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Seasonal changes in carbohydrate metabolism and its relationship with summer mortality of Pacific oyster *Crassostrea gigas* (Thunberg) in Marennes–Oléron bay (France)

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Abstract

This paper investigates the biological responses of *Crassostrea gigas* under traditional culture conditions on a mudflat in Marennes–Oléron bay. Summer mortality has been regularly observed in recent years in oysters reared using “on bottom” culture conditions. The present study attempts to provide a better understanding of the mortality phenomenon through biological parameters. Classical ‘field parameters’ such as mortality and growth rates, and quality index (dry meat weight/dry shell weight × 1000) were monitored. Additional parameters, as biochemical composition of oyster meat and glucose incorporation capacity, were included as potential new bioindicators. The work highlighted a critical timing (May–June) preceding the summer mortality and characterised by an arrest in lipid synthesis and a decrease in carbohydrate content. During this period, growth (especially gonad maturation) either slowed down significantly or even stopped. The first mortality event occurred during a growth renewal period at the end of June. Short-term analysis (15 days) provided information to identify such responses which may indicate a physiological stress and demonstrating the need for further investigation. The seasonal food availability (estimated from chlorophyll *a* levels) did not facilitate the mortality understanding which occurred after water temperature went above 18–19 °C. Nevertheless, this study shows carbohydrate anabolism contributed in the physiological stress leading to mortality events.

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Keywords: *Crassostrea gigas*; Summer mortality; Maturation; Glycogen incorporation; In vivo; Glycogenolysis; Marennes–Oléron bay

1. Introduction

Oysters harvested from public fisheries have been consumed throughout the world for millennia, gradu-

ally becoming a product of “traditional” aquaculture, as in Japan where oyster-farming has been practised for more than 1000 years (Farley, 1992). In Europe, the Pacific cupped oyster *Crassostrea gigas* was introduced from Japan and Canada (British Columbia) during the early 1970s to replace the ailing *Crassostrea angulata*, and became the main oyster species

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produced in European waters (Grizel, 1996; Gouletquer and Héral, 1997). Meanwhile, this species has become the leading aquaculture product at the world-wide level (FAO, 2004).

Since the beginning of the 1960s, ‘abnormal’ episodes of *C. gigas* oyster mortality (mortality rate >30% of the population) have increased throughout the world (Mackin, 1961; Imai et al., 1965; Sinderman, 1976; Beattie et al., 1980; Perdue, 1983; Farley, 1992). Oyster production in Japan and the West Coast of the United States was particularly affected in the 1960s and 1970s by summer mortality events that destroyed up to 60% of *C. gigas* livestock (Glude, 1975; Koganazawa, 1975). ‘Abnormal’ mortality episodes have also occurred in recent years (Gouletquer et al., 1998; Cheney et al., 2000). While some mortality events are clearly of pathogenic origin (Beattie et al., 1980; Farley, 1992; Renault et al., 1995), others occurred during exceptional climatic conditions (Mackin, 1961). In contrast, the specific causes and physiological pathways behind summer mortality events have until now remained unspecified.

In France, where *C. gigas* has been cultivated since the early 1970s, significant mortality (>30%) occurred in 1976–1977 (Parache, 1989) and then in the 1980s and 1990s at various oyster-rearing sites: (1) Arcachon bay on the south-west coast of France (Maurer et al., 1986) in 1982–1983; (2) Marennes–Oléron bay in 1988 and 1993; (3) rearing sites in Brittany and Normandy in 1994–1995 (Gouletquer et al., 1998). In Marennes–Oléron bay, oysters reared using the traditional “on bottom” culture and deployed directly on the mud show higher mortality rates than oysters reared in plastic bags deployed off-bottom on iron tables (Soletchnik et al., 1999; Soletchnik et al., 2005). Oyster summer mortality commonly occurs during the maturation period (Mori, 1979; Perdue et al., 1981; Maurer and Borel, 1986). Mori et al. (1965) and Tamate et al. (1965) compared Onagawa and Matsushima bays where low-level and highly significant summer mortality occurred respectively. They concluded that the main cause of summer mortality, in eutrophic Matsushima bay, was over-maturation of oocytes with “physiological disorder and metabolic disturbance”.

A comprehensive research program, called MOR-EST, has been developed recently in France to address

the ‘Summer *C. gigas* oyster mortality’ syndrome, specifically focusing on the interactions between pathogens, host and environment. Among the various tasks, in situ characteristics of abnormal oyster mortality events are critical to develop further experimental works at the laboratory level.

Although *C. gigas* is produced in all traditional French oyster areas, its biochemical cycle has been well described mainly without mortality event, and only in Arcachon bay (Maurer and Borel, 1986), Marennes–Oléron bay (Deslous-Paoli and Héral, 1988) and Normandy (Heude-Berthelin et al., 2001). These authors showed the increase of lipids and concomitant reduction of carbohydrate during the vitellogenesis process (Arcachon and Marennes–Oléron bays), when carbohydrate remained at a higher level in Normandy. The biochemical cycle in bivalves shows glycogen storage activity during favourable trophic conditions, followed by mobilisation and conversion of these reserves during the maturation period (reviewed by Martin, 1966 and Walne, 1970 in Gabbott, 1975). This cycle was confirmed in the Pacific oyster *C. gigas* (Mann, 1979; Perdue et al., 1981; Deslous-Paoli and Héral, 1988), with a late utilisation of glycogen (ripe stage) compared to the mussel *Mytilus edulis* (maturation stage) (Maurer and Borel, 1986). Turnover of stored glycogen is correlated with the annual reproductive cycle and food availability (Gabbott, 1975; Ruiz et al., 1992; Mathieu and Lubet, 1993). Glycogen metabolism pathways are controlled by glycogen synthetase, hemolymph glucose concentration and feeding conditions (Gabbott and Whittle, 1986). Gabbott (1975) suggested that vitellogenesis takes place at the expense of stored glycogen reserves in the blue mussel *M. edulis*.

Glucose incorporation into glycogen was first studied in the flat oyster *Ostrea edulis* by Fando et al. (1972), who reported that gill or mantle tissues incorporated significantly more glucose than muscle tissue by a factor of 5. Lenoir et al. (1989) focused on vesiculosis cells of the labial palps in the blue mussel (*M. edulis*). Berthelin et al. (2000a,b) then adapted the glucose incorporation method to *C. gigas*.

As low glycogen content has often been implicated in oyster mortality events during the reproduction period, a detailed examination of the relationship between bioenergetical pathways and

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