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Feeding mechanism and capture success of European whitefish (*Coregonus lavaretus* L.) larvae

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ABSTRACT

Key-words:
*feeding
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dimension,
Coregonus
lavaretus larvae*

Feeding success is a key factor for larval growth and survival, and is highly dependent on small-scale processes which occur during the predator-prey interaction. We studied the feeding mechanisms involved in the capture success of the European whitefish (*Coregonus lavaretus*) larvae using video recordings. The successful predatory sequence of this species consists of the following 5 events: encounter, pursuit (including fixation), strike, capture and ingestion. *C. lavaretus* larvae can exhibit an “S” shaped posture and always strikes on its prey from beyond. The mean fixation distance for wild larvae was 1.75 ± 0.71 mm and for reared larvae was 1.65 ± 0.76 mm. This distance was significantly different between failed and successful snaps, and seemed to be an important parameter to the capture success of *C. lavaretus* larvae. The analysis of the complexity in predator's swimming path showed that more convoluted approaches are less likely to lead to a fruitful attack.

RÉSUMÉ

Mécanisme alimentaire et succès de capture des larves du corégone lavaret (*Coregonus lavaretus* L.)

Mots-clés :
*mécanisme
alimentaire,
succès de
capture,
dimension
fractale, larves
de Coregonus
lavaretus*

Le succès alimentaire est un élément clé de la croissance et de la survie larvaire ; ce paramètre est fortement influencé par les processus se produisant à micro-échelle entre le prédateur et sa proie. Nous étudions ici les mécanismes alimentaires impliqués dans le succès de capture des larves du corégone (*Coregonus lavaretus*) à l'aide des enregistrements vidéos. Une séquence de prédation réussie consiste en la succession des 5 événements suivants : rencontre, poursuite (incluant la fixation), attaque, capture et ingestion. Lors de la fixation de la proie, la larve de corégone peut prendre une posture en forme de « S ». Ce prédateur attaque toujours ses proies par le bas. La distance moyenne de fixation est de 1.75 ± 0.71 mm pour les larves sauvages et elle est de 1.65 ± 0.76 mm pour les larves produites en pisciculture. Cette distance a été significativement différente entre les

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attaques réussies et celles ratées, et semble, de ce fait, être un des paramètres clés conditionnant le succès de capture des larves de corégone. L'étude de la complexité des trajectoires des prédateurs montre que les approches les plus complexes sont les moins susceptibles d'aboutir à une capture.

INTRODUCTION

The recruitment of pelagic fish species with high reproductive potential is highly variable, irrespective of marine (Koutsikopoulos and Le Cann, 1996) or fresh water species (Müller, 1992; Karjalainen *et al.*, 2000). Successful recruitment relies on adult spawning stocks (Helminen *et al.*, 1997), physical factors (Sirois and Dodson, 2000; Munk, 2007) and the availability of appropriate zooplankton prey (Rao, 2003). In addition, the accessibility of food not only depends on the relative prey abundance, but also on the predator's feeding adaptations (Pasternak *et al.*, 2006). An increasing research effort has been devoted to understanding the foraging behavior of fish larvae. Numerous aspects of predatory sequences like encounter rate (MacKenzie and Kiørboe, 1995), catch success (Drost, 1987; Domínguez-Domínguez *et al.*, 2002; Sarma *et al.*, 2003; Morales-Ventura *et al.*, 2004), attack success (Wanzenböck, 1992; MacKenzie and Kiørboe, 2000), and ingestion rate (Landry *et al.*, 1995) have been investigated. Previous studies also investigated the role of feeding mechanisms in the attack success of fish larvae and attributed the success of strikes to: (i) the aptitude of the creation of a suction flow in larval carp (Drost and Van Den Boogaart, 1986) and larval clownfish (Coughlin, 1994); (ii) the accuracy of larva and its strike speed in carp and pike larvae (Drost and Van Den Boogaart, 1986; Drost, 1987); (iii) the duration of the fixation time in cyprinids (Wanzenböck, 1992) and (iv) the capability of larvae to approach a prey without eliciting an escape response in larval cod (MacKenzie and Kiørboe, 2000). A clear outcome of these investigations is that capture success constraints are species specific.

Common whitefish (*Coregonus lavaretus* Linnée, 1758) is an endemic planktivorous salmonid, constituting a major component of western European inland commercial fisheries (Marttunen and Vehanen, 2004; Gerdeaux *et al.*, 2006). In Lake Geneva, the increase of whitefish catches is partly due to the change of stocking practices from only yolk-sac fry to the following different stages : yolk-sac fry, juveniles (< 3 cm) and fingerlings (5–6 cm) (Gerdeaux, 2004). For this genus, in which the highest pre-recruitment mortality occurs during the larval stage (Karjalainen *et al.*, 2000), little is known about the factors governing the catch success and the survival of its larval stages.

Although many studies have identified several mechanisms involved in the capture success of fish larvae, less attention has been paid to the role of the larvae's path complexity. The aim of this study was to explore the mechanisms acting on the feeding success of larvae of *C. lavaretus*, which accounts for a substantial proportion of the total catches of Lake Geneva's fishery (Gerdeaux, 2004). To analyze these mechanisms, we used standard cinematographic techniques and both scale dependent (distances and speeds) and scale independent (fractal dimension) metrics.

MATERIAL AND METHODS

> EXPERIMENTAL FISH LARVAE AND PREY

Wild whitefish larvae were caught in the deep peri-alpine lake, Lake Annecy (28 km², maximum depth 65 m, France) in April 2006 using a rectangular net (1.5:1 m) of 5 m length (1 mm mesh). The cod end of this net was equipped with a PVC receiver to collect the larvae. Trawls of 20 min were performed at an approximate speed of 1 knot. Larvae were kept in an aquarium and fed on wild zooplankton for one day before the experiment.

Reared larvae were obtained after the artificial fertilization of eggs produced from a broodstock originating from the Lake Geneva (582 km², maximum depth 309 m, France and Switzerland). When larvae emerged from the eggs, they were transferred in 1000 L tanks (density of 200~400 larvae.L⁻¹) filled with lake water. In rearing tanks larvae were fed on dry food pellets (INVE, 100–200 µm) and wild zooplankton.

The zooplanktonic preys used in our experiments were directly collected from the littoral zone of Lake Geneva. Water was filtered through a 200 µm mesh net and only organisms retained in the sieve were used as food. These were mainly composed by cladocerans (Bosminids and the two Daphnids *Daphnia hyalina* and *D. galeata*) and copepods (*Cyclops prealpinus*, *C. vicinus* and *Eudiaptomus gracilis*).

> EXPERIMENTAL SETUP

The animals were filmed in a small plexiglas tank of 10 x 8 x 3 cm (Length:Height:Depth) containing 0.24 L of filtered lake water. A dark-grey surface was put behind the aquarium in order to enhance the contrast of the larvae and prey. The 2D video set-up consisted of a single camera (Sony DCR PC120E) orthogonally oriented to the largest walls of the tank. The only light source was a fiber optic light (Zeiss KL Schott 8V 20 W) placed at ~10 cm above the tank. The light intensity was 48.9 µE.s⁻¹.cm⁻².

> EXPERIMENTAL PROCEDURE

The experimental procedure aimed to investigate the role of the feeding mechanism of whitefish larvae on its capture success. We carried out two experiments using larvae, as predators, facing two different prey types and densities. The two experiments were performed using non-starved larvae. In fact, preliminary observations showed that feeding larvae had fecal pellets protruding from the anus, suggesting that these larvae did not stop feeding once the gut was full.

In the first experiment, Exp1: 3 wild larvae (total lengths: 14.6, 12.6 and 14.0 mm, stages 1 and 2 according to the classification of Luczynski *et al.*, 1988) caught from Lake Annecy were put into the observation tank. A mixture of 500 individual zooplanktonic prey (total length range: 0.2~1.65 mm) caught from Lake Geneva were then added.

In the second experiment, Exp2: 4 reared larvae (total lengths: 15.3, 15.9, 15.1 and 15.5 mm, stages 2 and 3) were put into the vessel and 100 gently sorted adult *Cyclops* spp. (dominated by *C. prealpinus*, total length range: 1.0~1.65 mm) were added.

In both experiments predators and prey were acclimatized during 10 min in the observation tank. Afterwards the larval behavior was recorded for 50 min.

> DETERMINATION OF SWIMMING PATHS

A preliminary examination of the video recordings was performed in order to inspect the feeding patterns of whitefish larvae and to identify the preliminary set of predatory sequences (strikes, captures and escapes) to be analyzed. This analysis was conducted using the image processing software TrackIt (Iguana, v.2.0). This software permitted us to track zooplankters frame by frame at a time resolution, t_r , of 0.04 s. The coordinates of a larva corresponded to the position of the center of its eye (MacKenzie and Kiørboe, 2000), whereas the coordinates of a prey corresponded to the position of the center of its body. Each sequence resulted in a data base containing the spatial coordinates of each tracked predator or prey across time (x_i , y_i , t_i).

> BEHAVIORAL PARAMETERS

The following metrics were considered in this study: the apparent predator strike speed, the apparent prey escape speed, the apparent fixation distance, and the complexity of all trajectories during pursuit and attack phases using fractal dimension D .

We defined the investigated parameters as follows:

- Pursuit is the approach of the predator in the direction of a prey. As emphasized by MacKenzie and Kjørboe (2000) the pursuit can comprise repeated approaches if the prey exhibits escape drills. The fixation occurs during this event (Wanzenböck, 1992; MacKenzie and Kjørboe, 2000) and is defined as the disruption of the approach and the aiming at the prey (Wanzenböck, 1992). Georgalas *et al.* (2007) considered the “S” shaped posture as an event. However, we associated this posture with the aiming since this lineament did not accompany all the predatory sequences.
- Strike is the sudden jump of the larva toward a prey to engulf it (Heath, 1993).
- Success is the successful engulfment of a prey by a larva and failure is the escape of a prey from its predator. The capture success ratio is the number of successes divided by the total number of strikes.
- The apparent (2D) distance, d , traveled between two consecutive frames (a and b) is calculated as follows:

$$d = \sqrt{(x_b - x_a)^2 + (y_b - y_a)^2}.$$

- The apparent gross movement, D_g , during a given sequence is the sum of the distances moved from the first frame (1) to the last frame (i) constituting the sequence. It is estimated as follows:

$$D_g = \sum_1^i d_i.$$

- The swimming speed, S , of an event is estimated by dividing the gross movement D_g by the duration of the event (*i.e.*, predator strike or prey escape) T :

$$T = i \times t_r$$

$$S = \frac{D_g}{T}$$

where t_r is the duration of one frame and is equal to 0.04 s.

- The predator strike speed, SS , is the apparent speed of the snap of the predator. It was calculated between the frame where the larva showed the first sign of the snap launch and the frame where the larva reached the initial position of the prey.
- The prey escape speed, ES , is the apparent speed of the first jump exhibited by a prey in response to a larval attack. This escape, if performed, could be achieved by one or more jumps. It was calculated between the frame where the prey showed the first sign of an escape reaction and the frame where the prey stopped its movement. When a prey didn't perform any escape reaction, we assumed that $ES = 0$.
- The apparent fixation distance, FD , is the distance separating the predator from its prey during the aiming process. It was measured between the centre of the prey and the position of the larva on the frame preceding the strike.
- The apparent speed of an event occurring between two successive frames was calculated by dividing the covered distance by the time resolution t_r .
- The fractal dimension, D , measures the complexity of a trajectory. For a two dimensional path, it ranges from “1” to “2” with the value of “1” for a linear path and “2” for a more complex one. D was calculated using the counting box method described by Seuront *et al.* (2004a) which is based on the following formula:

$$N(\lambda) = k \times \lambda^{-D}$$

$N(\lambda)$ being the number of boxes occupied by a trajectory, λ the box size, and k a constant. The slope of the linear fit of the log-log plot of $N(\lambda)$ versus λ provides the value of D . In order to compare the complexity of predator paths between successful and failed attacks we

Table I

Mean values (\pm SD) of the different events occurring during whitefish larva strikes. *N*: number of observations; *SS*: mean predator strike speed ($\text{mm}\cdot\text{s}^{-1}$); *ES*: mean prey escape speed ($\text{mm}\cdot\text{s}^{-1}$); *FD*: mean fixation distance (mm).

Tableau I

Valeurs moyennes (\pm ET) des différents événements se produisant lors de l'attaque de la larve de corégone. *N* : nombre d'observations ; *SS* : vitesse moyenne de l'attaque du prédateur ($\text{mm}\cdot\text{s}^{-1}$) ; *ES* : vitesse moyenne de fuite de la proie ($\text{mm}\cdot\text{s}^{-1}$) ; *FD* : distance moyenne de fixation (mm).

Experiment	<i>N</i>	<i>SS</i> ($\text{mm}\cdot\text{s}^{-1}$)	<i>ES</i> ($\text{mm}\cdot\text{s}^{-1}$)	<i>FD</i> (mm)	Capture success ratio
Exp1 (wild larvae)	47	36.34 \pm 14.39	26.45 \pm 20.79	1.75 \pm 0.71	0.29
Exp2 (reared larvae)	45	36.81 \pm 25.80	15.97 \pm 23.83	1.65 \pm 0.76	0.46

pooled all individual trajectories for each situation. The coordinates of all trajectories were transformed so they started at (0,0). Then a global fractal dimension was computed for each situation by using all trajectories.

> DATA ANALYSIS

The non-parametric Spearman Correlation Test was used to evaluate the relationships between the following behavioral parameters: fixation distance, predator strike speed and prey escape speed. Wilcoxon Rank Sum Test was used to compare behavior variables between successful and failed strikes. Statistical analyses and the estimations of the fractal dimension were performed using MatLab software V. 7 (Mathworks inc., 2005).

RESULTS

A total of 47 and 45 events were analysed for Exp1 (wild larvae) and Exp2 (reared larvae), respectively.

> FEEDING ETHOGRAM AND KINEMATICS

The accurate analysis of all video recordings (*i.e.*, sequence by sequence and frame by frame when necessary) allowed us to describe the successful predatory sequence of *Coregonus lavaretus* larvae as follows: search, encounter, pursuit, strike, capture and ingestion.

Whitefish larvae only detected prey during swimming and hence appeared to be a cruise predator. During pursuit, larvae swam backwards to attain an appropriate aiming distance from the prey in 31.91% of the events in Exp1 and 6.25% of the events in Exp2. This pattern was not observed for the remaining sequences. Afterwards, larvae fixated the prey by keeping their head immobile and by wiggling the posterior part of their body. Before the strike, an "S" shaped posture was exhibited in 44.66% of the attacks of wild larvae and 31.25% of the attacks of reared larvae. *C. lavaretus* larvae always fixated its prey from below and stroked a few mms towards it to simply engulf it. During the attack, no prey was caught up in a flow towards the predator; showing no cues for the creation of a suction current.

Table I summarizes the mean values of the investigated parameters. The overall capture success ratio (capture/strike) was 0.29 for Exp1 and 0.46 for Exp2. The mean predator strike speed projected on the vertical plane oscillated around $36 \text{ mm}\cdot\text{s}^{-1}$ and the fixation distance was around 1.7 mm.

The fixation distance (FD) was positively correlated with the larva strike speed (SS) for both Exp1 ($r = 0.49$, $n = 47$, $P < 0.001$; Table II) and Exp2 ($r = 0.75$, $n = 45$, $P < 0.001$; Table II).

Table II

Correlation coefficients and *P*-values of Spearman correlation test. *N*: number of observations; *SS*: mean predator strike speed; *ES*: mean prey escape speed; *FD*: mean fixation distance.

Tableau II

Coefficients de corrélation et valeurs *P* du test de corrélation de Spearman. *N* : nombre d'observations ; *SS* : vitesse moyenne de l'attaque du prédateur ; *ES* : vitesse moyenne de fuite de la proie ; *FD* : distance moyenne de fixation.

	Exp1 (wild larvae)			Exp2 (reared larvae)		
	<i>r</i>	<i>N</i>	<i>P</i>	<i>r</i>	<i>N</i>	<i>P</i>
FD vs. SS	0.497	47	< 0.001	0.758	45	< 0.001
FD vs. ES	0.284	47	0.052	0.431	45	0.003
SS vs. ES	0.205	47	0.165	0.598	45	< 0.001

Table III

Mean values (\pm SD) of the different events of whitefish larva strikes for failed and successful strikes and *P*-value of Wilcoxon test. *N*: number of observations; *SS*: mean predator strike speed ($\text{mm}\cdot\text{s}^{-1}$); *ES*: mean prey escape speed ($\text{mm}\cdot\text{s}^{-1}$); *FD*: mean fixation distance (mm).

Tableau III

Valeurs moyennes (\pm ET) des différents événements se produisant lors des attaques réussies et ratées de la larve de corégone et la valeur *P* du test de Wilcoxon. *N* : nombre d'observations ; *SS* : vitesse moyenne de l'attaque du prédateur ($\text{mm}\cdot\text{s}^{-1}$) ; *ES* : vitesse moyenne de fuite de la proie ($\text{mm}\cdot\text{s}^{-1}$) ; *FD* : distance moyenne de fixation (mm).

Predator origin		<i>N</i>	<i>SS</i>	<i>ES</i>	<i>FD</i>
Exp1 (wild larvae)	Failure	33	37.90 \pm 13.92	37.19 \pm 14.75	1.90 \pm 0.76
	Success	14	32.12 \pm 16.03	1.14 \pm 3.42	1.41 \pm 0.44
	<i>P</i> -value	-	0.173	< 0.001	0.012
Exp2 (reared larvae)	Failure	24	44.15 \pm 29.20	28.68 \pm 26.66	1.91 \pm 0.84
	Success	21	28.41 \pm 18.58	1.36 \pm 3.13	1.35 \pm 0.55
	<i>P</i> -value	-	0.078	0.002	0.007

No correlation was found between prey escape speed (*ES*) and *FD* or between *ES* and *SS* in Exp1. In Exp2, both *FD* and *SS* were positively correlated with *ES*. This implies that the larvae could adjust their strike speed to the response of the prey.

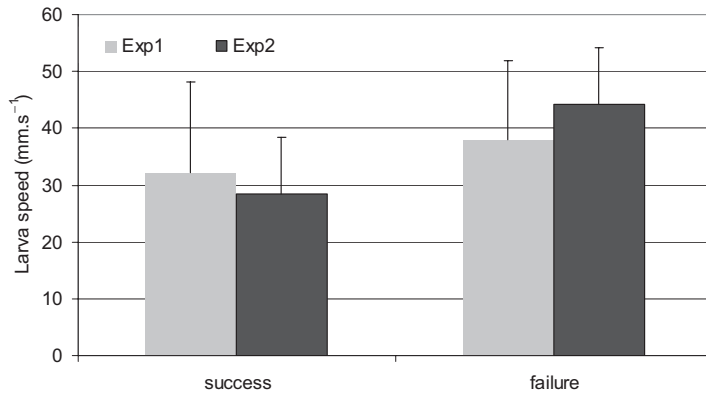
> COMPARISON OF FAILED VS. SUCCESSFUL EVENTS

Table III shows the results of the comparison between failed and successful events.

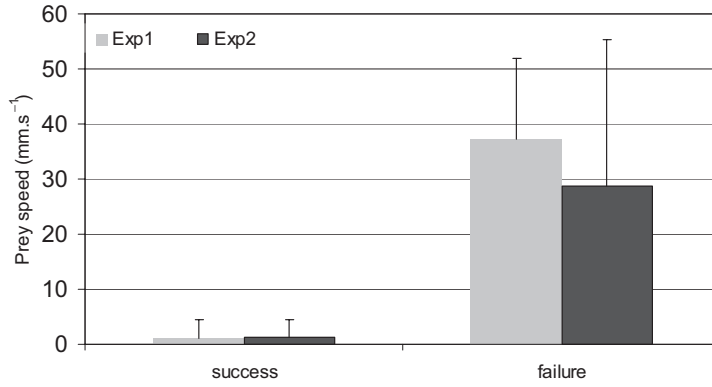
Strike speed (*SS*)

The mean strike speeds of larvae were lower for successful snaps compared with failed snaps (Figure 1A). However, these differences were not significant for Exp1 or for Exp2 (Table III).

A



B



C

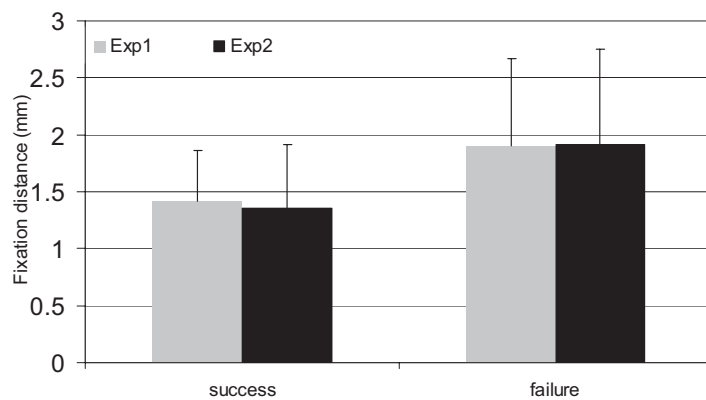


Figure 1
Mean predator strike speed (A), mean prey escape speed (B), and mean fixation distance (C) for successful and failed attacks; wild larvae ($n = 47$), aquaculture larvae ($n = 45$).

Figure 1
Vitesse moyenne des attaques (A), vitesse moyenne des fuites (B) et distance moyenne de fixation (C) pour les attaques réussies et les attaques ratées ; larves sauvages ($n = 47$), larves d'aquaculture ($n = 45$).

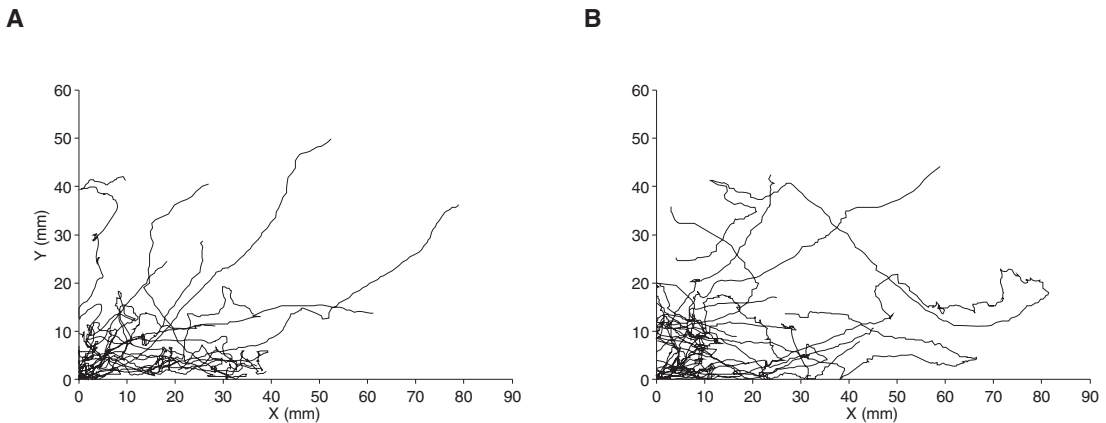


Figure 2

Paths of whitefish larvae during successful pursuits and attacks. (A) for Exp1 (wild larvae) and (B) Exp2 (reared larvae). All trajectories are plotted with (0,0) as starting coordinates and combined on the lower left side to facilitate representation.

Figure 2

Trajectoires des larves de corégone durant les poursuites et les attaques réussies. (A) pour l'Exp1 (larves sauvages) et (B) pour l'Exp2 (larves d'aquaculture). Toutes les trajectoires sont tracées avec les coordonnées (0,0) comme origine et sont combinées sur le côté bas et gauche pour faciliter la représentation graphique.

Escape speed (ES)

The mean escape speeds of prey (Figure 1B) were significantly lower in successful than in failed strikes for both Exp1 (Wilcoxon Rank Sum Test, $n = 44$, $P < 0.001$; Table III) and Exp2 (Wilcoxon, $n = 45$, $P < 0.01$; Table III). Nevertheless, an escape response was performed by only 14.28% of captured prey in Exp1 and 15.38% in Exp2.

Fixation distance (FD)

Figure 1C shows that the fixation distance was shorter in successful attacks compared with failed attacks. This trend was significant for both Exp1 (Wilcoxon, $n = 44$, $P < 0.05$; Table III) and Exp2 ($n = 45$, $P < 0.01$; Table III).

Fractal dimension (D)

The path complexity of successful events (Figure 2) was lower than path complexity of failed events (Figure 3) for both experiments. In fact, the fractal dimensions for successful events were lower than those for failed events (Table IV). The log-log plots of $N(\lambda)$ against λ were strongly correlated to the linear fit ($r^2 = 0.99$) for both experiments (Figure 4). This implies, as we will discuss later, that a convoluted pursuit was less likely to result in a successful event.

DISCUSSION

> FEEDING MECHANISM

An accurate portrayal of fish larvae's searching mechanisms facilitates the investigation of predator-prey interactions and provides insight into larval foraging efficiency (Browman and O'Brien, 1992). The analysis of the foraging behavior of common whitefish larvae in this

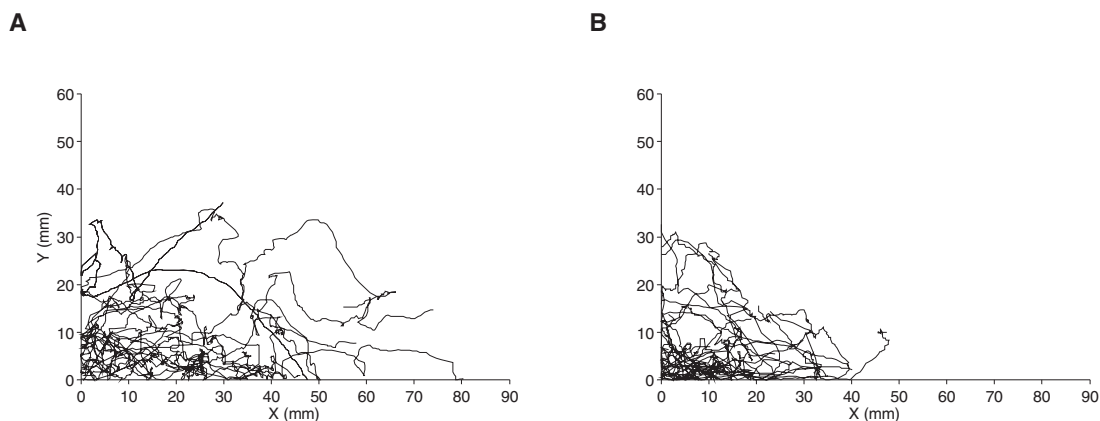


Figure 3
Paths of whitefish larvae during failed pursuits and attacks. (A) for Exp1 (wild larvae) and (B) Exp2 (reared larvae). All trajectories are plotted with (0,0) as starting coordinates and combined on the lower left side to facilitate representation.

Figure 3
 Trajectoires des larves de corégone durant les poursuites et les attaques ratées. (A) pour l'Exp1 (larves sauvages) et (B) pour l'Exp2 (larves d'aquaculture). Toutes les trajectoires sont tracées avec les coordonnées (0,0) comme origine et sont combinées sur le côté bas et gauche pour faciliter la représentation graphique.

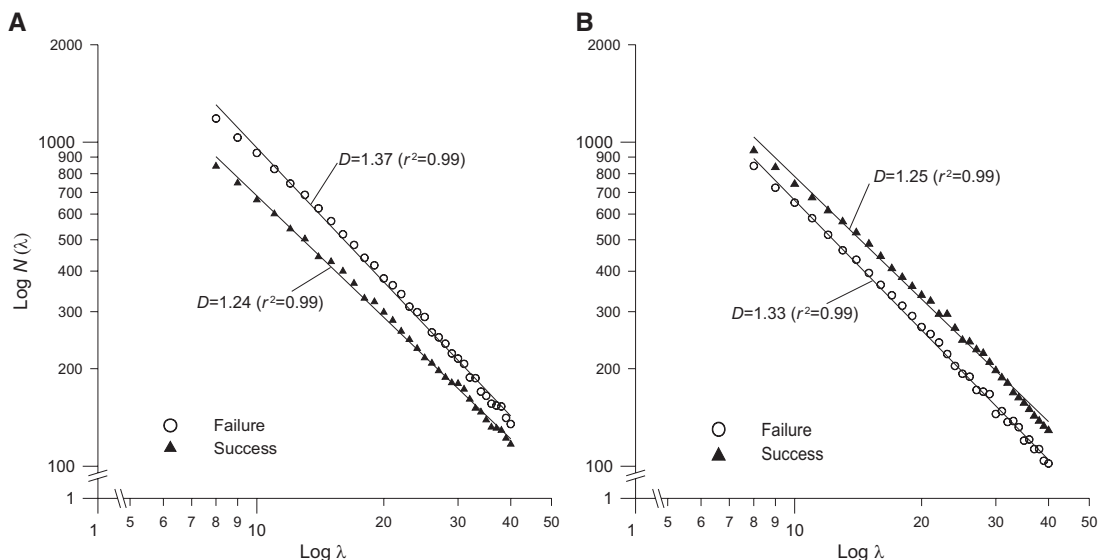


Figure 4
Scaling of the log-log plots of $N(\lambda)$ versus λ . (A) for Exp1 (wild larvae) and (B) for Exp2 (reared larvae). Solid triangles represent the paths of successful events and circled represent the paths of failed events.

Figure 4
 Ajustement des courbes log-log de $N(\lambda)$ en fonction de λ . (A) pour l'Exp1 (larves sauvages) et (B) pour l'Exp2 (larves d'aquaculture). Les triangles pleins représentent les trajectoires menant à une capture et les cercles représentent les trajectoires menant à un échec de capture.

Table IV

Fractal dimensions for failed and successful strikes for whitefish larvae (wild and from aquaculture) obtained for all trajectories shown in Figures 4 and 5. Confidence intervals (CI) correspond to fractal dimension estimates at 95%.

Tableau IV

Dimensions fractales pour les attaques réussies et les attaques ratées des larves de corégone (sauvages et de pisciculture) obtenues pour toutes les trajectoires des Figures 4 et 5. Les intervalles de confiance (CI) correspondent aux dimensions fractales estimées à 95 %.

Predator origin		N	D	CI	r^2	SD_{r^2}
Exp1 (wild larvae)	Failure	18	1.375	[1.343–1.406]	0.996	0.053
	Success	14	1.246	[1.223–1.270]	0.997	0.029
Exp2 (reared larvae)	Failure	18	1.331	[1.308–1.353]	0.998	0.016
	Success	12	1.258	[1.226–1.289]	0.995	0.059

study showed that these predators have the ability to locate prey while moving. We can accordingly classify their behavior as cruise predators, like herring (Munk and Kiørboe, 1985) and clownfish (Coughlin, 1993) larvae. Coughlin (1993) hypothesized that the prey location space for this type of predator could better be explained as a probability space rather than the boundary of the visual capabilities previously suggested by Browman and O'Brien (1992). The probability space is a succession of probability areas with the closest one being the one where the prey location probability reaches its maximum (Coughlin, 1993). The ability of a larval fish to detect a prey directly at the front of its head depends on the existence of an overlap of the visual fields of its two eyes (Coughlin, 1993). While analysing the pursuit sequences of whitefish larvae, we observed that these larvae seldom swam backward while orienting toward the prey before aiming at it. This result might suggest the existence of a limited perception area just in front of the snout of this larval species. Support for this hypothesis is given by the absence of binocular vision in larval fishes from the Coregoninae subfamily (Braun, 1978).

Blueback herring (*Alosa aestivalis*) and herring (*Clupea harengus*) have been shown to mostly attack their prey from below (Janssen, 1981; Thetmeyer and Kils, 1995). Coughlin (1993) also reported that clownfish larvae detected more prey items in the upper half of their perception field. Our results, showing that *C. lavaretus* larvae always aimed and attacked their prey from below, suggest that whitefish larvae have developed the same foraging mechanisms as these planktivorous predators. One should expect that efficient planktonic foragers have evolved toward mechanisms allowing them to detect prey items without being seen. Previous studies which investigated the benefits of searching and attacking the prey from below discerned different advantages for this strategy. On the one hand, planktonic organisms have higher contrast with the background and are more conspicuous when observed from below (Thetmeyer and Kils, 1995), especially when they are located outside the Snell's window (Janssen, 1981). On the other hand, the predator is hidden to its target prey when located below it (Thetmeyer and Kils, 1995). Finally, approaching from below could be a strategy of the predator to avoid casting a shadow that might warn the prey. In fact, rapid decreases in light intensity are known to trigger escape responses in copepods (Buskey and Hartline, 2003).

The results obtained in both Exp1 (0.29) and Exp2 (0.46) suggest that *C. lavaretus* larvae have a relatively low capture success rate. Low capture efficiencies ranging from 0.03 to 0.21 were also reported for early larval stages of other species of the genus *Coregonus* (Braun, 1963 in Drost, 1987) fed on mixed zooplankton. Indeed, when a larval fish shifts to external

feeding it has not yet fully developed optimal feeding abilities and its capture success could therefore be low (Rao, 2003).

> FEEDING KINEMATICS

The positive correlation between the SS and the FD for both Exp1 and Exp2 (Table II) could represent a strategy used by the predator to overcome the drawbacks of a longer strike distance associated with an increased risk of being detected.

Only Exp2 showed significant correlations between FD and ES, in fact for Exp1 the positive trend was weak (Table II, $P = 0.052$). However, it is worth noting that the fixation distance and the escape presumably occur in different planes, whereas our estimations, which are only projections on the vertical plane, underestimate the distances and speeds taking place in a different plane. As a general trend, although not statistically confirmed for Exp1, these results point toward that farther strikes are associated with faster escape responses of prey.

Hydromechanical perception of predators in copepods has been widely documented (Yen and Strickler, 1996; Kiørboe and Visser, 1999; Kiørboe *et al.*, 1999; Hwang and Strickler, 2001; Wagget and Buskey, 2007). It is also known that copepods can sense faster predators at a longer distance (Viitasalo *et al.*, 1998), and can adjust their escape response to the intensity of the mechanical stimuli (Heuch *et al.*, 2007). The positive correlation between strike speed and prey escape speed for reared whitefish larvae in this study supports these hypotheses and shows that the faster the larva is, the faster the escape response is.

We admit here the existence of a trade-off between the advantages of enhancing the strike speed (so as to decrease the strike duration and hence the risk of being perceived) and the disadvantages of diminishing it (in order to encompass the escape response of the prey). Accordingly, a successful snap should be quick enough to catch the prey off guard but not too fast in order to avoid eliciting an escape response. This balance can be achieved when the predator strikes on its prey from a closer distance (*i.e.*, short fixation distance).

> FACTORS GOVERNING THE CAPTURE SUCCESS

Differences in the predatory behavior were found between failed and successful strikes in both Exp1 and Exp2.

Comparison of the kinematics of failed *versus* successful attacks showed that successful events were characterized by a minor prey escape speed. We should note here, however, that only about 15% of captured prey elicited an escape response before being captured. This suggests that the fate of the prey probably depends on its ability to detect the predator rather than its ability to perform a successful escape response. As a result, the attack success of whitefish larva seems to be determined by events occurring upstream of the strike.

Viitasalo *et al.* (1998) and MacKenzie and Kiørboe (2000) attributed the capture success of fish larva to the ability of the predator to get within a strike distance close enough to the prey without triggering an escape response. This empirical observation was tested and confirmed by a mechanistic modelling approach (Caparroy *et al.*, 2000). Our study showed that a decrease in predator strike distance resulted in an increase of capture success for a planktonic predator. Our results, showing significantly higher fixation distances for failed strikes compared to successful strikes, corroborate the results of the above cited authors.

It has been documented that planktonic organisms may vary their path complexity in order to enhance their encounter rates (Coughlin *et al.*, 1992; Uttieri *et al.*, 2007a). The results of a simulation exercise comparing different search strategies by Uttieri *et al.* (2007b) implied that high fractal dimensions are more advantageous at high food concentrations, whereas less convoluted trails are enough when food is scarce. In this hypothesis an implicit assumption is that the escape responses of prey are the same for all search strategies irrespective of the search and/or pursuit's complexity. Although numerous studies on the mechanoreception capabilities of planktonic preys have been reported (Hwang and Strickler, 1994; Fields and

Yen, 1997; Hwang and Strickler, 2001; Burdick *et al.*, 2007), it remains unclear whether the complexity of the swimming path of a predator can influence the escape response of the prey. The present study supports that the contortion of the swimming path of European whitefish larvae is of primary importance to its capture success. In fact, for both of our experiments using wild larvae and reared larvae, low fractal dimensions values D were associated with success whereas high values of D were associated with failed events.

> LIMITATIONS OF THE APPROACH AND DATA

In our experiments, we recorded the projection of predator and prey paths on the vertical plane. Accordingly, all the distances and speed values of events not aligned parallel to the camera view were underestimated. To reduce such biases, MacKenzie and Kiørboe (2000) multiplied the average 2D distances and velocities by 1.225 to obtain 3D estimates. However, the shape of our experimental vessel, being 3 times larger than deeper, was designed to maximize the occurrence of events in planes not far from orthogonal to the camera axis and thus, to reduce the 2D biases.

As highlighted by Seuront *et al.* (2004b), most frequently used metrics in behavioral ecology are scale dependent. In other words we obtain a different value each time we change the time resolution. Keeping in mind that there is no particular scale at which these metrics can be precisely estimated (Seuront *et al.*, 2004b), we decided to contrast metrics of failed *versus* successful attacks, rather than trying to accurately estimate them.

While acknowledging the limitations of the approach and data provided by our experiments, we consider the videorecording approach to be a useful tool that can provide insight into the mechanisms acting at the individual scale. We want to emphasize that the results provided by our experiments can be viewed in a simplified context (*i.e.*, without turbulence) of whitefish larva – zooplankton interactions. Further research is therefore necessary to assess the mechanisms highlighted in this study at different levels of turbulence using different prey types and a three-dimensional video imaging technique.

CONCLUSION

Our study relied on both wild and reared larvae, which constitute the two components of the whitefish larvae stock in Lake Geneva. Although no direct comparison was made between the two groups, we could find no differences in the parameters involved in the capture success (*i.e.*, fixation distance and path complexity) of whitefish larvae. These results may serve as basis for further investigations required to elucidate the factors governing the feeding success of *C. larvaretus* larvae. Indeed, further works can be directed towards the reaction distance of planktonic preys available to whitefish larvae, and also the relationships between the swimming patterns of whitefish larvae and their prey. Such studies are needed to improve our knowledge of the feeding efficiency of whitefish larvae and may provide valuable tools to enhance the efficiency of commonly used techniques for artificial stocking of this species.

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