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A brief global agenda for advancing the study of molluscs

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Mollusca is the second largest phylum on Earth comprising more than 90,000 species. Molluscs are responsible for key functions and services in aquatic and terrestrial ecosystems. Despite their diversity and ecological and economic importance, several knowledge gaps exist concerning their basic biology. In this mini-review, I succinctly propose a new agenda for the study of molluscs for the next decade dividing it in four major topics that need urgent attention: knowledge shortfalls, monitoring at relevant spatial and temporal scales, conservation, and education and outreach. In this time of climate and biodiversity emergency, the study of molluscs and their conservation should be a priority and we cannot ignore their intrinsic and economic importance.

KEYWORDS

biology, conservation, ecology, education, human disturbance, shortfalls

Introduction

Mollusca is the second largest phylum on Earth, comprising around 90,000 species being up to 55,000 marine, up to 30,000 terrestrial and up to 7,000 freshwater (MolluscaBase, 2023). Molluscs are ubiquitous and can be found from the deep sea to the top of mountains playing a fundamental role in a wide range of ecosystem functions and processes (Vaughn and Hoellein, 2018; de la Chesnais et al., 2019; Floyd et al., 2020). They also provide a myriad of services vital to humans such as food, raw materials, purification of water, among others (Haszprunar and Wanninger, 2012; Michaelis et al., 2021; Zieritz et al., 2022). Despite their astonishing diversity and the important ecosystem services provided by molluscs, there are still considerable gaps in their basic biology. Fortunately, the opportunities to study them are increasing, even in regions of the planet (e.g., deep sea, caves, deep rivers and lakes) that were almost inaccessible until recent times (Haszprunar and Wanninger, 2012; Levin et al., 2019). At the same time, the myriad of molecular tools that are available nowadays, open a new frontier in different scientific fields, from taxonomy to conservation (Smith et al., 2012; Gomes-dos-Santos et al., 2020). New fields of research with high economic potential (aquaculture and food production) are also emerging because molluscs are considered a sustainable source of food with a low ecological footprint (Gephart et al., 2021). All these new advancements, plus the new challenges related to the increased human disturbance on ecosystems, will increase the future scientific and societal interest in this group of organisms and will open an incredible number of opportunities to study them. Here, I succinctly propose

a new agenda for the study of molluscs for the next decade dividing it in four major topics: knowledge shortfalls, monitoring at relevant spatial and temporal scales, conservation, and education and outreach.

Knowledge shortfalls

In the last decades, the scientific knowledge about molluscs increased steadily. According to Ponder et al. (2020), and until 2016, the Web of Science data reported a total number of 560000 items using the string “mollusc*”. Of the major molluscan classes, Gastropoda dominated the scientific productivity; followed by Bivalvia and Cephalopoda; all the other classes have a much lower number of publications. However, it should be noted that after 2002 the annual production of publications using bivalves supplanted those of gastropods. In the same vein, and when searching for keywords such as physiology, ecology, molecular and evolution we observe a dominance of physiological studies, followed by ecology, molecular and lastly evolution. Despite the huge number of studies published so far, there is a pressing need to cover the shortfalls that remain in relation to taxonomy, ecology, biogeography, physiology, genetics, evolution, among other key aspects (Lopes-Lima et al., 2021).

Taxonomy is the base for all the other scientific fields and an improper identification of organisms will lead to a cascade of conceptual and methodological errors and resulting flawed conclusions (Bortolus, 2008). Molecular tools can help resolve many of these taxonomic and systematic errors and there is place to an incredible acceleration in the number of studies dealing with taxonomy and evolution of molluscs in the near future (Smith et al., 2012). However, the use of these molecular tools (e.g., genomics) in molluscs is lagging much behind than other taxonomic groups, including other invertebrates such as arthropods (Gomes-dos-Santos et al., 2020). Anyway, these molecular tools cannot be seen as a panacea to resolve all problems, and classical expertise in taxonomy and systematics cannot be disregarded. In fact, the experience of a significant army of grey taxonomists should be urgently passed to the younger generations. For this, the investment (and recognition of their work) in personnel and curators employed in museums, universities and other institutions should increase and a much higher cooperation between taxonomists and other scientists working in different disciplines should be in place (Bortolus, 2008; Haszprunar and Wanninger, 2012). In the same vein, the above mentioned institutions are a repository of invaluable molluscan data that can be used in a myriad of studies in the field of global change biology (and other disciplines) being one of the best resources to reconstruct changes in morphology, species distribution and population dynamics, phylogeography, phenology and other life history events, discover of new species, among other possibilities (Meineke et al., 2018). Although the use of molecular tools can have a huge impact on future taxonomic and evolutionary studies they can also be used to improve aquaculture farming and breeding programs; to conserve threatened populations or species; to better understand the molecular mechanisms behind adaptation to changing environmental

conditions; to better understand immunological responses to certain diseases; to apply in medical and pharmaceutical disciplines; to better comprehend the biology and ecology of molluscs including the development of control or even eradication measures for invasive species; among many other possibilities (reviewed in Gomes-dos-Santos et al., 2020).

New resources and resulting information from the above mentioned topics need to be curated (and so subjected to a much higher public and private financial investment), digitized and freely available in accessible databases (Nelson and Ellis, 2018). These digital databases should also contain information about species autecology and habitat requirements, among other possibilities. The problem is that basic information about spatial and temporal patterns in distribution, abundance, biomass, population structure, abiotic tolerances, and biotic interactions in molluscs are most of the times unavailable or based in old sources of information without much recent updates. However, molluscs are highly amenable for experimental manipulations (bivalves and gastropods are easily manipulated in the field or in the laboratory, for example) and so there is much room for their use in ecological, physiological and biological theory. In the same vein, some species are highly invasive and cause important ecological and economic impacts, and so the interest in studying invasive molluscs (e.g. *Dreissena polymorpha*, *Mytilus* sp., *Corbicula fluminea*, *Crepidula fornicata*, *Pomacea* sp.) have been increasing rapidly and generating a lot of information, but often disregarding the study of native populations. Several new biological and ecological fields are emerging, although still not explored in molluscs, and have a high potential to be applied to this taxonomic group and include Internet Ecology and Culturomics, among others (Jarić et al., 2020; Correia et al., 2021). Also important may be the assessment of the key role of some molluscs on ecosystem functions and services and the assessment of their economic value. Some economic information exists regarding the provision of services mediated by molluscs (see van der Schatte Olivier et al., 2020) or disservices of invasive molluscs (for example Haubrock et al., 2022 for freshwater invasive bivalves), but the reality is that there is still much to be done regarding the assessment of regulating and cultural services. Despite that, people recognize the cultural importance of molluscs and some examples have shown how humans can use these organisms since ancient times (Haszprunar and Wanninger, 2012). The clam gardens (Jackley et al., 2016) and use of shells or pearls for aesthetic or religious reasons (Zieritz et al., 2022) are iconic examples.

Despite the huge knowledge gaps still in place in terms of taxonomy, distribution, abundance and population dynamics, evolution, abiotic tolerances, traits, biotic interactions, and the application and effectiveness of conservation measures, we predict a higher scientific and societal interest in these organisms that eventually will reduce some of these knowledge shortfalls.

Monitoring at relevant spatial and temporal scales

To cover the shortfalls mentioned above there is a need for further monitoring molluscs at relevant spatial and temporal scales. As in other taxonomic groups, a high spatial knowledge bias exist,

being molluscs in Europe and North America much more studied than in other continents (Ponder et al., 2020). Therefore, hyper diverse regions in South America, Africa and parts of Asia should be the target of future sampling campaigns. The same for some ecosystems (e.g. deep oceans, deep rivers and lakes, subterranean caves) where due to financial and logistic constraints their monitoring is much more challenging. In addition, molluscs can be widely present in anthropogenic habitats, where these systems may function as refuges and/or as ecological traps (Sousa et al., 2021). Given the expansion of these anthropogenic habitats in terrestrial and aquatic ecosystems and their potential conservation relevance for molluscs, a better monitoring of these systems are welcome. Because sampling is financially and logistically costly, a better cooperation with researchers working with other taxonomic groups will be crucial to reduce expenses and to better understand the role of molluscs at the community and ecosystem levels (Ponder et al., 2020). In the same vein, partnerships with the private sector should be pursued to increase investment in monitoring.

On the other hand, long-term studies are fundamental (Reinke et al., 2019), but few examples exist for molluscs (but see Edgar & Samson, 2004; Cowie et al., 2022; Grau et al., 2022; Nakamura et al., 2023). This temporal dimension need to be incorporated in molluscan monitoring programs more frequently because only long-term datasets could give insights about the heterogeneity of population and community dynamics, which can lead to novel and unexpected insights of possible factors explaining declining (or increasing) trends or even a better understanding of natural fluctuations. In addition, these long-term studies can serve as model systems, allowing the development of theory and methods to better comprehend the physiology, ecology, evolution and conservation of molluscan communities (Reinke et al., 2019). In particular cases, the use of questionnaires, interviews or similar approaches can be an easy way to assess local ecological knowledge about ancient abundance and distribution of particular species. Information given by elders could be extremely relevant in this topic (see Sousa et al., 2020).

Nowadays, an incredible array of new technological solutions are available for monitoring such as drones (could be especially informative for land-use changes), remote operated underwater vehicles, sonars, environmental DNA (eDNA), among many others. Molecular tools can be an incredible help in monitoring and in the last years eDNA, metabarcoding and other molecular techniques have been applied successfully to monitor molluscs in different habitats (West et al., 2020). These techniques will be helpful in resolving several taxonomic, evolutionary, physiological, biogeographic and ecological gaps (Haszprunar and Wanninger, 2012; Smith et al., 2012; Gomes-dos-Santos et al., 2020). When these molecular techniques evolve to give accurate information about abundance it can open the door for a myriad of biological and ecological assessments.

These new tools and technological advances can also be a help in the study of environmental features and biotic interactions. For example, in Tahiti, millimeter-sized smart sensors in tiny snails were used to assess the availability of refugia in forest edges free of predators (Bick et al., 2021). This is an incredible example of miniaturization and how electronic sensors and molluscs can be

used in physiology, ecology and conservation. In addition, citizen science and the use of digital applications (videos and photos available in social media and other internet platforms) can be helpful to collect an incredible amount of information regarding diversity and spatial and temporal data concerning distribution, density, population structure, and even assess the human perception about certain mollusc species. Citizen science programs can go much further than the usual collection of diversity and distribution molluscan data and being a way to collect information about phenotypic plasticity in relation to important environmental gradients. For example, in the Netherlands, researchers used a citizen-science approach (smartphone applications) to study the effects of urban heat on genetically determined shell color in a land snail. Data showed that snails in urban areas are more likely to be yellow rather than pink, an effect predicted on the basis of thermal selection (Kerstes et al., 2019).

Molluscs have also been extensively used as sentinels to assess ecosystem health, which is especially important given the myriad of disturbances imposed by human activities (e.g. pollution). Nowadays, in addition to the long tradition of using molluscs in ecotoxicology (lethal and sub-lethal tests, use of biomarkers, bioaccumulation of contaminants, etc), an incredible diversity of electronic sensors (Figure 1A) are available to measure different features (e.g. cardiac activity and distance between valves in

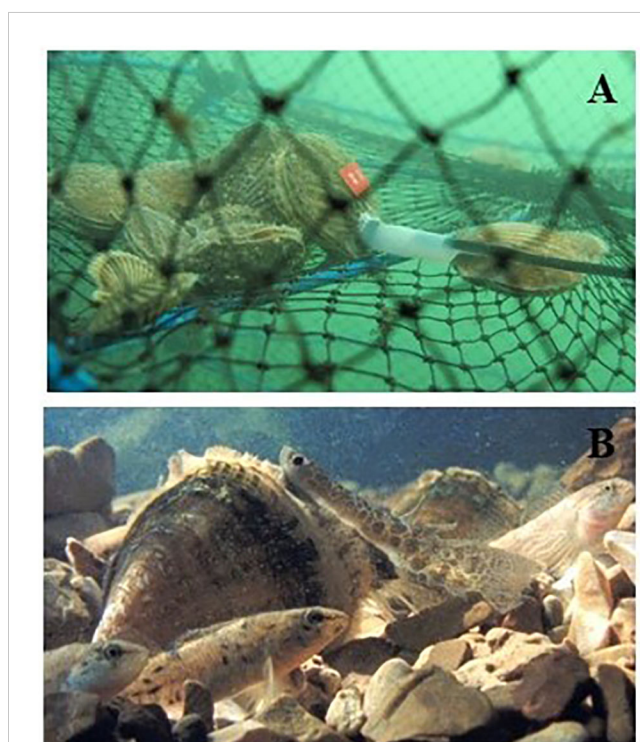


FIGURE 1
(A) The northern bay scallops (*Argopecten irradians irradians*) equipped with a sensor to measure the cardiac activity (Photo Credit: Steve Tettelbach); and (B) The freshwater mussel *Lamprolaima reeveiana* displaying a mantle flap lure that mimics a small fish (Photo Credit: Barnhart, M. C. 2008. Unio Gallery: <http://unionid.missouristate.edu>).

bivalves) that can be used to assess several human disturbances, from pollution to climate change (Andrade et al., 2016; Tomasetti et al., 2023). The miniaturization and storage capacity of this technology, combined with the use of artificial intelligence, plus the use of molecular techniques (e.g. genomics and transcriptomics), will turn possible the collection of data in real-time and use molluscs as early warning systems in a myriad of situations.

All these data retrieved in these monitoring programs should be publicly available and easily accessible to be used by other scientists and citizens. Platforms such as Global Biodiversity Information Facility, iNaturalist, Ocean Biodiversity Information System, MolluscaBase, National Center for Biotechnology Information, and the Barcode of Life Data System are some examples of repositories of information.

Conservation

Given the degree of human disturbances in natural ecosystems is not a surprise that many mollusc species went extinct or are highly threatened (Régner et al., 2009, 2015; Lopes-Lima et al., 2018). Pacific islands and freshwater ecosystems were (and still are) particularly prone to these extinctions (Cowie et al., 2022). However, and contrary to some recent influential studies documenting declining trends in invertebrates (i.e. the Insect Armageddon; Seibold et al., 2019), these extinctions or population collapses in molluscs did not get much scientific or societal attention. This situation is particularly worrisome because there is a lack of quantitative information concerning the conservation status of molluscs, mainly in South America, Asia and Africa, with many species not assessed (or data deficient) by the IUCN, which means that many extinctions and dramatic population declines continue unnoticed (Cowie et al., 2022).

This lack of information on the conservation status is dangerous and rigorous quantitative studies are necessary to assess the impacts of several threats that may include: ocean acidification and their sub-lethal and lethal effects; climate change and how mollusc species will respond in terms of physiology, phenology, and distribution (Saupe et al., 2014; Nicolai & Ansart, 2017; Silva et al., 2022); how the introduction of invasive species are affecting native molluscs due to changes in biotic interactions (Cowie, 2001; Sousa et al., 2014); how habitat degradation and fragmentation, fires, sand mining and exploration of karstic materials are affecting molluscs (Clements et al., 2006; Aldridge et al., 2023; Decker et al., 2023); how overexploitation of some species with commercial interest are affecting population dynamics (Beck et al., 2011); how certain diseases and parasites are affecting molluscs, including the recent discovery of cancer in marine bivalves that are spreading between different organisms and even between different species (Metzger et al., 2015, 2016), among others. Since most of these threats will not stop, and possibly will even accelerate, it is relevant to project for the future how species will respond to them, particularly to climate change (Silva et al., 2022). This information could be vital to find the best management measures to protect these populations/species from extinction.

To reverse the declining trends of these molluscs (and other) species their inclusion in protected areas may be a solution. Protected areas become a critical conservation tool, but despite their importance, very few studies include molluscs in conservation planning exercises (Nogueira et al., 2021, 2023). Anyway, it will be important that the design of future protected areas take into account this taxonomic group. The recent Kunming-Montreal Global Biodiversity Framework provides a unique opportunity for nations to designate new protected areas (or expansion of the existent ones) and should consider molluscs' needs. In addition, restoration of habitats is a priority for the next decade and a huge financial investment is planned to be in place. Molluscs cannot be ignored and need to be part of these restoration actions. These conservation and restoration actions should focus on the recovery of habitats but in some cases, this will be not sufficient and only translocation and/or reproduction in captivity and propagation of individuals can partially solve the problem. Recent methodological and technological advances are turning possible the production of juveniles ready to colonize new habitats, even in species with very complicated life cycles such as freshwater mussels (order Unionida) that need a suitable fish host to complete the life cycle (e.g. Nakamura et al., 2019). Despite the great advancements, these possible translocation or propagation actions need to be carefully scrutinized because there is always the risk of moving parasites and/or diseases (Brian et al., 2021). In the same vein, we cannot ignore the fundamental importance of genetic aspects and a special attention should be given to the assessment of genetic diversity and local adaptation for the success of the above-mentioned conservation initiatives.

The successes and failures of these conservation and restoration actions need to be reported and public available. These actions will also need a huge financial investment and so public-private partnerships and sustainable financing initiatives are necessary to restore and protect vital habitats for molluscs.

Education and outreach

The charisma of molluscs lag much behind of other taxonomic groups (Mammola et al., 2023). Even so, several species have incredible features such as color, size, peculiar life-cycle and amazing behaviors that can be used as a flagship in education and outreach actions. Amazing examples of natural history include octopus species that can throw objects or use defensive tools (Finn et al., 2009); solar-powered sea slugs, freshwater mussels with an incredible display of mechanisms to parasitize their fish hosts (Figure 1B; Modesto et al., 2018), the importance of reef sound for larvae settlement in oyster species (Williams et al., 2022), among many others. Therefore, and using some (or similar) of the above examples, it is possible to engage more people in the study and conservation of molluscs. Citizen science programs, even for the study of more complicated processes (see above example by Kerstes et al., 2019) than just the identification and distribution of species, can be a good way of engagement. Other education and outreach initiatives to raise public awareness for these animals may include Molluscan BioBlitz surveys (i.e. intense periods, usually 24h

of taxon inventories); festivals and workshops (e.g., activities for children and teenagers); educational exhibits at museums, zoos, and aquariums; engagement on social media and wildlife websites; and production of videos, educational posters, 3D printings or shells to increase engagement, among others. Malacological societies, museums, universities and other research institutions have a fundamental role in the development of these education and outreach programs. The involvement of retired malacologists and young enthusiasts, including undergraduate, master and doctoral students, in these actions is fundamental.

Conclusion

The next decade will continue to see an acceleration in the number of studies in molluscs using a diversity of new technologies and methods that will increase our ability to better understand their biology. New conservation and management challenges will arise in response to habitat loss and fragmentation, climate change, acidification, introduction of non-native species, pollution, and changes in land-use, and we need urgent measures to bend the curve of extinctions (at the population and species levels) in Mollusca. It is time to put molluscs in the global research and conservation agenda since these organisms have incredible biological features and are responsible for fundamental ecosystem functions and services that are vital to humans. These features, in addition to their intrinsic value, can be used to increase their charisma in science (and engage a new generation of scientists to study them) and society. In this time of climate and biodiversity emergency, molluscs cannot be overlooked and the preservation and protection of these extraordinary organisms should be a priority.

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