



Research Trends of Development on Pearl Bivalve Mollusks Based on a Bibliometric Network Analysis in the Past 25 Years

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Freshwater pearl mussels and marine pearl oysters are major producers of cultured pearls. With the development of pearl farming, pearl bivalve mollusks have attracted significant research attention over the past 25 years. To provide an overview of this research, we conducted a bibliometric analysis of publications from the Web of Science Core Collection database from 1995 to 2020. A network map generated by VOSviewer software was used to evaluate studies of pearl bivalve mollusks in terms of author, country, organization, journal, and keywords. A total of 2,288 publications were obtained, showing an annual increase in the number of papers. Researchers based in China were a major contributor to the field and there was active cooperation among authors. Research focused on mussel and oyster developmental biology, growth, culture mode, molecular biology, and ecological conservation. In recent years, hot topics, such as growth performance and traits, pearl formation and biomineralization, and immune response, have been widely discussed. Genomics, transcriptomics, proteomics, and metabonomics analyses were commonly used to analyze the regulatory mechanism of coding and non-coding genes. The interaction between the environment and farming activities showed the importance of sustainable development. Interdisciplinary research could solve some of the issues facing the pearl bivalve mollusk farming. In conclusion, our findings could serve as another way to understand research trends in pearl bivalve mollusks and contribute to future studies.

Keywords: pearl mussel, pearl oyster, aquaculture, bibliometric analysis, VOSviewer

INTRODUCTION

Cultured pearls are the response of pearl mussels or oysters to a tissue implant (Nagai, 2013). A tissue graft is inserted from a donor mollusk to a recipient mollusk, the mantle tissue of which then secretes nacreous material into the pearl sac, forming a cyst as part of the healing process (Haws and Ellis, 1999; Dan and Ruobo, 2002). This material is known as conchiolin and is formed of calcium carbonate and a fibrous protein (Ma et al., 2005). The growing pearl sac cell secretes nacre, and a pearl results once the nacre fills the growing pearl sac. Pearls can be farmed from two bivalve mollusks: freshwater pearl mussels and marine pearl oysters (Lucas, 2007). Freshwater pearl mussel refers not only to *Margaritifera margaritifera* but also to other freshwater mussel species that can also form pearls, such as *Hyriopsis* spp. in Asia and *Amblema* spp. in North America, both of

which belong to the family *Unionidae*. Marine pearl oysters occur in the genus *Pinctada* including *Pinctada margaritifera* and *Pinctada maxima* which are used for culturing South Sea and Tahitian pearls (Tisdell and Poirine, 2000). Commercial quantities of pearls can also be obtained from some species of the closely related winged oyster genus *Pteria* (Paul Southgate, 2011). Pearls have been used chiefly for adornment since ancient times (Nagai, 2013; Duncan Peter and Arne, 2019), and pearl powder is often used as a health product in traditional Chinese medicine, having antioxidant and anti-inflammatory effects on cells (Xu et al., 2001; Jian-Ping et al., 2010). Pearl extract is also used in the clinical treatment of various ulcers (Jian-Ping et al., 2010; Velasco, 2011) and wound healing (Li et al., 2013; Chen et al., 2019). In addition, marine pearl oysters are suitable for the restoration of polluted coastal environments (O'Connor and Gifford, 2008) because they have the highest pumping and filtration rates of any bivalve mollusk (Lucas, 2008).

Since Mikimoto succeeded in culturing blister pearls in 1893, pearls have been cultured worldwide by utilizing different bivalve mollusk species (Nagai, 2013), and the pearl farming industry has grown rapidly (Gueguen et al., 2016; Johnston et al., 2019). The black pearl oyster *P. margaritifera*, found in Tahiti and many other Pacific islands, including the Cook Islands and Fiji, is widely used for the production of cultured pearls (Kishore et al., 2018; Johnston B. et al., 2020; Johnston W. et al., 2020). Freshwater pearl mussels are widely used in various industries and created great wealth in China and Japan (Tisdell and Poirine, 2008; Bai et al., 2014b). Moreover, the industry of pearl farming has become a large part of financial income in some countries or regions (Southgate et al., 2006; Jiddawi, 2008; Johnston et al., 2019). The studies on pearl bivalve mollusks have been generated from various perspectives. Research has focused on a variety of factors relating to the aquaculture of these mollusks, including how pearls form and their color is determined (Chen et al., 2017; Li et al., 2017b), influence of nuclei implantation (Li et al., 2016; Wang et al., 2019), and different aquaculture methods (Muhammad et al., 2017; Ky et al., 2019).

However, pearl bivalve mollusks face multiple threats, not only in aquaculture settings but also in the wild. Red algal tides (Ericson, 2017; Nakayama et al., 2020) and disease (Sakatoku et al., 2018) have resulted in the decrease of specific species, which has also occurred as a result of environmental pollution, caused by water conservancy projects, overfishing, and water contamination (Cosgrove et al., 2016). Thus, in recent years, the global production of pearls has been in decline (Johnston et al., 2019; Mao et al., 2019; Saucedo et al., 2021). According to research released in 2019 by the South China Sea Fisheries Research Institute (SCSFRI) and Australia's University of the Sunshine Coast (USC), global pearl production had fallen by 60% and output value by 39% over the past decade (Changbo et al., 2019). Therefore, here we review studies on pearl bivalve mollusks to highlight areas for future pearl research on their conservation and further development of pearl aquaculture.

Bibliometrics is the use of statistical methods to analyze books, articles, and other publications (Broadus, 1987). Bibliometric methods were widely used to explore the distribution structure, quantitative relationships, and changes

in literature (Narin et al., 1994). It can quantitatively reveal the development history, research focus, and future research direction of academic fields (Narin et al., 1994; Daim et al., 2006). Bibliometrics has been applied in various fields, such as economics (Bonilla et al., 2015), physics (Rinia et al., 1998), ecology (Romanelli et al., 2018), and medicine (Geaney et al., 2015). Thus, the bibliometric analysis of previous pearl bivalve mollusk research could highlight hot topics and potential future research trends and directions.

MATERIALS AND METHODS

Data Collection

Given that there are two different bivalve mollusks used for pearl production (the freshwater pearl mussel and the marine pearl oyster), the topic search query phrase [TS = (pearl) AND TS = (mussel OR oyster OR bivalve)] in the Web of Science (WOS) search page (TS means topic) was used to compile a bibliography of all publications. The search time ranged from January 1, 1995, to December 23, 2020. The type of document was limited to research article, meeting reports, and reviews. Any irrelevant information was deleted manually.

In total, 2,288 results were selected from the Web of Science Core Collection for the next step. The Statistics plug-in in WOS was utilized to count the number of publications based on authors, organizations, journals, countries, or regions. All information was exported as plain text as a "Full Record and Cited Reference" so that it could be recognized by VOSviewer (Version 1.6.15).

Data Analysis

The VOSviewer software, supported by algorithmic clustering analysis based on bibliometric network data, can be used to visualize existing connections between bibliometric data. With the help of bibliometric maps, the network of relationships on this topic was examined among countries, research institutions, and authors.

For the 2,288 publications, the type of analysis was set as co-authored publication and the units of analysis were set as authors, organizations, and countries (regions included) to provide insights into any partnerships in this research. The minimum number of documents of an author (country or organization) was five. To merge synonyms by setting a thesaurus terms file, "Co-occurrence" and "Author keywords" were chosen to identify keywords to use to explore research hot spots, and the cited source of co-citations was also chosen to build a bibliometric map. The threshold of occurrences of a keyword was 10, whereas the minimum number of occurrences of the cited source of a co-citation was 20.

RESULTS

Publication and Journal Field

From 1995 to 2020, the number of publications on pearl bivalve mollusks increased, reflecting the increasing interest in

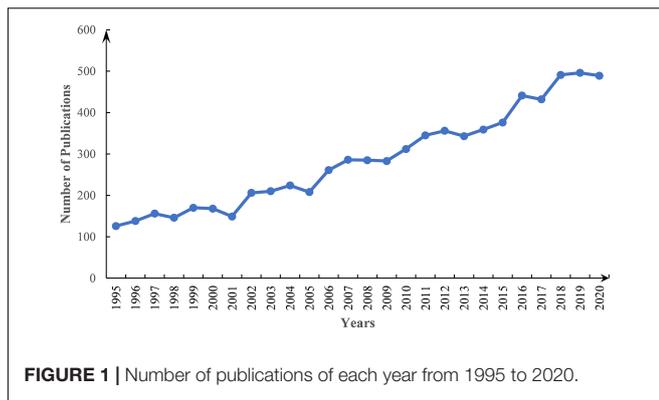


FIGURE 1 | Number of publications of each year from 1995 to 2020.

these species (**Figure 1**). The top five subject categories were selected based on the classification of subject categories in Journal Citation Reports (JCR) (**Figure 2**). The results showed that research in environmental sciences increased gradually, whereas the fisheries and marine freshwater biology research both increased significantly over the study time frame. In total, 2,288 publications were from 548 journals. The top 10 most productive journals accounted for ~31% of the total publications (**Table 1**). Among the pearl bivalve mollusks studies, *Aquaculture* was the most frequent publication, with 180 articles, cited 4,793 times, followed by the *Journal of Shellfish Research*, with 102 articles, and *Fish and Shellfish Immunology*, with 99 articles. In addition to these three journals, *PLoS ONE* and *Marine Pollution Bulletin* were more frequently cited (>1,100 times) by the 2,288 articles included in the bibliometric analysis.

Countries or Regions

The contribution of the China was especially prominent with the largest number of publications on pearl bivalve mollusks and the highest number of cited articles (**Table 2** and **Figure 3**). Also in the top five countries in terms of publications were Japan, Australia, and France, which all have a long history of pearl bivalve mollusk research. The United States represented the core of academic exchange and cooperation in pearl bivalve mollusks studies from 2010 to 2012, whereas contributions from China increased significantly after 2014. From 2016 onward, articles were published by researchers based in Italy, Poland, New Zealand, Portugal, and Belgium. In **Figure 3**, points representing a country that were joined to other country points indicated that researchers in those countries or regions worked with researchers from other countries or regions. Thus, this analysis indicated that research on pearl bivalve mollusks is a continuous and evolving research field.

Organizations

Chinese Academy of Sciences published the highest number of articles (**Table 3**), followed by the French Research Institute for Exploitation of the Sea (Institut Français de Recherche pour l'Exploitation de la Mer; IFREMER), James Cook University, and Tsinghua University. Publication from the Chinese Academy of Sciences was the most cited, followed by those from the IFREMER and James Cook University. The relationship

between different organizations was complex, as indicated by the numerous lines connecting to them, representing the tight cooperation between these organizations. IFREMER, Chinese Academy of Sciences, Chinese Academy of Fishery Sciences, and the University of Tokyo were the top four institutions in terms of frequency of cooperation. In **Figure 4**, the color scheme of yellow, orange, and red indicates that most organizations published articles after 2010.

Authors

The top 10 leading authors are listed in **Table 4**. Analysis of author productivity revealed that a few high-producing authors contributed significantly to the number of publications on pearl bivalve mollusks, especially R. Q. Zhang and L. P. Xie, who had the highest number of publications (~4% of the total number of publications) and which were also cited most frequently. The main authors contributing to pearl bivalve mollusk research were R. Q. Zhang, L. P. Xie, Y. W. Deng, X. D. Du, G. Le Moullac, P. C. Southgate, and M. X. He (**Figure 5**). The mode of academic development was more likely to be polycentric, indicating that authors collaborated with others both inside and outside of their research institutions, although collaborations among the main contributors were rare. Except for the studies by R. Q. Zhang and L. P. Xie, most other authors began to publish work only after 2014.

Cited Journals

Aquaculture, *Fish and Shellfish Immunology*, *Marine Pollution Bulletin*, *Hydrobiologia*, and *Nature* formed the major cores in terms of cited journals (**Figure 6**). Each cluster is represented by a different color and can be connected with other clusters. Thus, these journals represent the main publication sources for pearl bivalve mollusk research.

Hot Keywords

Obviously, the phrase “pearl oyster” occurs the most because it was the name of the study object (**Figure 7**). Around 2008, “spat,” “culture,” “*P. maxima*,” “gametogenesis,” and “larvae” were the significant keywords, suggesting that researchers were mainly focused on the development of oyster larvae especially for silverlip pearl oyster during this period. Around 2010, the growth of Pacific pearl oysters and blacklip pearl oysters was the most popular topic, followed by “growth,” “*P. margaritifera*,” and “*Crassostrea gigas*” becoming the focus of pearl bivalve mollusk research. Hot keywords that emerged around 2012 were “conservation,” “temperature,” “survival,” and “*Pinctada fucata*,” indicating that researchers began to focus on environmental problems, such as global warming and marine pollution which affect the survival of Akoya pearl oysters. In 2014, the focus transferred to “biomineralization,” “prismatic layer,” “nacreous layer,” “family,” and “shell formation,” which means the specific formation of pearls was notable. The hot keywords changed to “quality,” “gene expression,” “identification,” “molecular-cloning,” and “*Hyriopsis cumingii*” around 2016. In recent years, researchers have focused on using advanced molecular techniques to improve the quality of pearls especially for specific species of freshwater pearl mussels.

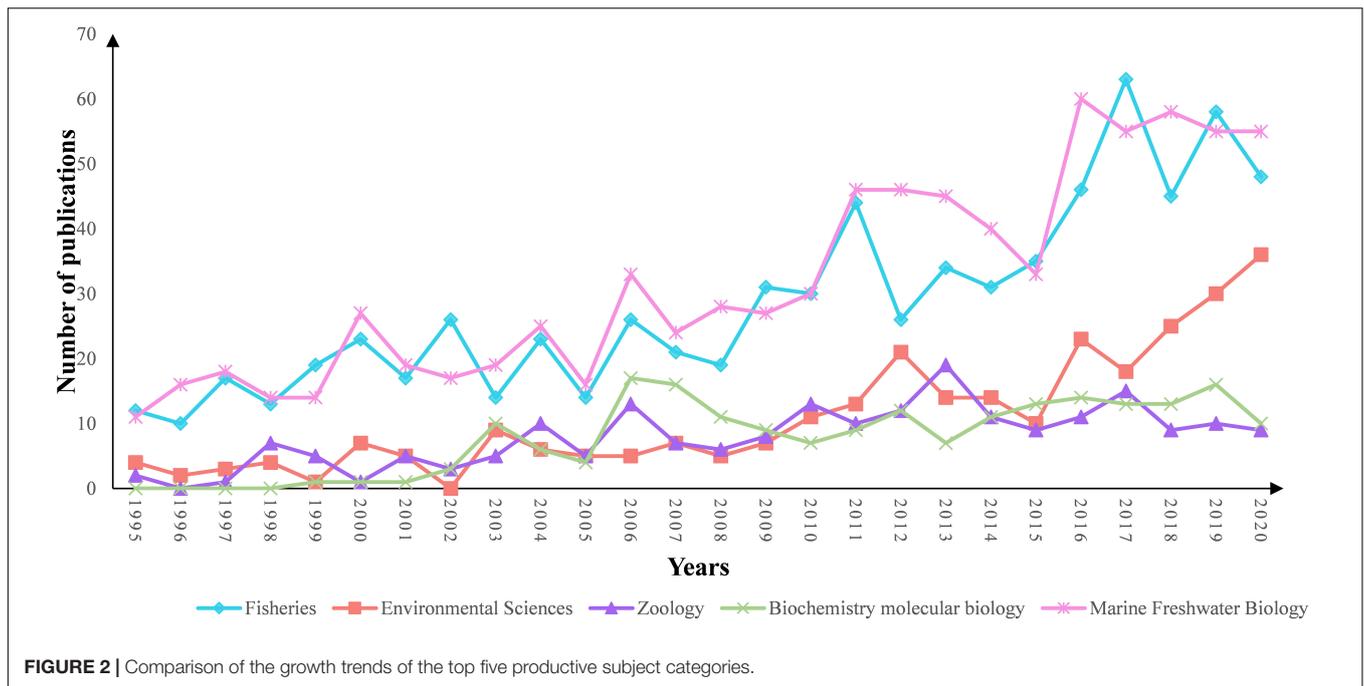


TABLE 1 | Among the studies related with pearl bivalve mollusks as the theme, the numbers of publications, the proportion of all publications, and the total times cited for the top 10 source journals ranked by the number of publications based on Web of Science (WOS).

Rank	Source journals	Number of publications	Proportion of all publications (%)	Total times of cited
1	<i>Aquaculture</i>	180	7.864	4,793
2	<i>Journal of Shellfish Research</i>	102	4.456	1,477
3	<i>Fish and Shellfish Immunology</i>	99	4.325	1,451
4	<i>Aquaculture Research</i>	80	3.495	841
5	<i>Aquatic Conservation Marine and Freshwater Ecosystems</i>	55	2.403	844
6	<i>Marine Pollution Bulletin</i>	47	2.053	1,131
7	<i>Marine Biotechnology</i>	43	1.879	1,096
8	<i>PLoS ONE</i>	39	1.704	1,179
9	<i>Aquaculture International</i>	38	1.660	366
10	<i>Comparative Biochemistry and Physiology B Biochemistry Molecular Biology</i>	38	1.660	1,003

TABLE 2 | Among the studies related with pearl bivalve mollusks as the theme, the numbers of publications, the proportion of all publications, and the total times cited of the top 10 countries or regions ranked by the number of publications based on WOS.

Rank	Countries or regions	Number of publications	Proportion of all publications (%)	Total times cited
1	China	673	29.401	10,301
2	Japan	288	12.582	6,057
3	France	266	11.621	5,546
4	Australia	237	10.354	4,756
5	United States	236	10.310	6,052
6	Germany	113	4.937	3,583
7	Mexico	77	3.364	687
8	England	64	2.796	1,376
9	Russia	64	2.796	717
10	Spain	58	2.534	1,287

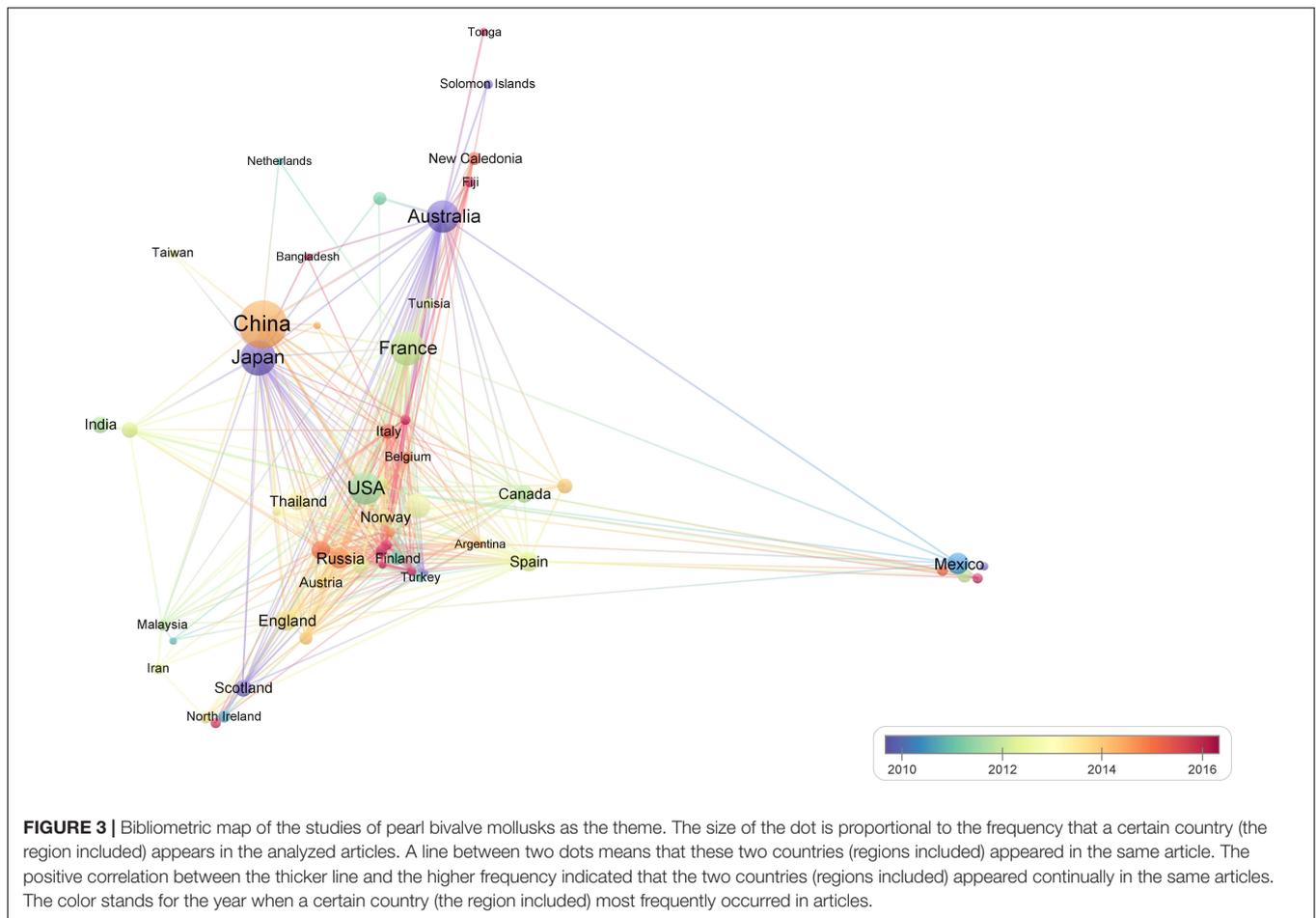


TABLE 3 | Among the studies related with pearl bivalve mollusks as the theme, the numbers of publications, the proportion of all publications, and the total times cited for the top 10 organizations ranked by the number of publications based on WOS.

Rank	Organizations	Number of publications	Proportion of all publications (%)	Total times cited
1	Chinese Academy of Sciences	229	9.991	3,632
2	IFREMER	151	6.806	2,776
3	CNRS	135	5.890	421
4	James Cook University	112	4.877	2,492
5	Tsinghua University	111	4.843	1,606
6	Guangdong Ocean University	97	4.232	899
7	Shanghai Ocean University	95	4.145	938
8	Chinese Academy of Fishery Sciences	77	3.360	1,079
9	Institut de Recherche pour le Developpement	69	3.010	424
10	Fisheries Research Agency of Japan	68	2.967	162

DISCUSSION

The transfer of hot spots in pearl oyster research fields showed that researchers have continued to focus on developmental biology, growth, culture mode, molecular biology, and ecological conservation of pearl oysters (Figure 7). From 2008 to 2010, researchers focused on the development, growth, and various culture modes of pearl oysters (Dauphin et al., 2008; Furuhashi et al., 2009; Welladsen et al., 2010),

whereas in 2012, environmental factors became a focus to enhance the survival of pearl oysters (Gum et al., 2011; Hüning et al., 2013). From 2014 until 2020, researchers were more likely to focus on identifying connections between the different traits of pearl oysters and selected genes to determine the underlying regulatory mechanisms of gene expression by using the integrated application of transcriptomics and metabolomics, which measure the expression levels of genes at different molecular levels (Li and He, 2014;

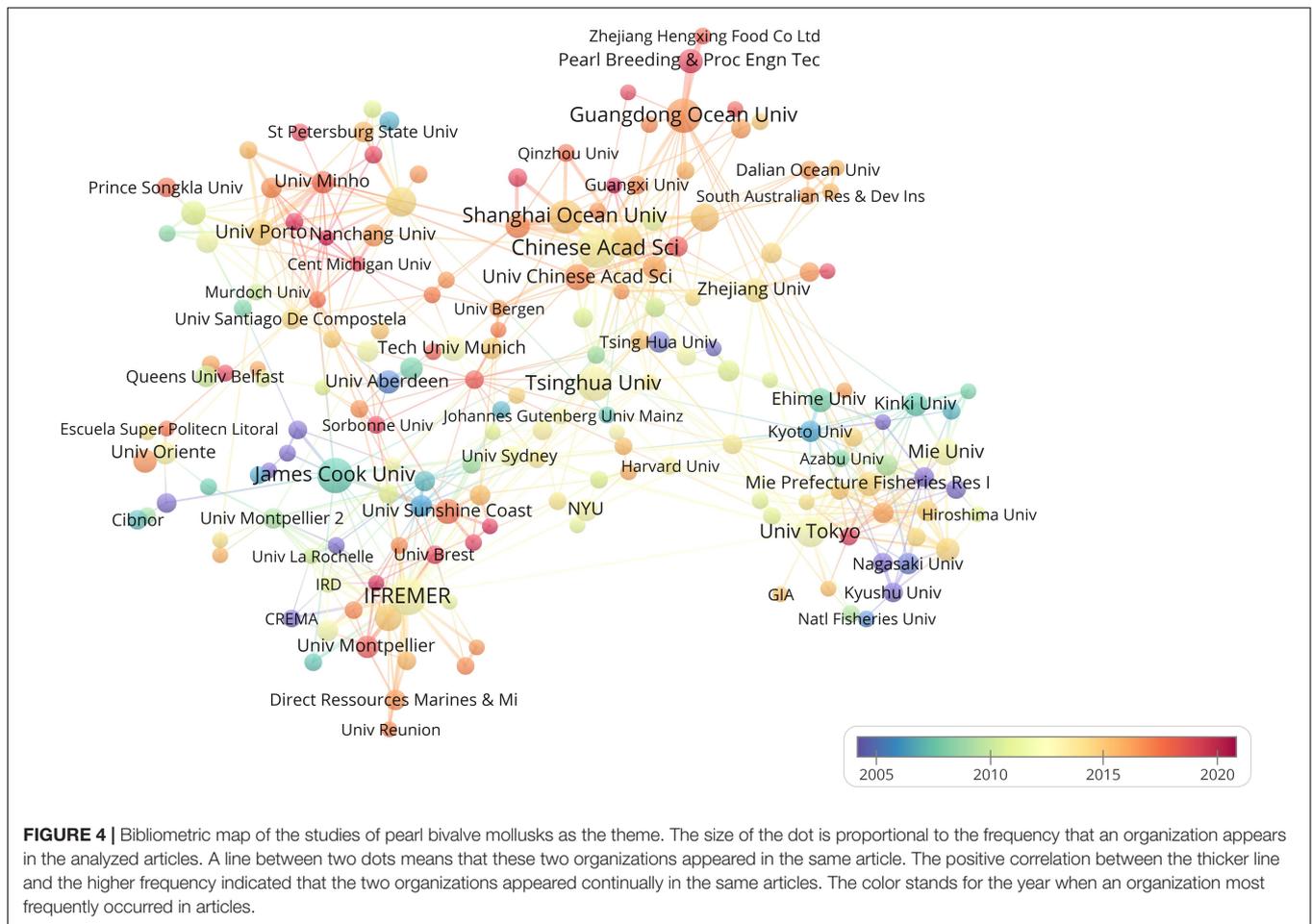


FIGURE 4 | Bibliometric map of the studies of pearl bivalve mollusks as the theme. The size of the dot is proportional to the frequency that an organization appears in the analyzed articles. A line between two dots means that these two organizations appeared in the same article. The positive correlation between the thicker line and the higher frequency indicated that the two organizations appeared continually in the same articles. The color stands for the year when an organization most frequently occurred in articles.

TABLE 4 | Among the studies related with pearl bivalve mollusks as the theme, the numbers of publications, the proportion of all publications, and the total times cited for the top 10 authors ranked by the number of publications based on WOS.

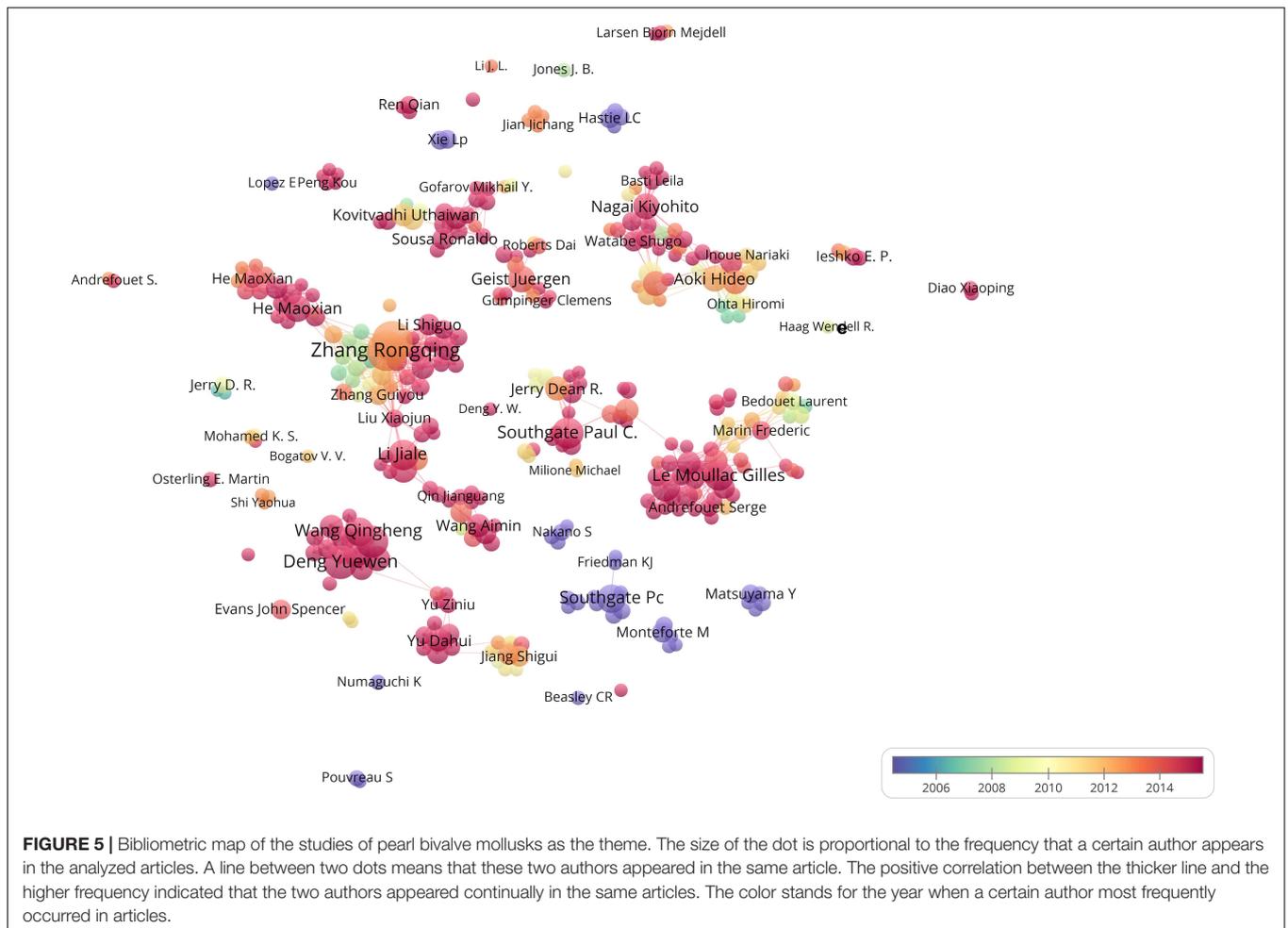
Rank	Authors	Number of publications	Proportion of all publications (%)	Total times cited
1	R. Q. Zhang	98	4.281	1,561
2	L. P. Xie	95	4.150	1,555
3	P. C. Southgate	77	3.364	494
4	Y. W. Deng	64	2.796	481
5	J. L. Li	55	2.403	430
6	X. D. Du	54	2.359	474
7	M. X. He	48	2.097	882
8	Q. H. Wang	42	1.835	392
9	G. Le Moullac	39	1.704	498
10	C. -L. Ky	37	1.616	377

Bai et al., 2015; Lemer et al., 2015; Zheng et al., 2016b; Yang C. et al., 2018).

Cross-Disciplines Technology

Some new interdisciplinary technologies have been applied in traditional pearl farming. Extenics is used to study the possibility of the expansion of a topic and the development of innovation in a formal way (Cai et al., 2013). The essence of extenics is to make all kinds of seemingly contradictory or unsolvable problems

solved (Liu et al., 2016). The combination of computer science and extenics brings forth new solutions for many problems across research fields. For example, an extenics-aided innovation system was used to provide a new method for pearl cultivations in China that produced pearls with a high yield but a low value (Yan et al., 2017). With the help of extenics and a mind map, Ye et al. (2019) studied the factors influencing the calcium content, water fluidity, water temperature, algae content, mollusk number, and so on in the cultivation of pearl oyster, providing a complete high-yield



breeding program for pearl farmers. Van Wynsberge et al. (2020) used Multiscale Ultrahigh Resolution (MUR) satellite-derived sea surface temperatures (SSTs) to simulate the oyster population and assist the research and management of pearl oysters. In addition, related techniques have been developed to examine pearl nuclei during pearl oyster aquaculture. Digital radiography was used to detect the pearl nucleus by optimizing the voltage, current, and exposure time (Yulianti et al., 2018). Using micro-CT in the live bivalves has advantages in that it is both non-invasive and rapid. Moreover, pearls can be evaluated in terms of their shape, size, smoothness, and dimension (Ding et al., 2021).

Interaction Between Farming and Environment

When discussing pearl farming, it is impossible not to mention the interaction between farming activities and the environment. Following the success of French Polynesia and the Cook Islands in marine pearl oyster aquaculture, other island states in the Pacific have also developed their own pearl mollusk aquacultural setups (Tisdell and Poirine, 2008). Basti et al. (2011) revealed that *Heterocapsa circularisquama* blooms negatively influence the early life stages of *P. fucata*. Ocean acidification results in

a reduced byssus diameter and amplified byssus nanocavity in *P. fucata* by altering the abundance and secondary structure of byssal proteins and affecting the metal ion content in distal threads (Li et al., 2017a). Researchers have also highlighted issues with diversity during pearl oyster aquaculture development. For example, Cartier used roving diver census methods to analyze coral reef bommies in a Polynesian lagoon and showed that pearl farming might not negatively alter the number and population structure of fish (Cartier and Carpenter, 2014). Gifford et al. (2004) argued that pearl farms could be regarded as biological filters to solve nutrient enrichment and pollution issues (Gifford et al., 2004). Lacoste et al. (2014) investigated the influence of nutrient regeneration on pearl oyster farming in French Polynesia, revealing that nutrient availability can be enhanced by pearl oyster culture. Thus, these studies did not reveal a significant crisis in marine pearl oyster culture. However, there are more problems associated with freshwater pearl mussel farming. The population numbers of *M. margaritifera* in Europe had been estimated to have declined >90% by the 1990s (Bauer, 1988), rendering this species highly endangered (Geist, 2010; Gum et al., 2011); therefore, many approaches were taken to protect these mussels, including from aquaculture (Preston et al., 2007; Schmidt and Vandr e, 2010) to molecular

hermaphroditic *P. margaritifera* from several gonadic samples of males and females at different development stages. The specific gene expression profiles identified sex differentiation and potential sex-determining genes in *P. margaritifera*: *pmarg-fem1-like*, *pmarg-dmrt*, and *pmarg-foxl2* are potentially involved in the sperm-oocyte switch (Teaniuraitemoana et al., 2014). Hybridization is documented as an efficient method to improve growth traits in pearl oysters. According to a transcriptome analysis, Yang J. et al. (2018) found that differentially expressed genes in hybrid families and their parental families might be associated with growth heterosis. Mitochondrial (mt) DNA is frequently used in comparative genomic analyses because its gene content and arrangement, as well as mt tRNA secondary structure, provides valuable phylogenetic information. Wu et al. (2012) described the sequence and characterization of the complete mt genome of the silverlip pearl oyster, *P. maxima*, observing a unique tRNA gene family in this genome and described a novel highly expressed ORF (*orfURI*), its potential function, and two possible mechanisms of origin. Piwi-interacting RNAs (piRNAs) are recently discovered small non-coding RNAs, the function of which is repressing transposable element activity. Huang et al. (2019) identified and characterized putative piRNAs by high-throughput sequencing in somatic and gonadal tissues of *P. fucata*. The discovery that piRNAs are highly expressed in a range of somatic tissues has enriched our understanding of the diversity and function of small RNAs in pearl oyster.

Pearl Formation and Biomineralization

The study of Takeuchi et al. (2012) provides the first opportunity to obtain insight into a bivalvian mollusk genome. Draft genome of the pearl oyster *P. fucata* provides a platform for the identification of selection markers and genes for calcification, the knowledge of which has a significant importance in the understanding of the molecular mechanisms involved in pearl biosynthesis and biology of bivalve mollusks. Liu J. et al. (2015) reported a global gene analysis during larval development of *P. fucata* based on a microarray and proposed a mechanism of how biomineralization-related genes regulate the larval shell formation process. Biomineralization refers to the dynamic physiological processes whereby living organisms elaborate mineralized tissues. Outer mantle epithelial cells (OME) secrete shell matrix proteins (SMPs) which determine the mineralogical and crystallographic properties of the shell. Researchers have identified many novel SMPs by using molecular biology techniques (i.e., gene cloning, *in situ* hybridization, and immunohistochemistry) coupled with high-throughput sequencing data (genome, proteome, secretome, and transcriptome), as well as confirming their corresponding functions during shell formation (Song et al., 2019). Using liquid chromatography-tandem mass spectrometry (LC-MS/MS) analysis of proteins extracted from the shells of *P. fucata*, Liu C. et al. (2015) identified 72 unique SMPs and combined with a draft genome. Bai et al. (2014a) compared the relative expression of seven housekeeping genes across different tissue types in the mantle or pearl sac by quantitative real-time polymerase chain reaction (PCR) and suggested that *Ubi*, *Rpl18*, and *EF1 α*

are suitable reference genes to facilitate the analysis of gene expressions during shell or pearl formation in the pearl mussel, *H. cumingii*. Using proteomic analyses combined with genomic and transcriptomic analyses with the addition of RNA-seq data, Zhao et al. (2018) showed that the gene expression profiles and SMPs from larval shells of the pearl oyster, *P. fucata*, and the Pacific oyster, *C. gigas*, are almost entirely different from those of adults in both species, which indicates that bivalves have two repertoires of SMP genes to construct larval and adult shells. Blay et al. (2018) analyzed the expression profiles of eight genes encoding nacreous and/or prismatic SMPs in the pearl sac of *P. margaritifera* during pearl biogenesis and identified three genes implicated in pearl surface quality by multivariate regression tree building. Thus, *SHEM9*, *ASP*, and *PIF* could be used as biomarkers for genetic improvement of *P. margaritifera* pearl quality. The study of Gao et al. (2016) suggested that the transcription factor *Pf-POU3F4* regulates the expression of the matrix protein genes *Aspein* and *Prismalin-14* in pearl oyster. Using high-throughput transcriptome profiling, Take et al. (2019) revealed the genes involved in the development of the pearl sac and pearls, as well as the sequential expression patterns of different SMPs secreted from the pearl sac during pearl formation in *P. fucata*. miRNAs are a class of non-coding RNA molecules with post-transcriptional regulatory activity in biomineralization. The study of Zheng et al. (2016a) added to the miRNA databases of *P. martensii* by deep sequencing and indicated pm-miR-2386 and pm-miR-13b as key factors regulating the formation of organic matrix or the differentiation of mineralogical cells during shell formation. Du et al. (2017) sequenced the highly polymorphic genome of the pearl oyster and conducted multi-omic and biochemical studies to study nacre formation, which is formed through a process of matrix-assisted biomineralization, as well as identified a large set of novel proteins participating in matrix-framework formation. Given that color is an indicator of pearl quality, Bai et al. (2013) identified genes involved in nacre coloring through comparative transcriptome analysis of tissues secreting purple and white nacre in the triangle sail mussel, *H. cumingii*. As nacre color has an effect on pearl color, Chen et al. (2017) studied the effect of tyrosinase on nacre color in *H. cumingii* (two types of purple-shelled and white-shelled freshwater pearl mussels) by cloning novel tyrosinase protein and tyrosinase-related protein genes (*HcTyr* and *HcTyp-1*, respectively) from the mantle. Results indicated that *HcTyr* and *HcTyp-1* are involved in the formation of nacre color in *H. cumingii*. The albino phenotype of *P. margaritifera* provides a new way to examine the molecular mechanisms underlying pigmentation. Using whole transcriptome RNA-sequencing analysis, Auffret et al. (2020) found that these genes were involved in five main molecular pathways, tightly linked to known pigmentation pathways: melanogenesis, calcium signaling pathway, Notch signaling pathway, pigment transport, and biomineralization.

Immune Response

Multi-omic studies have documented responses to nuclei insertion operation and diseases and in *P. f. martensii*, *P. maxima*, *P. margaritifera*, and *Pteria penguin* (Adzigbli et al., 2020a).

Bivalve mollusks have evolved an innate immune system with differentially expressed immune-related genes, which relies on the interaction between cellular and humoral factors to prevent them from potential infection because of their frequent exposure to microbial pathogens and environmental perturbations (Xu et al., 2010; Adzighli et al., 2020b). Matsuyama et al. (2017) used shotgun and 16s rRNA-based metagenomic analysis to identify genes that are present specifically in oysters affected by Akoya oyster disease. ERKs are conserved and related to protein-serine/threonine kinases that participate in the regulation of multiple biological processes. Zhang et al. (2018) cloned and identified a novel ERK from *P. fucata* (Pferk) that shared significant homology with other mollusk ERK proteins. Results suggested that PFERK was expressed in seven different tissues examined from pearl oyster in all developmental stages and is involved in innate mantle immunity *in vivo* and *in vitro*. Proteins in the tumor necrosis factor receptor (TNFR) superfamily have significant roles in inflammation, apoptosis, autoimmunity, and organogenesis. Two TNFR gene homologs (*PmTNFR1* and *PmTNFR5*) were characterized from *P. f. martensii*, and Wu et al. (2020) found RNAi inhibition of *PmTNFR1* and *PmTNFR5* gene expression. Results suggested that the NF- κ B signaling pathway may be activated by *PmTNFR1* and *PmTNFR5* and that these genes are closely related to allograft immunity in *P. f. martensii*. Long non-coding RNAs (lncRNAs) have regulatory roles in exoskeleton formation and immune response. Zheng et al. (2020) found a novel lncRNA, *LncMSEN2*, from the pearl oyster *P. f. martensii*, and its sequence was validated *via* PCR. High expression of *LncMSEN2* in mantle tissues and pearl sac detected by quantitative real-time PCR, *in situ* hybridization experiments, and RNAi experiments indicated that *LncMSEN2* may be a novel regulator of the mantle-shell defense system of pearl oyster.

CONCLUSION AND FUTURE DIRECTIONS

Cultured pearls are mainly produced by freshwater pearl mussels and marine pearl oysters, and the economic importance associated with pearl farming has focused the attention of

researchers from various fields on pearl bivalve mollusks. It is precisely because the market demands both the quantity and quality of pearls, which has focused research on these issues over the 25 years. Given that there are many internal and external factors affecting pearl production, researchers have reported corresponding solutions for specific topics, such as different culture modes, color formation, and growth performance of pearl bivalve mollusks. In the meantime, researchers have not ignored other threats to the pearl industry, in terms of environmental pollution and genetic characterization decline. With improvements in technology, genetic regulation technology will continue to be the most fundamental and effective technological method to regulate the character of pearls at the molecular level in the coming decades. However, for the sustainable development of the pearl industry, we need additional collaboration and cooperation among researchers and those involved in the industry to discuss and improve pearl bivalve mollusks research in the future.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

QC performed the bibliometric analysis and drafted the manuscript. WH collected the data and drafted the manuscript. ZB conceived the idea and supported the study. All authors contributed to the article and approved the submitted version.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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