

Calculation of search volume on cruise-searching planktivorous fish in foraging model

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Abstract: Search volume of cruising planktivorous fish was calculated based on its detailed behavior. To examine the factors influencing search volume, a series of experiments were conducted by varying ambient conditions, such as structural complexity, light intensity, and turbidity. *Pseudorasbora parva* were used in experiment as predator and *Daphnia pulex* was selected as prey. The shape of scanning area of *P. parva* showed elliptic and the search volume changed drastically depending on ambient conditions. Compared with the results of previous foraging model, the search volumes of the fish under previous study were larger (1.2 to 2.4 times) than those from our study. These results on the changes in feeding rate can be useful in determining microhabitat requirement of *P. parva* and other cyprinids with a similar foraging behavior. The calculated search volume is compared with other foraging model and the effect of zooplankton-planktivore interactions on aquatic ecosystem is discussed.

Key words : Prey encounter, *Pseudorasbora parva*, Reactive distance, Scanning area, Searching speed
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Introduction

A decline of zooplankton population in aquatic ecosystem due to planktivorous fish foraging bring about the destruction of the aquatic ecosystem balance (Aksnes and Giske, 1993; Manatunge and Asaeda, 1999). In a foraging model, the feeding rates of fishes provide an understanding of the mechanism of how prey are eliminated by visually feeding predators in aquatic ecosystems. Foraging and feeding ability of planktivorous fish depend on their visual ability and search speed (Asaeda *et al.*, 2001; Park and Park, 2005a), which determines the search volume and encounter rate of prey (Dunbrack and Dill, 1984; Beauchamp *et al.*, 1999; Flore *et al.*, 2000).

The exact shape and area of the cross-section of the visual field surrounding the fish (scanning area) and search speed is necessary to estimate the search volume. The shape of the scanning area of the reaction field can be calculated from bearing and elevation that describe the location of the prey relative to the foraging fish (Link and Edsall, 1996). The reactive distance is also an important factor that is used to calculate the maximum distance that a fish can locate the prey laterally (Beauchamp *et al.*, 1999).

Most previous studies on foraging model of planktivorous fish, the shape of scanning area and search volume have been only simply estimated (Eggers, 1977; Aksnes and Giske, 1993). The search volume was usually approximated by a cylinder with its slant and height equal to the reactive distance or maximum distance that prey are sighted laterally (consequently the shape of the

scanning area of reaction field was a circle) and the length equal to the distance traveled during the foraging period.

In this paper, we calculated the search volume of cruise-searching planktivore, *Pseudorasbora parva*, foraging on *Daphnia pulex* by measuring the scanning area and search speed. We analyzed the characteristics of search volume variation depending on several conditions that affects the fish's visual ability (structural complexity, light intensity and turbidity). The calculated search volume is compared with other foraging models and the effect of zooplankton-planktivore interactions on aquatic ecosystems is discussed.

Materials and Methods

Experiments:

P. parva, size range of 50-60 mm TL (total length), were used in experiments and *D. pulex*, 0.8-1.0 mm, was selected as the prey. The fish were trained to feed only on live zooplankton for one week before the experiments. The experiments were performed in a Plexiglas tank (60x30x30 cm), isolated by black curtains to avoid stress. The bottom and sidewalls of the tank were graduated with 1.1 cm grids for the use as coordinates. A series of experiments were conducted by varying the structural complexity, light intensity, and turbidity.

(a) Experiments for structural complexity: Brown cotton rope strands, 2 mm in diameter, extending vertically from top of the tank to the bottom at horizontal lattice points, were used to simulate the presence of structural complexity, which was represented with

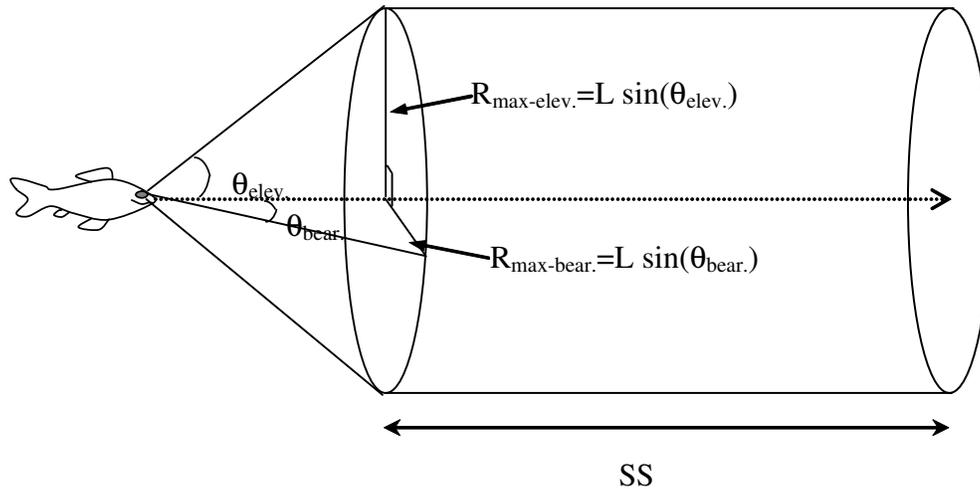


Fig. 1: Aspects of the search volume of cruising fish, where SS is search speed

the average distance between each strand. This distance was obtained by $(1/\text{density of strands})^{1/2}$, and varied from 63 cm (no strand, limited by experimental tank), 10.5 cm (about 100 strands per square meter), 7 cm (about 300 strands per square meter) and 5 cm (about 1,000 strands per square meter).

(b) Experiments for light intensity: Light intensities of 200, 100, 50 and 10 lux were provided by two fluorescent lamps installed 70 cm above the tank and partly covered with black paper.

(c) Experiments for turbidity: Four levels of turbidities, less than 1, 5, 10 and 15 NTU (Nephelometric Turbidity Units), were created by dissolving kaolinite in water. Settling was not observed during the experiments, indicating constant turbidity levels.

Fish were acclimated to each condition for at least 24 hr and were starved for 24 hr before each experiment. In all experiments, prey densities were maintained with 0.2 individual prey per liter and prey introduced while the fish swam in the opposite direction, at a distance from the fish.

Three video cameras were used for the detailed analysis of the search speed, reactive distance and bearing and elevation angles of the fish. The zoom video camera was focused on the details of fish behavior. Paired video cameras were installed at the top and the front of the tank to obtain the instantaneous coordinates (x , y and z) of prey and each part of the fish body (Dunbrack and Dill, 1984; Flore *et al.*, 2000). The analysis of recorded videotapes followed Priyadarshana *et al.* (2001).

The distance that fish moved during searching was determined using the grids on the tank. The time interval between two picture frames was measured by digital video image recorded automatically in the picture frame. This feature allowed the measurement of time intervals up to 0.033 sec. The moved distance divided by the time interval, determined by the two picture frames, produced an approximation of the search speed of the fish. At least

70% of search cases in experiment of each visual condition were analyzed to determine the mean and standard deviation of search speed.

Calculation of reactive distance and scanning area: The reactive distance, L was calculated by formula given by Flore *et al.* (2000).

$$L = \sqrt{(YZ)^2 + (XY)^2 + (XZ)^2}$$

Where, YZ = distance to prey from projection to transverse plane, XY = distance to prey from projection to horizontal plane, XZ = distance to prey from projection to sagittal plane.

Dunbrack and Dill (1984), defined the bearing angle (β) as the angle between longitudinal direction of the fish snout just before the orientation and the location of the prey, and the attack elevation angle (ϵ) is the angle between the attack trajectory and the horizontal plane (Fig. 1). The combination of bearing and elevation angles provides the shape of the scanning area of reaction field. When the scanning area of cruising fish is circular than it can be calculated as follows.

$$\text{Scanning area} = \pi R_{\max}^2, R_{\max} = L \sin(\theta)$$

Where, R_{\max} is maximum lateral sighting distance and θ is the angle from the longitudinal direction along fish's mid-body line to position of prey. When the shape of scanning area is ellipsoidal and the angle θ is different depending on the bearing and elevation angles because the range of R_{\max} is different in both angles than,

$$\text{Scanning area} = \pi R_{\max\text{-bear.}} R_{\max\text{-elev.}}$$

and maximum sighting distance in bearing angle, $R_{\max\text{-bear.}} = L \sin(\theta_{\text{bear.}})$ and maximum sighting distance in elevation angle $R_{\max\text{-elev.}} = L \sin(\theta_{\text{elev.}})$, where $\theta_{\text{bear.}}$ is the maximum bearing angle and $\theta_{\text{elev.}}$ is the maximum elevation angle (Fig. 1).

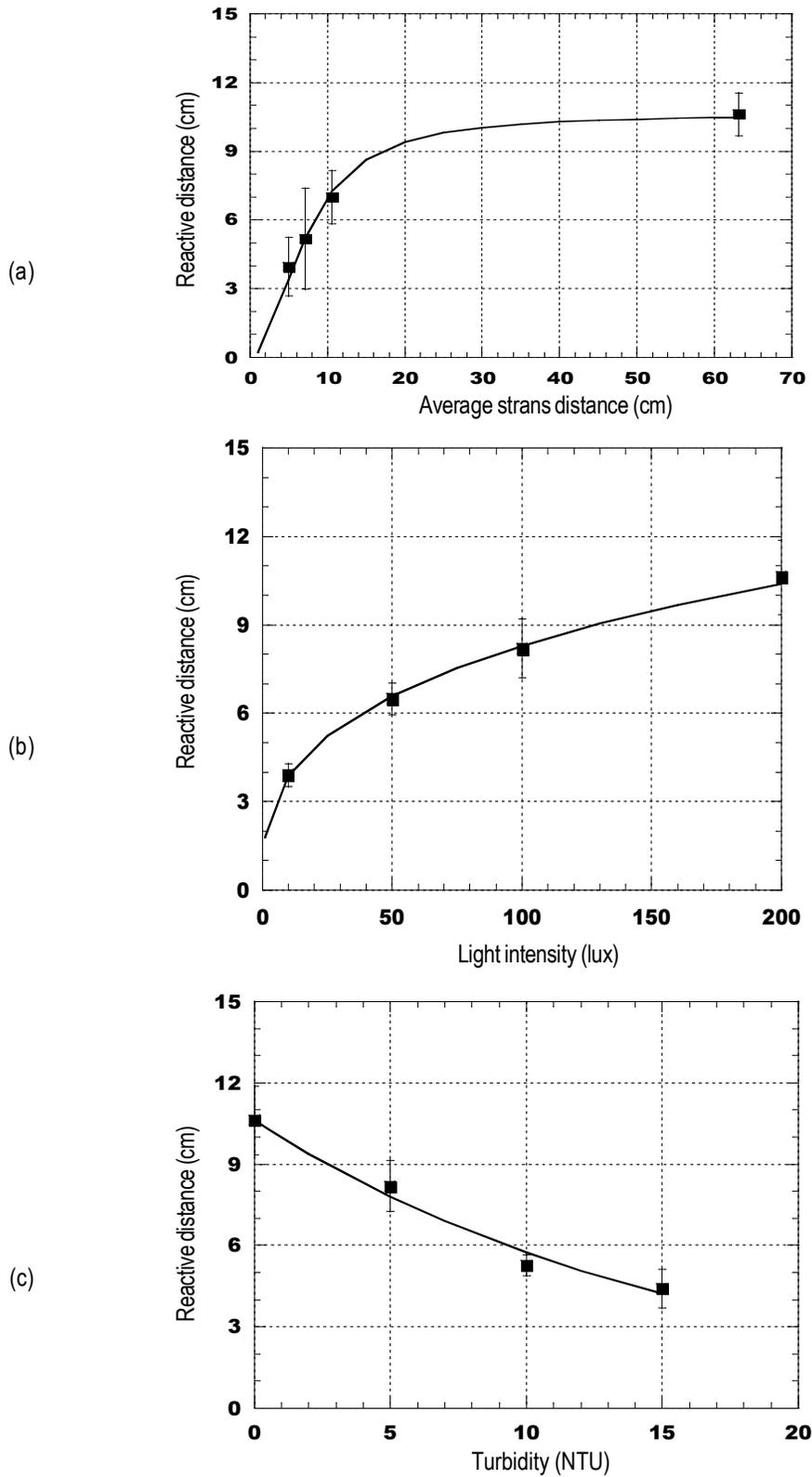


Fig. 2: The reactive distance variations depend on visual condition (horizontal bar represent \pm SD). Regression equations: (a) in structural complexity, $L = (10.62 \cdot \text{strans distance}^2) / (7.2^2 + \text{strans distance}^2)$, $r^2 = 0.883$; (b) in light intensity, $L = 1.803 \cdot \text{light intensity}(0.3313)$, $r^2 = 0.888$; (c) in turbidity, $L = 10.62e^{(-0.0616 \cdot \text{turbidity})}$, $r^2 = 0.884$



Calculation of search volume : The search volume can be calculated as;

$$\text{Search volume} = \text{Scanning area} \times \text{Search speed}$$

The scanning area of *P. parva* was estimated from the average reactive distance in all attack sequences and maximum lateral sighting distance in bearing ($R_{\text{max-bearing}}$) and elevation angles ($R_{\text{max-elev}}$).

Results and Discussion

Reactive distance variation depending on visual conditions:

In all attack sequences, the reactive distance changed with varying turbidity and structural complexity conditions. Fig. 2 shows the variation of average reactive distances in all experimental conditions as a function of each component. The reactive distance affected by structural complexity and the variation can be represented by saturation type (Fig. 2a). With increase in the average distance between strands from 5.0 to 10.5 cm, the reactive distance increased almost proportionally to the average strand distance. The reactive distance gradually converged to 10.5 cm. Increasing the strand distance to 20 cm, the reactive distance reached almost to the 90% of the final value. The reactive distance followed a power function for light intensity when varied from 10 to 200 lux and there was an exponential decrease with increase in turbidity.

The reactive distance changed with visual conditions in various patterns. The reactive distance is not significantly affected by the presence of strands at very low densities, however, decreasing the average strand distance from 10.5 cm, the average reactive distance decreased very sharply. The advancement of fish by one tail beat is approximately 60% to 70% of the body length (Videler, 1993; Priyadarshna *et al.*, 2001). Therefore, if the average distance of each strand is less than a one tail-beat advancement, the reactive distance is regulated by strands, even though the prey is recognized by the fish. If the average distance of each strand becomes larger than the distance a fish can see (visual distance), then the reactive distance depends more on the visual range, which is characterized by myopia of fish eyes independently of the distance of each strand (Luecke and Brien, 1981; Flore *et al.*, 2000).

Characteristics of scanning area depending on visual conditions: The bearing and elevation angles in all attack sequences were measured for calculating the scanning area (Table 1). In optimum conditions, at maximum light intensity (200 lux), minimum turbidity (less than 1 NTU), and no strand conditions, the left and right bearing angles and up and down elevation angles showed no difference. The range of the bearing angle (maximum = $\pm 68^\circ$) was substantially greater than that of the elevation angle (maximum = $\pm 44^\circ$), which implies that the shape of scanning area is elliptic rather than a circular.

Both angles were significantly symmetrical, even with increasing strand density. The range of bearing and elevation angles in 10.5 cm strand distance showed similar ranges as with no strand condition, and bearing angle showed a decreasing trend with

increase in strand density. The variation in both angles with light intensity showed a similar trend as with the pattern for structural complexity conditions where both angles decreased but were not significantly different at light intensities of 50 and 10 lux. The variation of both angles in turbidity conditions also showed the similar trend with its pattern depending on the light intensity condition (Table 1).

Following our observations, circular shape of scanning area of *P. parva* was not satisfying, because bearing angle was larger than the elevation angle, therefore, the shape of scanning area showed elliptic. The shape of the scanning area of reaction field (*i.e.* bearing and elevation angle) slightly changed under decreasing light intensity, increasing structural complexity and turbidity. Link Edsall (1996), found an elliptic shape for lake herring and showed that the cardinal bearing angle under high light intensities are much greater at low intensities, which were similar to the results of our study. Most previous models on planktivores were based on assumptions that the search volume of cruising fish was a cone with its slant equal to the reactive distance and a cylinder with its height equal to the swimming advancement (Eggers, 1977). According to our results, however, the scanning area had a more complex geometry and changed with variation of visual conditions (Park and Park, 2005b).

Calculation of scanning area and search volume: The scanning area depending on the visual conditions calculated through the maximum lateral sighting distance is shown in Table 2. Because the shape of scanning area was elliptic, the maximum lateral sighting distances of horizontal and sagittal planes were calculated accordingly. The scanning area rapidly decreased with decreasing strand distance. The variation of light intensity also affected the scanning area markedly, especially when the light intensity was reduced from 50 lux to 10 lux. Reduction rate of the scanning area from less than 1 NTU to 5 NTU (44%) was more than from 5 NTU to 10 NTU (68%). The search speed was also affected by structural complexity, light intensity and turbidity (Table 2).

The search volume was calculated from scanning area and search speed corresponding to each visual condition, and Table 3 (calculated method a) showed the variation of the search volumes in all visual conditions. The search volume increased with decreasing structural complexity and markedly changed when average distance increased from 5 to 10.5 cm. The search volume reduced about 90% at 5 cm strand distance compare to that of no strand condition.

The search volume showed approximately a linear relationship for light intensity variation. 203.4 liters per hour of search volume in 10 lux light intensity was in similar range with 5.0 cm of strands distance condition. The search volume decreased with increasing turbidity, and the reduction was significant when the turbidity was increased from 5 NTU to 10 NTU.

Eggers (1977), calculated the maximum lateral sighting distance using the reactive distance. He assumed that the shape of

Table - 1: Range of bearing and elevation angles of the reaction field under the visual conditions variation. Distribution; compares the distribution of bearing angles on left and right and elevation angles in the upward and downward direction (Mann-Whitney Test); Comparison; compares the bearing and elevation angles (Mann-Whitney Test)

Condition		Maximum (degree)	Mean (degree)	SD (degree)	Distribution ²	Comparison ³	
Optimum ¹	Bearing	68	38	16	S	D	
	Elevation	44	16	10	S		
Distance between each strand (cm)	10.5	Bearing	70	37	21	S	D
		Elevation	48	19	11	S	
	7	Bearing	63	31	16	S	D
		Elevation	48	21	11	S	
Light intensity (lux)	5	Bearing	57	28	15	S	S
		Elevation	34	20	10	D	
	100	Bearing	62	36	14	S	D
		Elevation	35	17	12	S	
Turbidity (NTU)	50	Bearing	59	25	22	S	S
		Elevation	34	17	14	S	
	10	Bearing	39	21	17	S	S
		Elevation	42	23	18	S	
Turbidity (NTU)	5	Bearing	65	36	18	S	D
		Elevation	42	18	13	S	
	10	Bearing	57	25	17	S	S
		Elevation	34	17	15	S	
15	Bearing	45	21	15	S	S	
	Elevation	38	18	17	S		

¹ no structural complexity, light intensity = 200 lux, turbidity = less than 1 NTU

^{2,3} All tests were performed with 5% significance level. S = Same, D = Different

scanning area is circular therefore, the maximum lateral sighting distances in bearing and elevation angles were same. On the other hand, Beauchamp *et al.* (1999) assumed that the shape of scanning area is circular and the maximum lateral sighting distance was reactive distance. A comparison of the search volumes calculated using the present study and those studies is shown in Table 3. The search volumes calculated using these methods for each experimental condition were about 1.2-2.4 times larger than the calculated values using the method proposed by our study.

When calculated with the method of Eggers (1977) and Beauchamp *et al.* (1999), the search volumes of *P. parva* with varying the visual conditions were 1.2-2.4 times larger than in our own calculations. Prey encounter rates are determined by the product of search volume and prey density (Beauchamp *et al.*, 1999; Manatunge Asaeda, 1999). If all attack sequences success to capture, however, feeding rates of our observations are 50% - 80% less than prediction values throughout the search volumes. Several factors might have caused this discordance; When visual foraging model apply to predict the feeding rate in nature, the problem is how we accurately measure the prey density so that these estimates and their variability correspond to the foraging capabilities of predators because prey are randomly distributed in nature. A visual foraging model for planktivores should improve predictive capability by providing a tool for estimating the expected proportional distribution of prey, based on temporal changes in

prey density distributions and the visual conditions of the water body.

The estimates for search volume are based on several critical assumptions. The model assumes that reactive distance represents the radius of a planktivore's visual field, however, prey might be detected at greater distance than reactive distance measured in laboratory experiments. If prey detection distances exceed reactive distance, then search volumes would be underestimated, based in proportion to (reactive distance²-detect distance²) detect distance². Therefore, the encounter rate predictions exceeded observed consumption rates.

Stomach content levels influence the feeding behaviour of fish (Ernsting, 1977; Brett, 1979), and in particular searching for food will reduce accordingly with the level of satiation (Gill and Hart, 1996; Andersen, 1998). Robinson and Pitcher (1989), studied the influence of hunger on swimming speeds of herring (*Clupea harengus* L.) and found that swimming speeds are highest at the maximum hunger state, decreasing with increasing satiation. As close to full satiation, the fish exhibited a swimming speed of 0.5 ~ 0.75 body lengths per second, which approximates the reported cruising speed of fish searching for prey (Beamish, 1978). Priyadarshana *et al.* (2001), reported prey density had a significant effect on swimming speed and feeding rate on *Ps. parva*; increasing prey density from 0.5 to 25 prey per litter caused the swimming speed to decrease three fold.



Table - 2: Variation of scanning area and searching speed depending on the visual conditions

Condition		Scanning area ¹ (cm ²)	SD	Search speed (cm sec ⁻¹)	SD
Optimum		228.9	17.0	6.71	1.00
Distance between each strand (cm)	10.5	106.8	10.5	5.66	1.18
	7	55.1	4.4	4.15	0.82
	5	23.2	2.2	3.06	0.50
Light intensity (lux)	100	107.3	10.7	5.57	1.44
	50	63.6	10.3	4.49	0.48
	10	20.1	4.3	2.81	0.71
Turbidity (NTU)	5	128.5	14.7	5.82	0.89
	10	41.5	6.7	3.70	1.03
	15	26.8	4.6	3.00	1.11

$$^1 \text{ scanning area} = \pi \times R_{\text{max-bear}} \times R_{\text{max-elev}}; R_{\text{max-bear}} = \sin(\theta_{\text{bear}}) \times L, R_{\text{max-elev}} = \sin(\theta_{\text{elev}}) \times L$$

Table - 3: Comparison of the search volume calculated with the present method (method a), Eggers (1977), Confer *et al.* (1978) (method b) and Beauchamp *et al.* (1999) method (method c)

Condition		Calculated with method a	Search volume (L hr ⁻¹) Calculated with method b	Calculated with method c
Optimum		5525.7	7375.4	8579.3
Distance between each strand (cm)	10.5	2177.1	2753.0	3117.7
	7	824.0	988.0	1244.5
	5	255.3	382.9	544.3
Light intensity(lux)	100	2150.0	3309.6	4245.2
	50	1027.9	1575.6	2144.4
	10	203.4	216.2	482.9
Turbidity(NTU)	5	2693.9	3648.8	4442.2
	10	552.4	828.4	1177.8
	15	289.0	331.9	663.9

Encounter rates do not necessarily equate to feeding rate (Christensen, 1996). Therefore, when translating encounter rates into predation rates, encounters will need to be discounted by varying probabilities of attack and capture success as a function of diel period, light intensity, size, or schooling / nonschooling status.

In conclusion, the shape of scanning area of *P. parva* showed elliptic, therefore, the method that calculate the scanning area also has to the characteristic of its shape. The search volume changed drastically depending on visual conditions. This information on the changes in the search volume may be helpful in determining microhabitat requirements of *P. parva* and other cyprinids with a similar foraging behaviour. However, several factors have to consider for accurate prediction of encounter rate and feeding rate, which is (1) efficient method for classifying the prey distribution, (2) control the difference between reactive distance and detect distance, and (3) characteristics of change of reactive distance and search speed depending on prey density and satiation level.

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