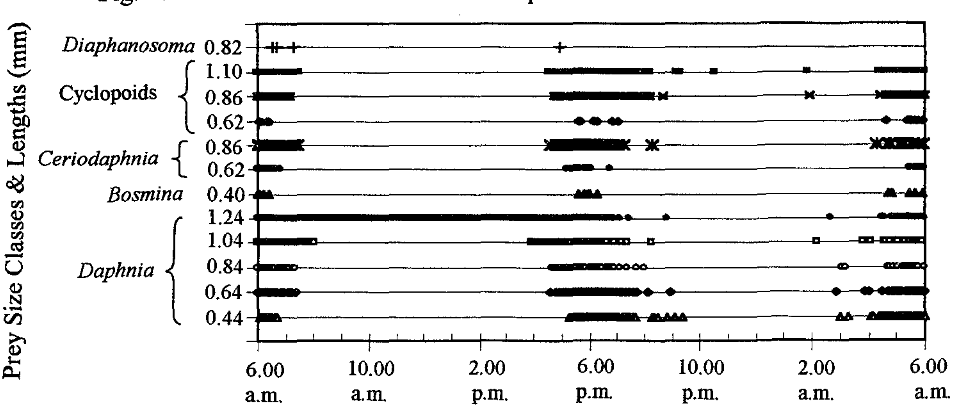


Fig. 5. The predicted foraging pattern of the white crappie of 100 mm in length. It was assumed that the fish foraged at a depth of 4 m and the water turbidity is 3 NTU. The light intensity at the water surface was defined by a sinusoidal function and was assumed to vary from 10 lux at 6.00 a.m and 10,000 lux at 12.00 noon.

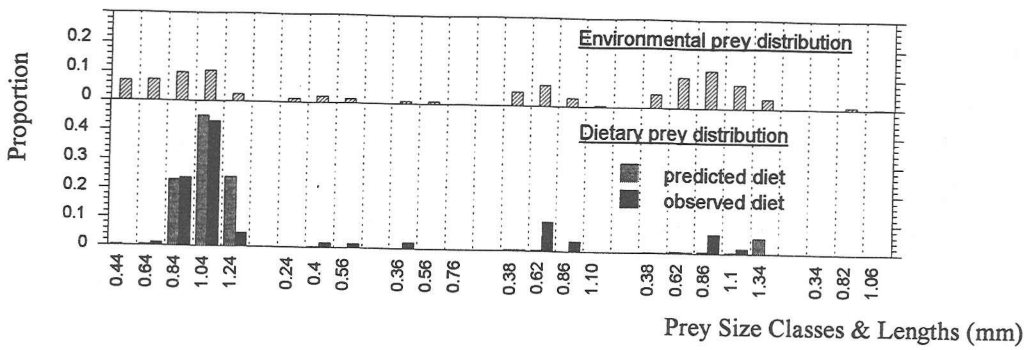


Fig. 6 Environmental distribution of zooplankton and comparison of the predicted and observed diets for white crappie. The fish diet was determined by performing a gut analysis. The 20 fish sampled were between 82-167 mm in length. The zooplankton were sampled at a depth of 6m where the light intensity was 1.74 lux and the turbidity was 3 NTU. Water temperature was 11.3 °C.

The model predictions agreed with the observations to an acceptable degree of accuracy. The coefficients used were for white crappie and they can be changed so as to accommodate the model for other fish species as well.

4.0 Discussion

Planktivorous fishes are the most important predators in the aquatic ecosystems because each fish species is planktivorous in juvenile stages, at least. Moreover, their effect as predators over other planktivores stems from the large feeding capacity they posses and the broad spectrum of food sizes that render nearly all zooplankton species endangered. The basic pattern of prey selectivity by any planktivore is the result of both prey density and prey vulnerability (less evading success, conspicuousness etc.). Therefore, the diet of a fish is composed either of the most abundant prey species when predation is non-selective, or the most vulnerable prey species when the predation is highly selective. The percent composition of prey species in the predator diet would be the same as that of the prey present in the former case, or an overrepresentation of some prey species in the diet in the latter case. The case we explored falls to this second category. The most vulnerable prey species is the most profitable in terms of energetic gain for the predator. The optimal criteria for prey selectivity is applicable in this case with most of the variables determined to acceptable accuracy. But this trend of size selectivity cannot be expected to continue for long because the optimal forager would shift to a less preferred but more abundant prey species as soon as the density of its preferred prey was greatly reduced. In this case too, the energetic considerations involved in predator behaviour are important rather than merely considering the prey within its energy values. The most profitable prey would then be neither the largest nor the most abundant prey species, but other species in between these two extremes.

In the early 1960's, Hrbácek (1962) noticed that the algal biomass was high in ponds with fish where zooplankton consisted mainly of small bodied species. Further, they observed in ponds without fish hat phytoplankton production was low and larger herbivores like *Daphnia* dominated the zooplankton community. Shortly after this, Brooks & Dodson (1965) developed the 'size-efficiency hypothesis' to explain these population shifts observed by Hrbácek. The large bodied zooplankters are much more efficient at grazing down phytoplankton biomass than their smaller competitors which are, moreover, restricted to foraging only on the smallest particles. Since fish foragers selectively on larger zooplankton, it causes a shift in the zooplankton community towards small bodied animals that have little impact on total algal biomass. Zooplankters feed on phytoplankton and large bodied herbivores have the added advantage of high efficiency in filtering. Therefore, when the predation pressure posed by planktivores is of low intensity, large bodied zooplankton dominate the and the lake water will be clear with lesser concentration of algae. But when the predation is intense, and size selective predation eliminates the large bodied zooplankton, the smaller bodied individuals have a better chance of survival with lesser capability of water filtration thus leading to murky waters. Therefore, the model results presented in this study could be used as a guide to understand the trophic relationships, which are dominant in a particular situation and appropriate management technique to be applied to the lake. This is the essence of biomanipulation, namely, constant management of the interaction between trophic levels. Either addition of or removal of planktivorous or piscivorous fish has to be decided on the trend predicted by the model.

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