Review article
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Environmental biology, life history traits and aquaculture of green ormer *Haliotis tuberculata*

Biologija okoliša, povijesne životne osobitosti i akvakultura petrovog uha *Haliotis tuberculata*

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ABSTRACT

Green ormer or European abalone is an ecologically and economically important mollusk that finds food in the marine ecosystem and is also a delicacy for humans. Therefore, numerous studies have been conducted on this species in order to cultivate it as successfully as possible in new habitats. Mollusks are affected by bottom trawling and seafood disturbance while seasonal variations in oceanographic factors also affect their physiology, stress responses, and survival. In this review, an overview of numerous studies on the distribution and influence of various ecological factors on this species is presented, along with a morphological description of green ormer. In addition, the factors that influence maturation, reproduction and growth, as an important part of the breeding process, are presented. Emphasis is also placed on the natural diet as well as the diet in breeding farms. The physiology of this species lists numerous factors that affect its growth, especially antioxidant stress. There are a considerable number of knowledge gaps in the history of ormer aquaculture, which are pointed out together with their solutions, providing the opportunity to expand the cultivation of this species.

Keywords: mollusks, aquaculture, morphology, physiology, growth

SAŽETAK

Petrovo uho je ekološki i ekonomski važan mekušac koji hranu nalazi u morskom ekosustavu, a također je i zanimljiva delikatesa za ljude. Stoga su na ovoj vrsti provedena brojna istraživanja kako bi se što uspješnije mogla uzgajati u novim staništima. Na morske mekušce utječu ribolov pridnenim kočama i uznemiravanje plodova mora, dok sezonske varijacije oceanografskih čimbenika također utječu na njihovu fiziologiju, reakcije na stres i preživljavanje. U ovom istraživanju dat je pregled brojnih studija vezanih uz rasprostranjenost i utjecaj različitih ekoloških čimbenika na ovu vrstu, te je dat morfološki opis petrovog uha. Osim toga, prikazani su čimbenici koji utječu na sazrijevanje, razmnožavanje i rast, kao važan dio procesa uzgoja. Drugi fokus bio je na prirodnoj prehrani ove vrste, kao i prehrani na uzgajalištima. Pri fiziologiji ove vrste navode se brojni čimbenici koji utječu na njezin rast, posebice antioksidativni stres. U povijesti akvakulture ukazuje se na nedostatke u znanju i njihova rješenja kako bi se petrovo uhu moglo uzgajati na novim područjima.

Ključne riječi: mekušci, akvakultura, morfologija, fiziologija, rast

INTRODUCTION

Green ormer *Haliotis tuberculata* (Linnaeus, 1758) is a member of the family Haliotidae, order Archaeogastropoda. The family Haliotidae has one genus (Haliotis) with 70 species (Geiger, 2000), but the green ormer is the only species of the family Haliotidae that is commercially harvested in Europe (Mgaya and Mercer, 1994). It is also an ecologically and economically important mollusk (gastropod) that finds food in the marine ecosystem and is also an interesting delicacy for humans (Cook, 2014). Due to environmental changes such as disease incidence and global warming, as well as overfishing, many species of the genus Haliotis have experienced population declines worldwide (Travers et al., 2009). Fishing for ormer has much less impact on populations of this species in Europe than in Asian countries. In France and Spain, their population has been overexploited, leading to a ban on fishing in 1973 (Mgaya and Mercer, 1994). Although significant resources have been invested in establishing and expanding farms throughout Europe, production has yet to be defined. Unfortunately, there are still some technical barriers to the production of viable juvenile ormer stages. The steady increase in abalone aquaculture production worldwide has generated increasing interest in the application of new technologies to green ormer for aquaculture as well (Mgaya, 1995). This review study outlines the basic characteristics of this species as well as the challenges and constraints to improving its production.

Distribution

Green ormer is distributed in the Mediterranean Sea and the North Atlantic region (from the Canary Islands to the English Channel) (Coleman and Vacquier, 2002; Mgaya and Mercer, 1994). Densities are highest at the northernmost end of its range (Clavier, 1992). It has a sizable abundance also in the Northern Adriatic (Topić Popović et al, 2021)

Juveniles and adults are usually found in waters up to 10 - 15 m (Mojeta and Ghisotti, 2003), on weed-covered rocks and boulders. Although migrations of several hundred meters through various substrates have been recorded (Werner, 1993), this species prefers solid bottom.

Ecological requirements

Green ormer is an economically and ecologically important marine species because it provides food sources for other species and contributes to the ecosystem balance. Organisms living on the bottom are strongly influenced by microclimatic conditions and water mass characteristics (Clark et al., 2020). Summer heat waves are considered the greatest threat to mollusks (Rodrigues et al., 2015). For ectothermic animals such as green ormer, temperature is the most important parameter affecting distribution. Maximum growth occurs at a temperature of 20 °C. They grow and feed less well at lower temperatures (Peck, 1989) and die when exposed to temperatures below 4°C for extended periods (LaTouche et al., 1993). Differences in salinity do not significantly affect population density. For example, they can tolerate brackish water areas (Fretter and Graham, 1962) with up to a 24‰ increase in salinity (Peck, 1983).

Morphology

The main feature of green ormer is a round, flattened and elongated ear-shaped shell that protects the soft body. The shell is perforated with 5-7 holes (Figure 1) up to 9 cm long and 6.5 cm wide (Avant, 2007), The color of the shell varies from red to grayish depending on the environment and the type of algae they eat. Wavy spiral ridges separated by furrows can be seen on the outside, marking the growth lines. The dorsal part of the large, muscular foot is surrounded by an epipodium covered with small sensory organs and tentacles (Graham 1988). Sensory organs and tentacles are located on the dorsal part of the large muscular foot. The mouth contains a toothed radula for crushing food. The conical appendage is a gonad that surrounds the digestive gland and is located in the posterior half between the shell and foot. The color of the abalone varies from green to grayish, with a curved foot (Briones-Labarca et al., 2012).

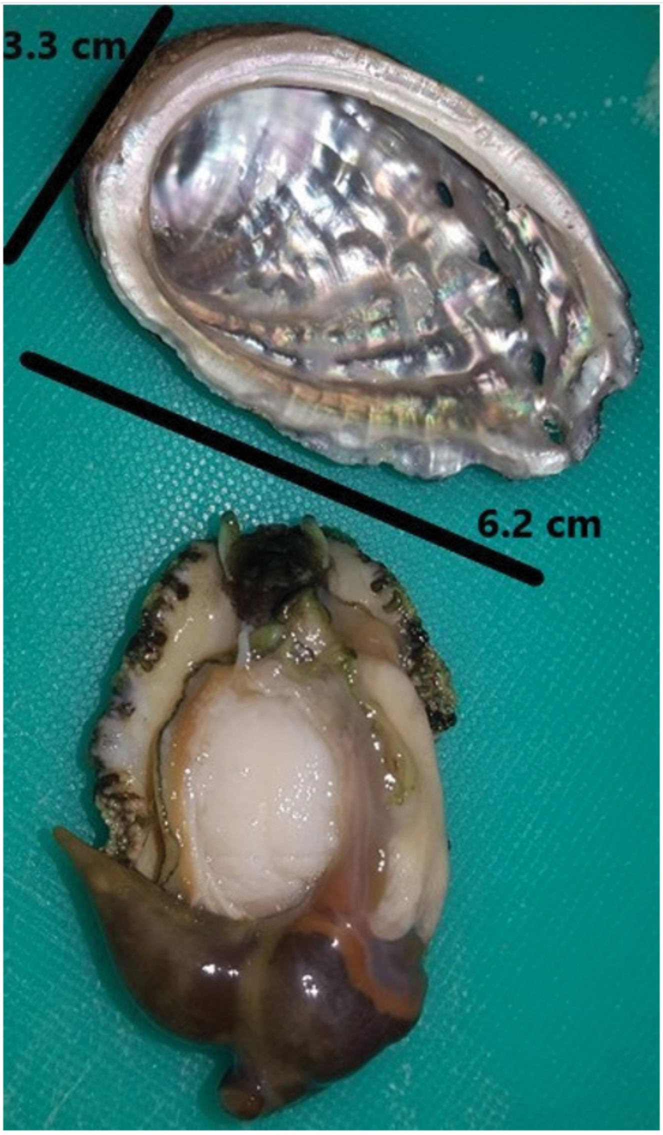

Figure 1. Green ormer from the Adriatic Sea (photo Krbavčić Jambrošić, M.)

Reproductive behavior

The pelagic-benthic life cycle of the green ormer makes it very sensitive to environmental changes, as it includes the larval planktonic stage and then the critical metamorphosis to a benthic juvenile (Byrne et al. 2011). Spawning and larval settlement occur during a short summer period between August-September. During this warm season, water temperature is near its maximum and water flow is reduced. Prince et. al. (1987) suggest that adult populations probably choose conditions of low water movement for spawning to reduce the dispersal of gametes and larvae. Green ormer has lecitho trophic eggs that are significantly heavier than water. The actively swimming juveniles are an integral part of the plankton. The plankton phase of this species is generally short, lasting only 4-5 days (Koike, 1978). Larval settlement is strongly influenced by temperature; the lower it is, the longer the transition to the benthic phase (Forster et al., 1982). Juveniles live in areas protected from prevailing tidal currents, but adults are also found in unprotected areas (Clavier and Chardy, 1989). Temperature most determines their behavior during spawning, as their reproductive peak is for a short period in late summer when water temperature reaches its maximum (Mgaya and Mercer, 1994).

Ormers are dioecious gonochoristic animals. The difference between the sexes can be seen in the conical appendage on the right side of the shell. The gonads are differently colored; males are cream or off-white with a greenish tinge, while females are usually dark green with various shades of gray-green. After spawning, however, the gonads of both sexes are cream-colored, making it impossible to distinguish between the sexes (Forster, 1962). There are also no differences between the sexes in the appearance of the shell. The timing of sexual maturity in the wild varies from place to place, but generally, males become sexually mature earlier than females and have a smaller shell size (Mgaya and Mercer, 1994). Both males and females release their gametes directly into seawater. Fecundity is very high, and it has been found that there is a linear relationship between carapace length and fecundity (Sluczanowski, 1986).

Age and growth

The diameter of an unfertilized egg is about 180 µm, while fertilised eggs have a diameter of 210 µm in diameter. The time required for the larva to hatch from the egg membrane depends on the water temperature and is about 13 hours at a temperature of 20 ± 1 °C. The embryo is classified as a trochophore larva when the stomodeum is formed and the cilia are fully developed along the prototrochal belt (Fretter and Graham 1964), when the apical region becomes flat and the velum is fully developed with long cilia. Trochophore larvae become veligers when the apical region becomes flat and the velum is fully developed with long cilia. This occurs within 35-41 hours after fertilisation. Veliger larvae begin settlement after four to five days and then immediately use a serrated radula to scavenge benthic biota. After three years, they reach a size of about 45 mm, indicating rather slow growth. Ormer live up to fifteen years or longer and reach a length of about 12.3 cm (Peck, 1989).

Feeding and habitat

Green ormers are herbivores and belong to a group of organisms called holobionts. They have a specific microbiota in their digestive system with catabolic abilities to break down complex food components. This has been well-studied in large terrestrial herbivores, but not in marine organisms. Green ormers feed primarily on red, green, and brown macroalgae, which contain a specific composition of complex polysaccharides and an epiphytic microbiota. Gobet et al. (2018) found that the digestive microbiota of ormers changes with a monospecific algal diet, with the microbiota in the digestive gland dominated by *Mycoplasma* and *Vibrio species*. Their distribution is related to an optimal supply of floating algae carried by the currents. The amount of such floating algae determines the ormer density where the habitat is suitable (Clavier and Chardy, 1989).

Their feeding and movement occur mainly at night and decrease with lower temperatures (Mottet, 1978). When they feed, they are usually inactive, waiting for drifting algae. The diet of juvenile ormers is encrusting coralline algae and associated epibiota. Adults prefer algae such as *Palmaria palmata*, *Delesseria*, *Griffithsia*, *Laminara* spp, *Ulva lactuca*, *Chondrus crispus* and *Enteromorpha intestinalis* (Mercer et al., 1993). Ormers can consume up to 39% of their weight in seagrass per day (Mottet, 1978).

The preferred habitats of green ormers are those that provide optimal footing to escape predators and movement by waves and sea currents. These are rocky sublittoral areas with numerous cracks and ledges in the rocks and especially the undersides of large rocks on sandy substrates (Forster et al. 1982). In such areas, they are well protected from predators and direct light.

Physiology

As mentioned earlier, temperature is the most important factor for most metabolic processes in green ormers. Outside their optimal temperature range, they adjust basic physiological functions to maintain their metabolism (Morash and Alter, 2015). At elevated metabolic demands, ormers may show signs of oxidative stress, produce reactive oxygen species (ROS) and activate antioxidant enzymes (Sokolova and Pörtner, 2003). The most important variables determinating their responses to the environment are temperature and oxygen (Topić Popović et al., 2021).

Assessment of their antioxidant capacity and lipid peroxidation, such as total antioxidant status (TAS) and formation of reactive thiobarbituric acid substances (TBARS), are valuable tools for biomonitoring (Deschaseaux et al., 2011). In addition, changes in superoxide dismutase (SOD) and glutathione peroxidase (GPx) activities in mollusks are biomarkers of antioxidant responses associated with oxidative stress caused by excessive ROS production during cellular metabolism (Vosloo et al., 2013). During their life cycle, changes in biochemical composition are also expected, mainly related to the specific requirements of gamete formation, spawning, and food availability associated with seasonal variations (Arranz et al., 2021). The content of fatty acids (saturated fatty acids - SFA, monounsaturated fatty acids - MUFA and polyunsaturated fatty acids - PUFA) and most individual fatty acids show seasonal changes in the tissues of other marine snail species (Mateos et al., 2010). Lipids are particularly important energy reserves of aquatic organisms (Arts et al., 2001).

They are the main source of energy for metabolism, an important material for the construction of cell membranes, involved in many biochemical processes, physiology, and the reproductive cycle of mollusks, and reflect specific seasonal biotic and abiotic changes in the environment in which the organisms are found (Pázos et al, 1997; Arts et al, 2001; Vance and Vance, 2002). In the assessment of stress and other pathophysiological changes, analysis of tissue biochemical properties and histopathological analysis of tissue are important factors that can provide information about on the degree of stress and metabolic, functional, and morphological tissue disturbances (Fazio et al., 2013). It is known that even trace elements (metals) in shellfish tissues are subject to seasonal variations. This may be related to diet, changes in the quality of sea currents or river inflows, the reproductive cycle, or changes in the size of individuals (Frías-Espericueta et al., 1999), and the same is possible in marine gastropods. Although all organisms require small amounts of essential elements for their physiological activities, metals such as arsenic, cadmium, mercury, or lead are not critical for metabolism and could be toxic to marine organisms and pose a potential risk to human health (Torres et al., 2020).

Green ormer uses calcium carbonate ($CaCO_3$) to make their shells and are among the invertebrates most affected by ocean acidification. Ocean acidification and associated changes in seawater carbonate chemistry threaten the survival of calcifying organisms. Aquatic organisms, such as the European abalone, are particularly sensitive to pH changes in their early development stages. This is particularly evident larval survival rates, which were significantly lower under acidified conditions in the experiment by Wessel et al. (2018). Acidification leads to an altered biomineral architecture, resulting in a more brittle shell. It is concluded that abalone metabolism is maintained at lower pH at the expense of shell growth and integrity, which may be a problem for aquaculture (Avignon et al., 2020).

Mass mortality of numerous organisms has been observed in aquaculture (Chang et al., 2005; Raimondi et al., 2002). In the case of green ormer, it was observed during the spawning season when sea temperature was above 17 °C and the bacterial pathogen Vibrio harveyi was present (Travers et al., 2009).

Aquaculture and knowledge gaps

Market demand for haliotids was increasing, so intensive research on their cultivation began in the 1990s (Mgaya and Mercer, 1994). Ormer production was 203 374 mt in 2019 (FAO, 2021), with China being the largest producer with 180 267 mt in 2019. The main species grown there are *H. discus hannai* and *H. diversicolor*. Other important producers include the Republic of Korea, South Africa (*H. midae*), and Australia (*H. rubra*, *H. laevigata*, and a hybrid of these two species) (Nguyen et al., 2022). Although production is increasing in many countries, there are still many problems that need to be overcome, such as abalone disease viral ganglioneuritis, slow growth, and high production costs, especially for juveniles (Wu and Zhang, 2016). Abalone is valued as a gastronomic delicacy and has been cultivated in Portugal and France since the early 2000s (Hannon et al., 2013; Lachambre et al., 2017; Roussel et al., 2019a).

As the demand for green ormer as food is constantly increasing and the supply from fisheries is questionable, the topic of cultivation of this species became more important. The main advantages of the ecological and profitable abalone aquaculture business are the minimization of effluents and the use of a local and cheap sustainable resource as feed (Troell et al., 2006). Cultivation of this species began as early as 1968 (WFA), and Koike (1978) conducted laboratory rearing of fertilized eggs to hatching. Hayashi (1982) succeeded in rearing juveniles up to one year of age. A marine rearing program (Flassch and Aveline, 1984) took place at an experimental farm in France. In Ireland, several laboratories were attempting to breed ormers. In Galway, the first and second generations of ormers have been successfully bred in a hatchery (Moylan and Mercer, 1993). There is also a program for marine rearing of ormers in cages (Hensey, 1993; Ward, 1993). Before spawning begins, adults must be exposed to elevated water temperatures. Individuals are ready to spawn after 89 days at 18 °C (Flassch and Aveline 1984).

Various techniques have been tried to promote spawning, e. g. heat shock (Flassch and Aveline, 1984), treatment of seawater with ultraviolet light (Hayashi, 1982), exposure of mature juveniles to hydrogen peroxide solution (Morse et al. 1977). For high quality fertilization, a sufficient sperm concentration of about 200 000 ml^{-1} is required, which is achieved by adding sperm to a known concentration of eggs in the spawning pool (Flassch and Aveline, 1984).

After fertilization of the eggs, the larvae are transferred to a tank containing corrugated PVC sheets lined with a thin layer of benthic diatoms (Moylan and Mercer 1993). Koike (1978) found that a flagellate, *Tetraselmis suecica*, was very effective as a supplemental food for the spawn. However, Moylan and Mercer (1993) reported that *T. suecica* is not always suitable because it is not a benthic microalga and coating lasts only a few days. At this stage of rearing, it is recommended that they be fed to finely chopped mixed algae (Koike et al., 1979; Mercer et al., 1993).

Further rearing to marketable size can be done by three methods: by rearing in a tank (on land), in marine cages above the ground, and in marine cages on the ground. A suitable location for marine rearing is critical (LaTouche et al., 1993). For both methods good water quality, fast water currents, high quality feed, and good protection from bad weather conditions are important. Depending ot the breeding strategy and availability of algae in natural environment, it may be interesting to feed abalone eith certain species of algae. A mixed diets allow for a good muscle development and growth results and should probably be preferred over a monospecific diet to avoid deficiencies in essential nutrients and high pressure on an algal resource (Roussel et al., 2019b). Ormers should be maintained at optimal densities when intensively cultured because stocking density is inversely proportional to growth rate (Mgaya and Mercer, 1994). The production cycle takes 3 to three and a half years for the stock to reach the market size of 65 mm shell length (Bossy, 1990).As this species has become increasingly economically important to European aquaculture, the commercial farming of *Haliotis tuberculata* has recently begun in Europe (Roussel et al., 2019b), hatcheries have been expanded and improved breeding programs were initiated. Roussel et al. (2010) note that the original genes of Atlantic populations could be used in selection programs, for example, for disease resistance. However, the European Mediterranean abalone, is not used for selection because of its small size. In addition to the differences in morphology between the Mediterranean and Atlantic populations, it was discovered that they also belong to a different genetic cluster.

CONCLUSION

Ormers can be so easily overfished that numerous regulations have been enacted to manage and conserve this resource. Ocean acidification could negatively impact larval recruitment and the persistence of abalone populations in the near future. To further increase the production of this species, it is important to study the effects of stress on abalone physiology. This would allow producers to adjust breeding while reducing stress, preventing mortality, and increasing production. In order to mitigate the effects of overfishing, abalone could become a promising aquaculture species in the Adriatic Sea and other fisheries exploited seas. However, it is always advisable to conduct marketing studies and cost analysis before starting farming, as their results can help optimize technical standards and production plans.

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