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Full Length Research paper

Predation patterns in heterobranchus longifilis Larvae: An analysis of their first exogenous feeding

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Two-day-old post hatch *Heterobranchus longifilis* larvae (4.06 ± 0.1 mm, 2.75 ± 0.06 mg and 0.35 ± 0.03 mm average standard length, weight and mouth width, respectively) were introduced into glasswares and exposed to a wide range of live zooplankton (prey size range: 42 to 876 µm) at a density of 2,944 individual/larva/day for 14 days. The 180 guts examined showed that food intake changed markedly with age and size. Larger preys were preferred as larvae increased in age and size. *Chilodonella uncinata* and *Lepadella ovalis* (size range: 42 - 125 µm) dominated the larval gut from day 2 - 4 post hatch. *Brachionus quadridentatus, Alona monachanta* and *Chydorus sphaericus* (225 - 346 µm) were predominant at days 5 and 6, while *Asplanchna priodonta, Bosmina longirostris* and *Daphnia ambigua* (485 - 876 µm) dominated from day 7 - 14 post hatch. Results from another 146 stomachs batch revealed that 2 to 4 day old post hatch fry preyed on larger prey (225 - 876 µm) at disproportionate mouth-width to prey ratio from 1: 1.2 to 2 when solely introduced and adequate. Initial recognition of prey by 2 - 4 day old larvae was longer but thereafter feeding became more voracious and intermittent with shorter resting periods compared with older larvae. Active feeding in *H. longifilis* larvae decreased with age while the length of feeding and rest period increased with age.

Key words: Prey selection, behaviour, *Heterobranchus longifilis*, exogenous.

INTRODUCTION

Fine- tuning of larval nutrition is important at the transition from endogenous to exogenous feeding in order to avoid high mortalities usually encountered during this first critical stage in larval life. Kimpe and Micha (1974) and Horvat et al. (1978) earlier identified this period as the next critical phase after spawning. Natural food is a prerequisite for early larval rearing of African catfish, *Clarias gariepinus* and *H. longifilis* (Msiska, 1981; Verreth and DenBieman, 1987; Villegas, 1990; Fermin and Bolivar, 1991; Kerdchuen and Legendre, 1994; Xi et al., 2002; Hagiwara et al., 2007; Ajah, 2008). Zooplankton always served as an important first source of natural food during intensive larval rearing of Atlantic salmon (Reinersten et al., 1984; Holm, 1985a and b; Holm, 1986), carp (Jana and Chakrabarti, 1993), two flat fish *Pleuronectes platessa* and *Limanda limanda* (Bels and Davenport, 1996), American shad (Johnson and Dropkins, 1996). *H. longifilis* (Kerdchuen and Legendre, 1994; Ajah, 1998; Ajah, 2008) brook charr (McLaughlin et al., 2000; McLaughlin, 2001), endangered fish golden bubblebee goodeid, *Allotoca dugesi* (Domínguez-Domínguez et al., 2002), Artic charr (Benhaïm et al., 2003) and whitefish (charal) (*Chirostoma riojai*) larvae (Morales-Ventura et al., 2004).

Survival during early fish larval stages depends largely upon the availability of appropriate prey. The paper seeks to elucidate the particular type and size of live food organism fish larvae/frys/fingerlings can swallow at any given stage of growth and development. These findings can be used to improve growth and performance of juveniles in rearing tanks.

MATERIALS AND METHODS

Prey selection and larvae nutrition

A total of 1,840 two-day old *H. longifilis* Val. larvae (average individual weight of 2.75 ± 0.06 mg, 0.4 ± 0.03 mm mouth width and 4.06 ± 0.06 mm standard length) raised in the Hatchery Complex of the Institute of Oceanography, University of Calabar, Calabar,

Table 1. Prey composition per aquarium per day (± s. d. of density in aquarium).

Species (size in µm)	Culture tanks density (org/L)	Density (org/aquarium/day)	Composition (%)
C. uncinata (40.3 × 23.1)	102	326,400	27.72
L. ovalis (93.6 × 70.3)	94	300,800	25.54
B. quadridentatus (432.9 × 128.7)	44	140,800	11.96
A. priodonta (685 × 356)	36	115,200	9.78
A. monachanta (392 × 231)	25	80,000	6.79
C. sphaericus (476 × 351)	24	76,800	6.52
B. longirostris (523 × 482)	18	57,600	4.89
D. ambigua (688 × 541)	15	48,000	4.08
E. gracilis (1240 × 300)	10	32,000	2.72
Total	368	1,177600 ± 108958.055	100

Source: Ajah 1995. N.B.The nutritional values of most live foods used in this study have been well researched and compiled by Hepher (1990). Consequently, analyses of their nutrient contents were not embarked upon.

Nigeria were used for this research. The first 1,200 larvae were reared in three 100 L rectangular glass aquaria (25 x 40 × 100 cm, respectively, for w × h × l) with netted inlet and outlet water pipes of 96 mm diameter. Each aquarium received 400 two-day old larvae at 50 larvae/L.

Flows through system were maintained throughout the experiment. Aeration at 4.5 ± 0.6 mgO_2L^{-1} was supplied via an air-blower of 1.5 horsepower (model: Siemens). The water level was kept at the 10 cm mark making room for 8 L of water per aquaria and the water flow rate averaged 45 ± 7.6 mls/s. Feeding was at 1,177,600 ± 108,958 mixed zooplankton/aquarium/day drawn from their monoculture tanks (three 10 m^3 circular tanks, 4 oblong 1 m^3 concrete tanks, 3 fibre glass tanks of 0.6 m^3 each and six 40 L glass aquaria). The larvae were fed with 2,944 ± 256 prey/larva/day given in two installments. These monocultures were developed in both the laboratory and semi-controlled outdoor tanks (Ajah, 1995) with mono species compositions as in Table 1. The zooplankton species compositions were standardized for three years (1992 - 1995) to ensure stability in composition (Ajah, 1995). Same results will be gotten at any time/year given same conditions and culture methods so long, there is no change due to cyclomorphosis and the culture organism's size remains the same.

Behavioural pattern during feeding

For closer observation of feeding behaviour a total of 40 *H. longifilis* larvae of various ages' vis-à-vis 2 - 4, 5 - 6, 7 - 10 and 11 - 14 days old were stocked at 10 larvae per 2 L Erlenmeyer flask. The flasks were placed in an illuminated culture cabinet lined with silver material (aluminum foil) (Ajah, 1995). A total of 29,440-mixed live zooplankton was put into each of the four flasks containing larvae of a particular age. Duration of feeding was monitored using a stopwatch. A hand lens was used in observing the opening of larval mouth during feeding. Further confirmations of feeding was by timely removal of all the larvae and dissecting immediately for gut examination.

Exposure to exclusively larger prey

Six aerated 2 L Erlenmeyer flasks kept in the culture cabinet were stocked with each of 2 days old *H. longifilis* larvae at 10 larvae/flask giving a total of 60 larvae/L is a total of 24 larvae. Mono species cultures of *Eudiaptomus gracilis* (1240 × 300 µm), *B. longirostris* (523 × 482 µm), *Physocypria inflata* or *A. priodonta* (685 × 356 m) were separately administered in two installments per day into the first four flasks to ascertain their acceptance as exclusively mono species prey. The remaining two flasks received a mixture of larger prey at same densities and feeding regime as above. Zooplankton counts were usually done using Sedgwick rafter (model: Ajah 001).

Predator-prey ratio

The predator: prey ratio was calculated by dividing the mouth width of the larvae by the length of the prey.

Gut analysis

Sampling was carried out everyday for 14 days on larvae fed on mixed live foods. A total of 180 randomly sampled larvae guts comprising 10, 15, 15, 40, 35, 10, 10, 8, 8, 5, 8, 8 and 8 each for days 2 to 14-post hatch/feeding, respectively, were examined.

Again, twenty randomly selected guts were examined from each of the 100 larvae exposed to mono species cultures in 4 flasks. Twenty six guts were examined from the two-mixed zooplankton flasks, composed of 2 -14 day old larvae exposed to mixed prey.

A total of forty guts were each examined when fed on the small and large prey. Ten guts were analyzed at day 2 and 15 each at days 3 and 4 with small prey. For the larger prey size 10 guts each were analyzed at days 7 and 8 while 8 guts each were analyzed from days 9 -14 except day 11 that only 5 guts were examined.

All examinations commenced few seconds when active feeding terminated. The fish caught were immediately dissected and the contents introduced into plastic containers. The contents were slightly diluted with borehole water.

Two drops of 4% formaldehyde solution was added to demobilize the organisms in the gut and latter examined after sedimentation using counting chamber (model: Ajah 001) with a light microscope at ×100 magnification.

The dominance, occurrence and numerical methods were adopted. The dominance method indicated the number of stomachs where each food item occurred as the dominant/main food item expressed as a percentage of the total food items. The numerical method gave the relative abundance of a particular food item in the stomach while the percentage occurrence indicated the number of stomachs each item was found over the total number of stomach examined.

Table 2. The sized ranges of food organisms consumed in percent at various larval ages and guts examined at each stage are represented.

Days 2 - 4	Days 5 - 6	Days 7 - 14
Small prey size: 42 - 125 µm	Large prey size: 225 - 345 µm	Larger prey size: 485- 876 µm
Composition (%)	**Composition (%)**	**Composition (%)**
*C. uncinata (*85)	*B. quadridentatus* (39.99*)*	*A. priodonta (*28)
*L. ovalis (*15)	*A. monachanta (*30) *C. sphaericus (*30)	*B. longirostris (*24)
		*D. ambigua (*47.5)
	Copepoda (0.01)	Copepoda 0.5%
Larval size: 4.06 - 6.0 mm s.l	Larval size: 6.1 - 8.0 mm s.l	Larval size: 8.1 - 15 mm s.l
Mouth width 0.4 - 0.6 mm	Mouth width 0.6 - 0.8 mm	Mouth width 0.8 - 1.5 mm
Total guts examined 40	Total guts examined 40	Total guts examined 73

RESULTS

Prey selection and larval nutrition

When *H. longifilis* larvae were exposed to adequate quantities of properly mixed zooplankton species as shown in Table 1, gut anaylsisi revealed that within the first 3½ days post hatching, results indicated that initial concentration of feeding was on smaller food organisms- ciliates like *C. uncinata* and rotifer (*L. ovalis*), with *Chilodonella* being more consumed (85%) than *Lepadella* (15%) (Table 2).

By the eve of the 4th day, they have started shifting to large rotifers- *B. quadridentatus* (40%). A few stomachs containing copepod had not more than one copepod each.

Towards the end of the 6th day, further consumption of the largest group of zooplankton types present in the mixture was observed. Most stomachs predominantly comprised rotifer- *A. priodonta* (28%), Cladocera- *D. ambigua* (48%), *B. longirostris* (24%) while up to two copepods was observed in only two of the guts examined.

Behavioural pattern during feeding

When the larval feeding behaviour was monitored, using 2 L Erlenmeyer flasks, the following findings were made:

It took the younger larvae (2 - 4 days old post hatch) longer time (average of 1½ min) to notice/sense their prey organisms but thereafter, fed more voraciously and incessantly, allowing shorter resting intervals (5 - 10 s) in-between meals. Active feeding lasted for average of 30 s. Quite terrific wagging of the tail and body movements as well as very rapid movements was observed during this period. Older fish larvae (5 - 6 days old) recognized their prey within 60 s of introduction. They fed for 5 - 7 min on the average and rested for 10 - 15 s. Fish larvae of 7 - 14 days old post hatch with average standard length 13 ± 0.2 mm jumped on their prey with the fastest rapidity (5 - 10 s) following introduction of prey. Duration of feeding ranged from 22.5 - 31 min and period of rests increased to 2 min. At this stage, traces of real competition were observed. Larvae upon the slightest confrontation by the other changed location and continued feeding.

Predator-prey ratio

Based on the findings in Table 2, predator: prey mouth width (mw) ratio of 2 days old larvae (mw = 0.4 mm) fed large prey was 1: 0.5 to 1: 0.86. When larger prey, like *A. priodonta, B. longirostris, D. ambigua and E. gracilis were* introduced, the ratio increased from 1: 1.2 to 1: 2.2. Difficulty in swallowing this larger prey increased with the presence of appendages as in *E. gracilis,* although the high population densities of prey created room for a sizeable number to be caught though quite often by chance.

The Ostracods were rather evasive. They aggregated at the edge of the aquarium until pursued out by the predators. As soon as they are scattered, their chances of being preyed upon increased. However, this evasion was not possible when round bottom 2 L Erlenmeyer glass flasks were used. It was much easier to lay hold on the Cladocerans than either the Copepoda or Ostracoda. *A. priodonta* besides its very large size, its rotator/folding habit and the speed at which it does this, made it more difficult to catch.

Exposure to exclusively larger prey

The introduction of larvae during its most active stage (2 - 4 days old post hatch, Figure 1) into a pool of only larger zooplankton species such as cladoceran (*B. longirostris, D. ambigua)* copepoda (*E. gracilis*), ostracoda (*P. inflata* etc.) and rotifera (*A. priodonta*) left the fish larvae with no other choice than to prey on these larger prey.

Examination of the 26 guts via the numerical method for 2 days post hatch indicated the presence of the following prey per gut within ten minutes of feeding:

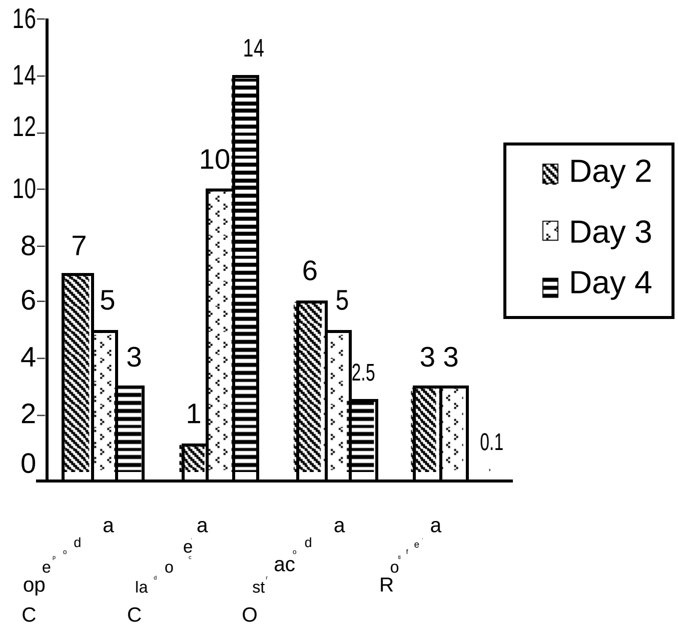

Figure 1. Average prey composition per *H. longifilis* gut upon exposure to only large prey. The numbers of samplings were: 12, 8 and 6, respectively, for days 2, 3 and 4 post hatch.

average of 7 copepoda (4 cyclopoids, 2 harparticoids and 1 nauplius), 1 cladoceran, 6 ostracoda and 3 rotifera (Figure 1) . The 3rd day post hatch witnessed 5 copepoda, 10 cladoceran, 5 ostracoda and zero rotifera per gut while 3, 14, 2 and 0, respectively, were observed during day 4-post hatch.

DISCUSSION

Prey selection

According to Visser (1982), (1) preference for the more popular prey increases when the total prey density increases, (2) preference for the relatively scarce prey increases when the total prey density increases. Diet shift from zooplankton to benthic invertebrates was not due to reduced zooplankton availability, but was instead related to changes in gill raker structure (Qin and Fast, 1997).

Milinski (1982), feeding three-spined sticklebacks with *Daphnia* showed that more successful competitors concentrated on large prey, whereas the poorer competitors fed as generalists but not unselectively. Holm (1987) did not notice any significant size selection in salmon when *Bosmina* was the main prey item. Knight (unpublished data) advised that large food granules should be fed at the early fingerling stage but an admixture of the smallest granules is advisable if a tank still contains very small fish fry. An admixture of the various prey sizes in adequate proportions gave preference to the smaller prey as starter diet by *H. longifilis* larvae. Holm (1987) stated that depending on the fish size, salmon selected different food types on days 40.

Upon exposure of *H. longifilis* larvae to adequate quantities of properly mixed zooplankton species within the first 3½ days post hatching, initial concentration of feeding was on smaller food organisms-ciliates like *C. uncinata* and rotifer (*L. ovalis*), with *Chilodonella* being more consumed (85%) than *Lepadella* (15%).

Between days five and six there is a complete shift to large rotifers like *Brachionus* (40%) and cladocerans like *Alona* (30%) and *Chydorus* (30%). By the end of the first week to that of the second week basically, larger cladocerans prey sizes such as *Daphnia* (48%) and *Bosmina* (24%) and *Asplanchna* (28%), a rotifer plus a few copepods (0.5%) were consumed. Hurst and Conover (2001) found out that the diets of young- of-the-year striped bass (*Morone saxatilis*) captured in winter were dominated by gammarid amphipods and shrimp species with generally higher consumption in early winter than late winter.

Behavioural pattern during feeding

Fish larvae naturally prefer smaller prey organisms at first few days of post- hatch unless exposed to solely large prey from the start. Smaller prey is preferred to larger prey by small larvae when the prey is dense and mixed.

The first recognition of the prey by younger larvae (2 - 4 days old) is usually longer but soon after begins more voracious and intermittent feeding with shorter resting periods. Larger fish juveniles recognize and capture its prey within a much shorter time, spend longer time during feeding and resting. The incessant feeding tendency coupled with shorter resting periods could be attributed to higher metabolic rates often noticed among younger organisms.

It took the very young larvae (2 - 4 days old) longer time to detect the presence of food due to incomplete development of the gustatory and chemoreceptor organs but become much more voracious thereafter. The much older (7 - 14 days old) were more sporadic in capturing their prey, fed for longer time intervals and also rested for longer time than the younger (5 - 6 days old) and the youngest (2 - 4 days old).

Clearly, multiple levels of selection and signaling are operating visual and size selection, free amino acid feeding signals, but also further signals such as spit out signals. Holm and Walther (1988) indicated that both the high spit- out rate of depleted daphnids and the positive response to *Daphnia* extract explained the importance of taste during the early feeding of Atlantic salmon.

Predator-prey ratio

Based on the findings in Table 2, predator: prey mouth width (mw) ratio of 2 days old larvae (mw = 0.4 mm) fed large prey was 1: 0.5 to 1: 0.86. When larger prey, like *A. priodonta, B. longirostris, D. ambigua* and *E. gracilis* were introduced, the ratio increased from 1: 1.2 to 1: 2.2. Difficulty in swallowing this larger prey increased with the presence of appendages as in *E. gracilis*, although the high population densities of prey created room for a sizeable number to be caught though quite often by chance.

The Ostracods were rather evasive. They aggregated at the edge of the aquarium until pursued out by the predators. As soon as they are scattered, their chances of being preyed upon increased. However, this evasion was not possible when round bottom 2 L Erlenmeyer glass flasks were used. It was much easier to lay hold on the Cladocerans than either the Copepoda or Ostracoda. *A. priodonta* besides its very large size, its rotator/folding habit and the speed at which it does this, made it more difficult to catch..

Exposure to exclusively larger prey

H. longifilis larvae do go for excessively large food organisms (*A. priodonta, B. longirostris, D. ambigua* etc.) in comparison to its mouth width provided such is in slow motion, attractive and abundant. While larval shad mainly consumed copepods (37.7%) and cladocerans (37.4%), juvenile shad ate chironomids (43.1%) and ostracods (28.4%) both thus, exhibiting diet variation in diet composition and feeding periodicity (Johnson and Dropkins, 1996).

Brodeur (1998) while working on juvenile pollock (*Theragra chalcogramma*) observed general selection of larger prey sizes relative to what was available. Consequently, as predator size increased, choice of prey skewed towards the bigger prey. Brodeur (1998) observed a general increase in prey width with increasing predator size while Qin and Fast (1997) observed that at both the laboratory and field trials, snakehead diets changed as fish size increased. Ware (1973) has shown that motion of prey increases the reactive distance of trout to their food. Aloo and Dadzie (1995) noticed a switch to crayfish and fish at comparatively smaller length-class while absence of zooplankton from the diet might be due to the small sample size of the juvenile bass.

Ajah (1998) found out that the larvae fed on copepod alone from days 4 post hatch did not grow since they were unable to capture their evasive prey. However, such evasiveness was very pronounced due to paucity of prey organisms (480 individual copepod/larva/day).

When the concentration of this supposedly evasive prey (Holm, 1985b; Ajah, 1998) was increased in this experiment during days 2 - 4 post hatch to 2,944 individual copepod/larva/day, larvae were able to capture up to seven copepods within 10 min of feeding and then grew. Storebakken (1985) reported that Atlantic salmon in nature select food items according to high occurrence and not, for example, in accordance with the nutritional appropriateness such as the protein: lipid ratio found to be optimal in aquaculture. Holm and Moller (1984) showed that food selection in salmon yearlings was influenced by occurrence, high occurrence allowed size selection. Visser (1982), working with three-spined sticklebacks, found that preference for the preferred prey (*Daphnia*) increases when the total prey density increases. Morales-Ventura et al. (2004) stated that survival during early fish larval stages depends largely upon the availability of appropriate prey.

Larval behaviour and prey capture

McLaughlin et al. (2000) examined the prey capture success of recently emerged brook charr (*Salvelinus fontinalis*) foraging in shallow, clear and still- water pools, and found that fewer than 42% of attacks ended with ingestion either because of difficulty distinguishing suitable prey from unsuitable items or because of difficulty capturing evasive prey. Probabilities of capture upon attack and ingestion upon capture depended upon where attacks were directed in the water column, the fish's level of activity at the time of attack, its fork length and the sampling date. In general, success was higher for larger, sedentary fish attacking prey in the lower portion of the water column than for smaller, active fish attacking prey at the water surface. Bels and Davenport (1996) made a comparison of food capture and ingestion in juveniles of two flatfish species, *P. platessa* and *L. limanda* and found relatively minor differences between species, but plaice captured and transported food more quickly than dab.

The low water depth reduced the energy loss by the larvae in search of food and enhanced the aggregation of the diet (Ajah, 1997). Vivekanandan (1976) earlier reported that the depth of the water column influences the food intake of air-breathing fishes. The frequency of items attacked was only a moderate predictor of the frequency of prey ingested.

Poor capture success is an important aspect of the early life history of brook charr in particular and probably of young salmonines in general. The ostracods were rather evasive. They aggregated at the edge of the aquarium until pursued out by the predators. As soon as they are scattered, their chances of being preyed upon increased. However, this evasion was not possible when round bottom 2 L Erlenmeyer glass flasks were used. It was much easier to lay hold on the cladocerans than either the copepoda or ostracoda. *A. priodonta* besides its very large size, its rotator/folding habit and the speed at which it does this, made it more difficult to catch.

Job and Bellwood (1996) indicated that visual acuity of *Premnas biaculeatus* larvae improved substantially between early feeding (days 3 post-hatch) and the pre-settlement (days 10 post-hatch) larvae. The prey capture success with rotifers ranged from 96% at 3 days post-hatch to 100% at 10 days post-hatch. *H. longifilis* fish larvae recognized their prey faster with age and fed and rested longer with age. At older stage, traces of real competition were observed. Larvae upon the slightest confrontation by the other changed location and continued feeding.

Domínguez-Domínguez et al. (2002), larval feeding behaviour of the endangered fish, *A. dugesi* on three zooplanktonic preys, viz. *B. calyciflorus* (Pallas), *Moina macrocopa* (Goulden) and *D. pulex* (Leydig) showed that capture success (capture/attack) ranged from 0.80 - 0.98 with *Brachionus*, 0.72 - 0.94 with *Moina* and 0.17 - 0.46 with *Daphnia*. Prey preference experiments were conducted using *B. calyciflorus, M. macrocopa* and *D. pulex* at a fixed ratio of 5: 2: 2 ind. mL^{-1}, respectively and revealed a positive selection for rotifers and *Moina*, but avoidance of *Daphnia*.

The abundance of food at all times eliminated all forms of competition and/or cannibalism. Each fish larva rose from rest to find more than enough to feed upon. Some were lured to feed by the body movements/feeding habits of others.

Feeding was not continuous, since each larva, fry or fingerling needed periods of rest, which increased as larval size increased. Live zooplankton is preferred to dry feed (Holm, 1987; Ajah, 1997, 2008; Hagiwara et al., 2 007).

Benhaïm et al. (2003) young arctic charr, *S. alpinus*, shortly after the onset of exogenous feeding, large fish (0·11 - 0·14 g) were more active and fed mainly from the water surface. Small fish (0·06 - 0·09 g) moved less and made fewer foraging attempts. McLaughlin (2001), behavioural diversification in brook charr (*S. fontinalis* Mitchill) foraging in still-water pools along the sides of streams exhibit conspicuous variation in foraging behaviour. Some charr are sedentary and eat crustaceans from the lower portion of the water column. Others are mobile and eat insects from the upper portion of the water column.

In conclusion, *H. longifilis* larvae select food when exposed to a wide range of properly mixed prey and generally will prefer the smaller as first exogenous food. Where only large preys are available, it can still commence preying on such up to a disproportionately predator: prey mouth-width ratio of 1: 1.2 and above, provided the prey was introduced early enough and in large amount. Thus, *H. longifilis* larvae could be start-fed with large food organisms like copepods, ostracods and cladocerans provided that preys are introduced in large quantities from days 2 - 4 post hatch being the most active stage. At the end of days 4, fish larval activity and motivation by hunger slightly reduces and consequently attraction to food reduces if not fed within the period.

The younger larvae do not easily recognize its prey but as soon as prey presence is established, feeding is more voracious, incessant with very short resting periods in comparison to older larvae.

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