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The onset of exogenous feeding in marine fish larvae

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Abstract

The onset of exogenous feeding in fish larvae can be considered as the period from which the ingestion is possible up to the moment when larval growth is detected. The main characteristic of this phase is that the source of nutrient and energy necessary to continue the larval development changes from the yolk reserves to the ingested food. To achieve this transition with success it is necessary that all structures and organs related with food uptake, digestion and assimilation are ready in due time and that the appropriate food is available. This review will focus on the most relevant processes during this short period of early life history of marine fish: gut anatomy, digestive capacities, feeding behaviour and metabolism.

At the opening of the mouth and anus the yolk is completely or almost exhausted. The gut is a simple tube histologically differentiated in foregut, midgut and hindgut. The pancreas, liver and gall bladder are functional. From the first moment of feeding the larvae are able to ingest, digest and assimilate food particles. The digestion starts in an alkaline environment with the contribution of pancreatic enzymes as well as cytosolic enzymes. The main limitations at the beginning of exogenous feeding are mouth gape, restricting the particle size and larval length, restricting swimming capacity and hunting success. After the opening of the mouth, the organogenesis continues. A quick growth and differentiation of the digestive tract is necessary to reinforce digestion and nutrients absorption. A few days later the larval length and jaw size have increased enough to allow a more effective predation.

Keywords: Marine fish larvae; First feeding; Digestive activity; Feeding behaviour; Energetics

Contents

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1. Introduction

The onset of exogenous feeding is a crucial moment in developing fish larvae. This stage has been associated with massive mortalities both in nature and in laboratory populations. After the exhaustion of yolk reserves, deprivation of food in nature (Hunter, 1981; Theilacker, 1986) as well as inappropriate food quality and feeding procedure in reared populations reduce remarkably the survival in the first days or weeks. Survival during the first days of feeding is highly variable depending on fish species, spawn quality, rearing procedures and age at which it has been recorded. For instance, survival values up to 82% in *Mugil cephalus* (Tamaru et al., 1994), 41% in *Gadus morhua* (Baskerville-Bridges and Kling, 2000; Puvanendran and Brown, 2002), 75% in *Dicentrarchus labrax* (Cahu et al., 2003), 91% in *Sparus aurata* (Yúfera et al., 2005), 85% in *Solea senegalensis* (Yúfera et al., 2005), 60% in *S. solea* (Palazzi et al., 2006), 46% in *Sciaenops ocellatus* (Brinkmeyer and Holt, 1998), 38% in *Melanogrammus aeglefinnus* (Hamlin and Kling, 2001) and 25% in *Hippoglossus hippoglossus* (Olsen et al., 1999), have been measured during the first few weeks after the mouth opening under the best rearing conditions. Survival can fall sharply when not all the feeding and environmental requirements are properly met. This is especially dramatic in the research of new species or new diets (Kaji et al., 1996; Fernández-Díaz and Yúfera, 1997; Cahu et al., 1998; Hamlin and Kling, 2001; Robin and Vincent, 2003; Papandroulakis et al., 2005; Yúfera et al., 2005).

The understanding of the early ontogeny of digestive functionality as well as of the nutritional and environmental requisites for triggering properly the coordinate series of hormonal and digestive processes occurring in this sensitive period is of primary importance in designing inert feeds for first feeding larvae. The start of feeding can be considered as the period from which the ingestion is possible up to the moment when larval growth is detected, in some cases when the moment for irreversible starvation has been attained. The main characteristic of this phase is that the source of matter and energy necessary to continue the larval development changes from yolk reserves to exogenous feeding. To achieve this transition with success it is necessary that all structures and organs related with food uptake, digestion and assimilation have to be ready in due time and the appropriate food be available.

This review focuses on the key aspects related with the acquisition of nutrients of external origin during this short period of development in marine teleosts. Most of the available information about this transitional stage has been obtained from laboratory experiments in species with interest for aquaculture. Such information is still relatively scarce and patchy in comparison with embryo and growing larval stages.

2. Valid period for start feeding

Before first feeding, the yolk is utilised for the embryo development with an efficiency characteristic for each species (Bagarinao, 1986; Arul, 1991; Parra and Yúfera, 2001). There are other factors affecting the yolk absorption rate and the conversion efficiency into embryo tissues, such as the yolk amount at fertilization (depending on the maternal conditions) and the temperature (Howell, 1980; Polo et al., 1991; Buckley et al., 2000; Hardy and Litvak, 2004). All these circumstances determine the potential existence of a mixed endo- and exogenous-feeding period and the resistance to starvation and, in general, the readiness of larvae to the start the exotrophic life. The concept of point of no return (PNR) is associated to a critical stage with massive mortalities after the moment for first feeding. The moment for irreversible starvation is defined as the moment after which 50% of larvae cannot start to feed and therefore cannot survive even in presence of food. The period between the mouth opening and the PNR depends mainly on water temperature (McGurk, 1984; Arul, 1992; Dou et al., 2002, 2005) and larval length (Miller et al., 1988) ranging from 3 days in temperate waters to 20 days in cold waters approximately. Nevertheless, the anatomical and digestive structures start to be affected and degraded before the PNR is attained (Theilacker, 1978; Yin and Blaxter, 1987; Yúfera et al., 1993b; Gisbert et al., 2004a) and the larvae lose progressively the energy reserves available for swimming and predation. Therefore, a relatively short starvation period may induce deformities as well as permanent feeding and digestive problems that will seriously affect these larvae surviving beyond PNR (Gwak and Tanaka, 2001; Dou et al., 2002). Obviously, a nutrition limitation has consequences at any stage of the development but the resistance to starvation increased with larval age and length (Ehrlich et al., 1976; Miller et al., 1988).

Thus, the moment for irreversible starvation marks the end of the valid period for start feeding in the worst scenario, that is, food scarcity or individual disadvantage against larvae of the same cohort. Nevertheless, the ingestion in the last part of this period does not guarantee survival up to the juvenile stage. Contrarily, a short delay in start feeding does not seem to affect the anatomical structures and the capacity for growth and