

Feeding behaviour and prey size selection of gilthead seabream, *Sparus aurata*, larvae fed on inert and live food

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Abstract. Prey selection shortly after the onset of feeding by laboratory-reared gilthead seabream, *Sparus aurata* L., larvae was studied using larvae fed on two types of microcapsule (hard- and soft-walled) having diameters ranging from 25 to 300 μm . Preferences between inert food and live prey (rotifers and *Artemia* sp. nauplii) were also studied. Seabream larvae were able to ingest inert food from first feeding. Larvae of all size classes ingested hard microcapsules with diameters in the range 25 to 250 μm . However, larvae with a total length (TL) below 4 mm preferentially selected particles 25 to 50 μm in diameter, larvae of TL 4 and 5 mm preferred particles 51 to 100 μm in diameter, while larvae above 5 mm TL preferred particles 101 to 150 μm in diameter. With soft microcapsules, larvae always preferred particles larger than in the previous case, and above 4.5 mm TL they preferentially selected particles 201 to 250 μm in diameter. In addition, the gradual increase of preferred diameters with increasing TL was more pronounced when larvae were fed on soft particles. Mean values for prey width/mouth width ratios were approximately 0.24 and 0.30 when larvae were fed on hard-walled and soft-walled microcapsules, respectively, irrespective of the absolute value of larval length. When a mixed diet of live and inert food items was offered, live prey were always preferentially selected, even if the prey width/mouth width ratio was apparently not favourable. Only a physical constraint such as excessive prey width could counter this preference for living prey vs inert microcapsules. These results contribute to our knowledge in larval feeding behaviour, especially in the presence of inert food, and represent a fundamental step in developing prepared food for marine fish larvae.

Introduction

The gilthead seabream *Sparus aurata*, inhabits the Mediterranean Sea and North Atlantic Ocean (Bauchot and

Hureau 1986). This species is commercially cultured in Mediterranean countries, and the standard system for intensive larval rearing is based on living prey during the first weeks, usually rotifers (*Brachionus plicatilis*) and *Artemia* sp. Weaning occurs after the about the fifth week. As with other cultured marine fish species, a certain amount of research effort is focused on the replacement of live prey by inert food (Tandler and Kolkovski 1991).

Prepared diets have proved relatively successful in rearing freshwater fish from first feeding (Luczynski et al. 1986, Appelbaum and Van Damme 1988). For marine species, results are very limited but do show that some growth can be achieved when larvae are fed on an artificial diet alone (Adron et al. 1974, Barnabé 1976, Kanazawa et al. 1982, Appelbaum 1985). Generally, results with inert food were better when live prey were also given (Gatesoupe et al. 1977, Kanazawa et al. 1982, Szlaminska and Przybyl 1986, Ehrlich et al. 1989, Fermin and Bolivar 1991, Tandler and Kolkovski 1991).

The problems encountered with prepared food are related to the intrinsic nature of the inert particles (size, texture, digestibility, leaching of nutrients) and to the methods for administering them (culture technique), as well as to insufficient knowledge of the feeding physiology, nutritional requirements and behaviour of the larvae in the presence of such food.

The importance of prey size as a factor influencing first feeding and the efficiency of early growth is well documented (see e.g. reviews by Hunter 1981, Pascual and Yúfera 1987). Problems associated with the size of inert food particles have been described by several authors (Wankowski and Thorpe 1979, Knights 1983, Dabrowski and Bardega 1984). Particularly small particles cannot be easily detected by larvae, whereas very large ones can be difficult to ingest and may even promote a blockage of the digestive valve (Walford et al. 1991).

The importance of developing an inert food for marine fish larvae is obvious. With this aim in mind, the purpose of the present paper is to examine the feeding

behaviour of *Sparus aurata* larvae in the presence of non-living prey shortly after the onset of feeding. To achieve this objective we have determined prey size preferences of larvae by using microencapsulated inert food in order to avoid differences among prey other than size. Two different types of microcapsules have been tested separately in order to assess the effect of food hardness on prey size preferences. In addition, selectivity when both inert and living food is offered simultaneously has been studied.

Material and methods

Sparus aurata eggs were obtained through natural spawning from a captive broodstock kept at a constant temperature of $19.5 \pm 0.5^\circ\text{C}$ and a salinity of 33 g l^{-1} . Larvae hatched from these eggs were cultured in 300-liter tanks at the same temperature and salinity and under permanent light intensity (Polo et al. 1992, Yúfera et al. 1993). The initial stocking density was 35 to 50 larvae l^{-1} . Constant slight aeration was provided, and the oxygen level ranged between 4.8 and 8.8 mg l^{-1} . Rotifer *Brachionus plicatilis* and microalgae *Nannochloropsis gaditana* ($3 \times 10^5 \text{ cells ml}^{-1}$) were supplied from Day 3, from which time 10 to 15% of the seawater was replaced daily. From Day 14, *Artemia* sp. nauplii were added.

Selective feeding behaviour was studied in larvae ranging in length from 3.5 mm (first feeding) to 7 mm (20 to 25 d old), comprising seven length classes (3.51 to 4.00 mm, 4.01 to 4.50 mm, etc.). Two experiments were performed, the first with larvae fed on microcapsules alone, and the second with larvae fed on a mixed diet of microcapsules and living food.

Protein-walled microcapsules with diameters ranging between 25 and 400 μm were used as inert food. Two types of microcapsule with differing rigidity were tested separately: type A microcapsules were prepared with a hard wall and appeared rigid while type B were prepared with a soft wall and appeared deformable (based on UK patents 2200863 and 2103568, respectively). Frequency histograms of the diameters of both microcapsule types are shown in Fig. 1.

Two strains of *Brachionus plicatilis* with two different body sizes, strain S-1 (L-type) and strain Bs (S-type), as well as *Artemia* sp. nauplii, were used as living prey. The biometric characteristics of both rotifer strains (Yúfera et al. 1993) and *Artemia* sp. nauplii are summarized in Table 1.

Experiments were carried out in 2.5-liter beakers at a density of 20 to 30 larvae l^{-1} , slight aeration, permanent illumination (1000 lux) and a temperature of 19.5°C . Larvae of different ages were taken from the rearing tanks. Food was supplied at the start of the experiment. Larvae were fed on microcapsules *ad libitum* and, in the experiments with a mixed diet, live prey formed 10 to 30% of the total number of food items offered. After a period of 0.5 to 3 h, depending on larval age, larvae were removed and anaesthetized with ethyl-4-amino-benzoate for examination under a light microscope. Total length (TL) of each larvae was measured and gut contents were determined by measuring the diameter of any microcapsules present, as well as the number of natural prey in the case of mixed feeding. All experiments were performed in triplicate using larvae from different spawnings, and the data were pooled into the different larval size classes with between 20 and 70 larvae in each class by the end of the study.

Feeding selectivity was estimated by Chesson's α index (Chesson 1983):

$$\alpha_i = \frac{ri/pi}{\sum_{j=1}^m (rj/pj)} \quad (1)$$

where ri = percentage of a particular prey i in the gut in a mixture of m prey types, and pi = percentage of the same prey i in the environment. This index may vary from 0 to 1.

In the experiments with microcapsules alone and using the extremes of the range of the capsule diameters ingested in preliminary

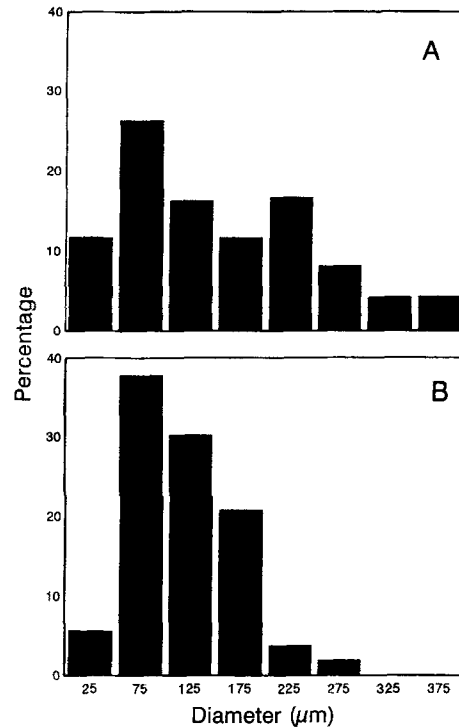


Fig. 1. Distribution frequency of diameters of the microcapsules offered in the experiments. (A) hard type; (B) soft type

Table 1. *Brachionus plicatilis* and *Artemia* sp. Length and width (mean \pm SD) of the living prey used in the experiments

Species	Length (μm)	Width (μm)
<i>B. plicatilis</i> Bs strain	140 ± 19	113 ± 17
<i>B. plicatilis</i> S1 strain	240 ± 28	156 ± 22
<i>Artemia</i> sp. nauplii	451 ± 29	176 ± 13

tests, six size classes of capsules were established (25 to 50, 51 to 100, 101 to 150, 151 to 200, 201 to 250 and 250 to 300 μm), with a preference for a given size occurring at $\alpha > 0.166$. The experiments with a mixed diet were carried out with hard-walled microcapsules, and only those microcapsules whose diameter had already been established as suitable for ingestion were considered in calculating α . In this case, with two prey types, the neutral value of Chesson's index was 0.5. Differences of the observed α from non-selective feeding were analysed using t -tests (Chesson 1983).

In addition, the relation between mouth width and larval length in the range 3.5 to 7 mm TL was determined. Mouth width was measured as shown in Hunter (1981) and the data were fitted by linear regression. Similarly, the relation between mean prey width in the gut and the corresponding larval length was determined by means of a linear regression. The ratio of prey width to mouth width (PW/MW) for a given larval length was extrapolated from the above regressions. To calculate the PW/MW ratio for living prey, the mean width of each type of organism was used because it was not possible to measure individual prey in the gut.

Results

Selective feeding by *Sparus aurata* larvae on inert particles is shown in Fig. 2. Larvae of practically all the size

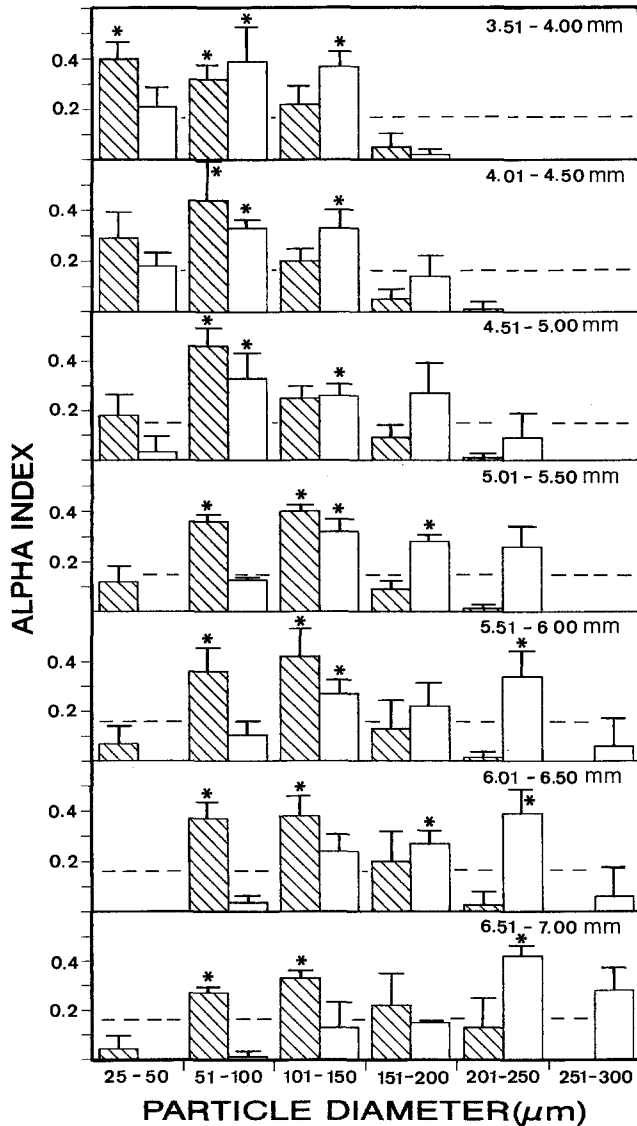


Fig. 2. *Sparus aurata*. Selection (α index) of different diameters of hard-walled and soft-walled microcapsules (hatched and open bars, respectively) by larvae of different size classes. Dashed lines represent the point of neutral selectivity ($\alpha=0.166$) with six classes of particle diameter. Vertical lines indicate magnitude of SD obtained from triplicate experiments. Asterisks indicate selection greater than neutral value ($P < 0.05$)

classes ingested microparticles within the range 50 to 200 μm . However, with increasing larval length a preference for increasing diameters of microcapsules was observed. In the case of hard microcapsules, larvae always positively selected particles between 50 and 100 μm in diameter (all $P < 0.05$), the selection of microcapsules larger or smaller than this varying according to larval length. Thus, larvae below 4.0 mm TL showed positive selection for particles with diameters $< 50 \mu\text{m}$, while larvae above 5.0 mm showed positive selection for particles with diameters between 101 and 150 μm . Finally, larvae above 6 mm TL tended to select particles 151 to 200 μm in diameter, although a non-significant difference from the neutral value was found, and these larvae ingested almost no particles smaller than 50 μm .

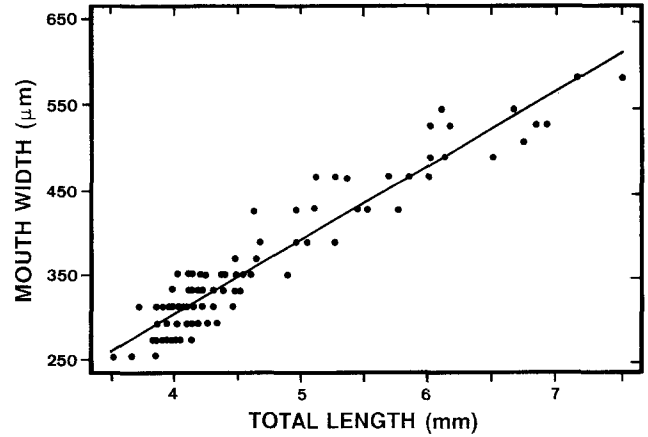


Fig. 3. *Sparus aurata*. Mouth width as a function of total length of larvae. Each data point represents a single larva

When fed on soft-walled microcapsules, larvae always selected larger particles than in the case of hard-walled microcapsules. In fact, larvae below 4.5 mm TL positively selected particles between 50 and 150 μm in diameter ($P < 0.05$), and above this length larvae started to select progressively particles in the range 151 to 200 and 201 to 250 μm , and from 6 mm TL they ingested without difficulty particles $> 250 \mu\text{m}$.

MW and TL of larvae were related according the formula:

$$MW = 44.542 + 87.635 TL; r = 0.952, n = 113, P < 0.001 \text{ (Fig. 3).} \quad (2)$$

The mean diameter of ingested particles increased with larval length (Fig. 4), and consequently with increasing mouth width. This increase was more pronounced in the case of soft particles (slopes significantly different ANOVA $P < 0.001$).

When a mixed diet of living prey and microcapsules was offered, a preference for living food was evident, the alpha index generally being ≥ 0.8 ($P < 0.05$; Table 2). This tendency was obvious with both rotifer strains from first feeding. However, *Artemia* sp. nauplii were ingested only by larvae above 4.5 mm TL, and they were positively selected by larvae above 5.5 mm TL. In this case of mixed diet, it is also interesting to remark that individual larvae showed differences in preferences, having a considerable proportion of larvae that showed exclusively one prey type, either living prey or microcapsules, within the gut (Table 3).

The PW/MW ratio decreased with increasing larval length in the case of living prey because a fixed value for the width of each prey type was used (Table 4). However, it is worth noting that this ratio stayed almost constant (approximately 0.24 with hard-shelled particles and 0.30 with soft-shelled particles) when larvae were fed on microcapsules alone and the mean diameter of particles in the gut contents was measured directly. Nevertheless, larvae were able to ingest particles with a PW/MW ratio varying from 0.1 to a maximum of between 0.8 and 0.6, depending on larval length.

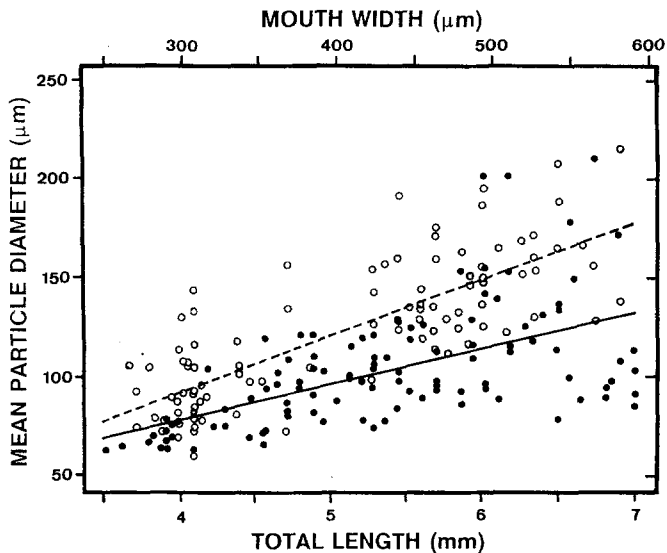


Fig. 4. *Sparus aurata*. Mean diameter (D) of ingested particles in relation to larval total length (TL). Hard microcapsules (filled circles and continuous line): $D=17.81 TL-7.24$; $r=0.566$; $P<0.001$. Soft microcapsules (open circles and dashed line): $D=28.38 TL-20.65$; $r=0.806$; $P<0.001$. For comparison, corresponding scale of mouth width values obtained from Fig. 3 has been included

Table 2. *Sparus aurata*. Values of α index (mean \pm SD of three replicates) for living prey in larvae fed with a mixed diet of microcapsules (MC) and live prey [*Brachionus plicatilis* strains Bs (Bs) and S1 (S1), and *Artemia* sp. nauplii (AN)]. $\alpha=0.5$ represents neutral selectivity with two prey types. Asterisks indicate selection greater than neutral value ($P<0.05$). TL: Larval total length

TL (mm)	Diet					
	MC+Bs		MC+S1		MC+AN	
	Mean	SD	Mean	SD	Mean	SD
3.5–4.0	0.88	$\pm 0.22^*$	0.75	$\pm 0.01^*$	–	–
4.0–4.5	0.89	$\pm 0.04^*$	0.83	$\pm 0.03^*$	0.0	–
4.5–5.0	0.91	$\pm 0.01^*$	0.88	$\pm 0.10^*$	0.29	± 0.41
5.0–5.5	0.95	$\pm 0.05^*$	0.83	$\pm 0.12^*$	0.45	± 0.14
5.5–6.0	–	–	–	–	0.75	$\pm 0.07^*$

Table 3. *Sparus aurata*. Percentage of larvae showing one prey type exclusively or a mixture of living prey and microcapsules in gut. Bs: small type *Brachionus plicatilis*. S1: large type *B. plicatilis*. AN: *Artemia* sp. nauplii. MC: microcapsules. LP: living prey. MC+LP: mixture of living prey and microcapsules

Diet	Gut content	Larvae length class (mm)				
		3.5–	4.0–	4.5–	5.0–	5.5–
Bs+MC	MC	11.3	41.4	10.5	10.0	–
	LP	59.4	41.7	28.1	25.0	–
	MC+LP	29.3	16.9	61.4	65.0	–
S1+MC	MC	55.7	36.7	24.3	33.2	–
	LP	27.3	27.5	41.4	28.6	–
	MC+LP	17.0	35.8	34.3	38.2	–
AN+MC	MC	–	100	87.5	63.9	51.4
	LP	–	0	6.3	12.2	24.3
	MC+LP	–	0	6.2	23.9	24.3

Table 4. *Sparus aurata*. Prey width/mouth width ratio of larvae when fed on microcapsules and living prey. TL: Larval total length; H: Hard-walled microcapsules; S: soft-walled microcapsules; Bs: *Brachionus plicatilis* strain Bs; S1: *B. plicatilis* strain S1; AN: *Artemia* sp. nauplii

TL (mm)	Prey				
	H	S	Bs	S1	AN
3.5	0.241	0.331	0.439	0.607	0.680
4.0	0.243	0.322	0.371	0.513	0.579
4.5	0.241	0.314	0.321	0.443	0.500
5.0	0.241	0.310	0.283	0.391	0.442
5.5	0.240	0.306	0.253	0.350	0.395
6.0	0.239	0.303	0.229	0.317	0.357
6.5	0.247	0.308	0.215	0.297	0.330

Discussion

The above results confirm that gilthead seabream can ingest microencapsulated feeds from the onset of exogenous feeding. The ability of *Sparus aurata* to ingest inert food was reported by Kentouri and Divanach (1982), and this ability has also been observed in other marine species, such as *Pagrus major* (Kanazawa et al. 1982), *Pleuronectes platessa* (Adron et al. 1974), *Plecoglossus altivelis* (Kanazawa et al. 1982), *Dicentrarchus labrax* (Barnabé 1976, Gatesoupe et al. 1977), *Solea solea* (Appelbaum 1985) and *Lates calcarifer* (Walford et al. 1991).

The progressive increase in body opacity, as well as the more rapid breakdown and disintegration of microcapsules in the gut with increasing larval age, restricted the maximum larval length in our experiments to about 7 mm (ca. 3 wk after hatching). This period was long enough to observe trends in prey selection in relation to size and hardness of prey. Thus, selection of the size of inert food by seabream larvae is a function of larval length, and more specifically of mouth width as was reported by Hartman (1958) and Shirota (1970) for other species feeding on natural prey. This change in size selection of living prey during larval growth has been described for several fish species (Detwyler and Houde 1970, Stepien 1976, Oozeki et al. 1992, Ghan and Sprules 1993), including *Sparus aurata* (Kentouri and Divanach 1986, Polo et al. 1992). From the start of feeding, larvae accept a wide range of particle sizes, but growing larvae prefer prey of a size much smaller than the maximum they can ingest and tend to maintain a constant relation between the diameter of ingested particles and the mouth width. This finding is in agreement with the results of other authors using other fish species (Wankowski and Thorpe 1979, Hunter and Kimbrell 1980, Knights 1983, Hasan and Macintosh 1992). Nevertheless, fish larvae also accept prey much larger than the preferred size when faced with a wide spectrum of natural prey (Hyatt 1979, Hunter and Kimbrell 1980, Kamler 1992). In the present study, seabream larvae ingested without difficulty particles with diameters up to 60–80% of the mouth width, and it is significant that, although such large prey represented only a small proportion of the total ingested items,

they accounted for a considerable proportion of the total biomass in the gut.

On the other hand, when live and inert food were offered simultaneously, larvae preferred living prey even though the prey width/mouth width ratio was not the preferred value expected from the trials with non-living prey alone. This preference could be, to a great extent, a consequence of pre-conditioning to living prey, but more specific experiments are required to confirm any interpretation because the high variability observed in the individual preferences (Table 3). Greater acceptance of living as opposed to inert prey has been observed by several authors working with different fish species (Barnabé 1976, Rösch and Appelbaum 1985, Ehrlich et al. 1989). In these studies, living prey probably appear more attractive or are more accessible. With respect to this last point, the present findings using particles of different hardnesses indicate that the characteristic of deformability is an advantage as far as ingestion is concerned. The importance of the structural characteristic of the food items was recognised by Hartman (1958) working with *Salmo gairdneri* fry fed on two different prey organisms, and more recently by Knights (1983) studying *Anguilla anguilla* fry fed on soft paste or a dry compound. It seems that, besides mouth width, the possible abrasive effect on the oesophagus of swallowing hard food items may also help to determine prey size preferences by fish larvae.

Obviously, a condition sine qua non for any organism to be a potential prey is the physical capability of the fish to catch and eat it. This is the reason why *Artemia* sp. nauplii were not ingested by larvae at first feeding but were eaten when the larvae had attained a given size. Once the physical constraint had been overcome, nauplii were positively selected, despite the PW/MW ratio not being optimal in terms of the preference shown for inert particles. It is interesting to note that only when above 4.5 mm TL were larvae able to ingest *Artemia* sp. nauplii ($176 \pm 13 \mu\text{m}$ width), this threshold corresponding to the length at which they begin to select soft microcapsules in the range 151 to 250 μm .

Villamar and Langdon (1993) working in larval shrimp demonstrated the usefulness of microcapsules for nutritional and energetic studies. Results on prey selection found in the present study as well as further data on ingestion rates obtained by us (Yúfera et al. in preparation) confirm the microcapsules as an important tool in behavioral and bioenergetic studies also in fish larvae.

In fish culture, current efforts to replace live food are based mainly on testing mixed diets, either using inert food as a supplement to live food, or using live organisms as a supplement to promote enzymatic activity (Kissil 1984, Tandler and Kolkovski 1991, Walford et al. 1991, Kamler 1992). Whatever is done, it is important to take into account the fact that if larvae preferentially ingest living prey even when these are present at a very low concentration in comparison to inert food, the larval maintenance ration of such living prey must not be surpassed if a correct assessment of inert diets is to be possible. Furthermore, individual larvae within a population show differences in preferences, some preferring live food, others inert food, some preferring large prey, others

small prey, all in the same experiment. Consequently, generalizations of growth and survival data could overestimate the true nutritional quality of the inert component of a diet.

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