

Influence of temperature on gonadal development of *Ruditapes philippinarum* (Adams and Reeve, 1850) with special reference to ingested food and energy balance

Marina Delgado ^{a,*}, Alejandro Pérez Camacho ^{b,1}

^a Institut de Recerca i Tecnologia Agroalimentaries, Centre de Aquicultura, Carretera del Poble Nou, Km 5.5. E-43540 Sant Carles de la Ràpita, Tarragona, Spain

^b Instituto Español de Oceanografía, Muelle de Ánimas s/n, E-15001 A Coruña, Spain

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Abstract

This study evaluated the influence of temperature on gonadal development in *Ruditapes philippinarum* under controlled dietary conditions, in order to distinguish between the effect of temperature alone and the associated effect of temperature on ingestion. The experiment was therefore divided into two groups: group L (at temperatures of 14 °C and 18 °C, with a daily ingestion rate of 470–550 µg organic weight of phytoplankton per g clam live weight) and group H (at temperatures of 18 °C and 22 °C, with a daily ingestion rate of 1000–1100 µg organic weight of phytoplankton per g clam live weight). Both ingestion and respiration rates were calculated for each of the diets and temperatures. Gonadal development of the different groups of clams was monitored over the 70-day experimental period by means of image analysis techniques and calculation of the soft tissue dry weight of a standard clam.

Experimental results show that when the amount of food ingested is similar a difference of temperature between 14 °C and 18 °C, or between 18 °C and 22 °C, has no significant effect on the rate of gonadal development, the effect of temperature possibly being masked by the differences in the respective energy balances.

When a higher temperature coincides with a higher ingestion rate, as is often the case with naturally-occurring populations of bivalves, then gonadal development is greater, and faster, at the higher temperature, although this is mainly due to the greater amount of food ingested.

When, in experimental (or environmental) conditions, a high temperature (18 °C) is associated with a low ingestion rate, a situation of negative energy balance arises, associated with a slow rate of gonadal development that takes place at the cost of the animal's energy reserves. When the temperature is reduced to 14 °C, there is a decrease in the ingestion rate and lower energy consumption, leading to a situation of positive energy balance. In these conditions gonadal development is slow and the surplus of available energy is, presumably, used to accumulate energy reserves, as is often the case during the stage of growth prior to the onset of gonadal development in many bivalves that inhabit geographical areas with noticeable seasonal variations.

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* Corresponding author. Tel.: +34 977745427; fax: +34 977714138.

E-mail addresses: Marina.Delgado@irta.es (M. Delgado), alejandro.perez@co.ico.es (A. Pérez Camacho).

¹ Tel.: +34 981205362; fax: +34 981229077.

1. Introduction

Seasonal fluctuations in environmental parameters determine to a great extent the reproductive cycle of bivalves. Temperature has traditionally been assigned a major role, although the existence of sufficient nutritional reserves in the animal or the abundance of food in the natural environment also play a major part in the evolution of the reproductive cycle (Sastry, 1970, 1979; Gimazane, 1972; Pérez-Camacho et al., 2003).

Environmental factors, by acting on the components of the energy balance equation (Bayne and Newell, 1983), determine the amount of energy that is available for reproduction and/or somatic growth, and can have a considerable impact on reproduction. Environmental stress can also limit energy reserves and lead to the adoption of strategies such as delaying the production of gametes or reabsorbing already formed gametes, designed to ensure the survival of the adult specimens at the cost of a reduced level of reproductive activity (Gagdil and Bossert, 1970; Callow, 1979).

Most studies that have evaluated the influence of environmental parameters on gonadal development of bivalves in the natural environment suffer from a temporal and spatial coincidence of factors such as temperature and food availability that make it difficult to study their separate effects. With specific reference to *R. philippinarum*, there is usually an *a posteriori* relation established between the environmental conditions (temperature, chlorophyll, salinity) and gametogenesis, spawning period or conditioning index (Holland and Chew, 1974; Beninger and Lucas, 1984; Laruelle et al., 1994; Xie and Burnell, 1994).

In the case of studies performed under controlled experimental conditions the effect of these environmental factors is not usually sufficiently well separated, their superposition masking the interpretation of the results and preventing the effect of each of the factors on the reproductive cycle from being evaluated independently. An increase in temperature speeds up most of the physiological processes, including clearing and ingestion rates as well as those for respiration and growth (Walne, 1972; Griffiths and Griffiths, 1987; Hoffman, 1983). This notwithstanding, in many studies of the influence of temperature on reproduction in bivalves the same amount of food is usually offered to the specimens, regardless of the experimental temperature, and ignoring the effect of temperature on the various physiological rates, in particular the rate at which food is ingested (Saucedo et al., 2001; Martínez and Pérez, 2003).

When experiments are conducted at a constant temperature the amount of food available conditions the

ingestion rate of bivalves. There is usually a direct relation between ingestion rates and the amount of food present in the water, as has been shown by several different studies carried out by our research group (Beiras et al., 1993; Albentosa et al., 1996; Pérez-Camacho et al., 2002; Delgado and Pérez-Camacho, 2002). However, what is commonly controlled in studies on the influence of the amount of food on reproductive cycles is the quantity of food offered, rather than the amount of food that the bivalves actually ingest (Muranaka and Lannan, 1984; Chaparro, 1990).

If the purpose of a study is to evaluate the effect of environmental factors on reproduction, then it is essential to control food ingestion and metabolic energy consumption, since these two parameters are the principal indicators of the amount of energy available for somatic and/or gonadal growth.

In accordance with the above, in the present study on the influence of temperature on the reproductive process of *R. philippinarum* it was proposed to study this factor on its own, eliminating the associated effect of temperature on ingestion. In order to do so, ingestion was controlled in our experiments, which were conducted at temperatures of 14 °C, 18 °C and 22 °C, and food availability was regulated to ensure that the ingestion of food by clams kept at the different temperatures remained the same, regardless of temperature. At the same time gonadal development was monitored by means of image analysis techniques and the calculation of soft tissue dry weight of a standard clam.

2. Materials and methods

2.1. Biological material

The clams (*R. philippinarum*) were gathered from a beach in the Ría de Arosa (NW Spain), with specimens measuring between 33 and 44 mm being selected for the purposes of the experiment. The initial average length of the clams was 36.3 ± 0.22 mm for experimental conditions 18L, 18H and 22H, and 38.8 ± 0.22 mm for experimental condition 14L.

2.2. Design and experimental conditions

The experiment was performed in 12 l plastic tanks, containing natural sea-water filtered through 1 µm in a flow-through circuit at a variable rate of l/hr, depending on the different ingestion rates. Water salinity was 33‰.

The aim of the experiment was to verify the effect of temperature on gonadal development over temperatures ranging between 14 °C and 22 °C, which are those

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