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Polar Animal Genetic Resources: Current Situation and Development Strategies

Chen Songlin[1, 2], Xu Wenteng[1, 2], Chen Zhangfan[1, 2]

1. Yellow Sea Fisheries Research Institute, Chinese Academy of Fishery Sciences, Qingdao 266071, Shandong, China
2. Laboratory for Marine Fisheries Science and Food Production Processes, Pilot National Laboratory for Marine Science and Technology (Qingdao), Qingdao 266237, Shandong, China

Abstract: In this article, we review the current status of polar animal genetic resources and propose development strategies based on existing problems. Sequencing of the genomes of polar animals started comparatively late, and to date, whole-genome sequencing has been conducted for only 13 polar animals. In recent years, however, the transcriptomes of 31 polar animals have been sequenced, and transcriptome research has focused on adaptation to polar environments, molecular mechanisms underlying the responses to pollutant stress, transcriptome changes during different developmental stages or within different tissues, and exploitation of functional genes. Given the late initiation of studies on polar animal genetic resources, the depth and width of related research is currently limited. Such studies are, nevertheless, strategically important. We accordingly recommend China to establish a key research and development program "Exploration and application of biological gene resources in polar animals" to support the work in this field, which focuses on the genetic dissection of important traits, the functional analysis of specific genes, and the development of genetically engineered products.
Keywords: polar animal; genome; transcriptome; genetic resource

1 Introduction

The polar environment is extremely harsh. The climate is cold and dry and food resources are typically scarce. The polar days and nights can last for up to several months each year, which predictably disrupts the metabolism of animals and make it difficult to maintain biological rhythms. How can polar animals survive in this hostile environment? Which regulatory genes are involved in adaptation to the extremely cold and highly saline environments? How do marine fish manage to resist freezing? In which ways do terrestrial polar animals keep warm? These are among the numerous questions to which scientists avidly seek the answers. However, the coldness of the polar regions has for long restricted research in the life sciences. In recent years, the rapid development of polar survey and sample acquisition technologies has, nevertheless, greatly facilitated research on polar animals. Elucidating genome structures, examining gene function, and determining the molecular mechanisms that underly the adaptation of polar animals to the cold environment, particularly fishery animals, is not only of scientific significance but also has considerable application value and potential.

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Corresponding author: Chen Songlin, researcher of the Yellow Sea Fisheries Research Institute of Chinese Academy of Fishery Sciences. Major research field is exploitation and application of aquatic gene resources. E-mail: chensl@ysfri.ac.cn
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2 Current research and application status of the genetic resources of polar animals

2.1 Current status of polar animal genomic research

2.1.1 Research on the genomes of polar animals is currently in the initial stages

As of September 2018, the genomes of over 380 animal species had been sequenced, the details of which have been published in 385 papers (Fig. 1a). To date, however, the genomes of only 13 polar animals have been sequenced and reported in 12 papers, accounting for less than 3% of the total (Table 1). This relative paucity of sequence data can primarily be ascribed to the difficulty in obtaining polar animal samples and late initiation of the related genomic research.

Table 1. A list of the polar animals with sequenced genomes.

Latin name	Genome size	Author/year	Journal name
Gadus morhua	830 Mb	Star et al., 2011	Nature [1]
Ursus maritimus	2.53 Gb	Miller et al., 2012	PNAS [2]
Notothenia coriiceps	637 Mb	Shin et al., 2014	Genome Biology [3]
Balaenoptera acutorostrata	2.76 Gb	Yim et al., 2014	Nature Genetics [4]
Belgica antarctica	99 Mb	Kelley et al., 2014	Nature Communications [5]
Aptenodytes forsteri	1.26 Gb	Li et al., 2014	GigaScience [6]
Pygoscelis adeliae	1.23 Gb		
Salmo salar	2.97 Gb	Lien et al., 2016	Nature [7]
Parachaenichthys charcoti	795 Mb	Ahn et al., 2017	GigaScience [8]
Delphinapterus leucas	2.32 Gb	Jones et al., 2017	Genes [9]
Tigriopus kingsejongensis	295 Mb	Kang et al., 2017	GigaScience [10]
Salvelinus alpinus	2.2 Gb	Christensen et al., 2018	Plos One [11]
Dissostichus mawsoni	824 Mb	Chen et al., 2019	GigaScience [12]

As shown in Fig. 1, research on the genomes of animals started in 1998, and the number of related published articles has increased significantly since 2010. It was not until 2011, however, that the first genome of a polar animal, the Atlantic cod, was sequenced [1] (Fig. 1b). Contrary to popular belief, polar animal resources are not exceptionally scarce. Although it is true that there are relatively few mammalian species in polar regions, there are hundreds of fish species. Therefore, despite the reasonable diversity of polar animals, the genomic research is significantly lagging.

2.1.2 Foreign research institutions play a dominant role in polar genomic research

With the exception of the genomes of the penguin and Antarctic toothfish, which were sequenced by Chinese scientists, the first affiliation of researchers who sequenced the genomes of the other 10 polar animal are all located in countries other than China: the Arctic charr and beluga whale (2 species sequenced in Canada); the Antarctic midge and polar bear (2 species sequenced in the USA), the Atlantic cod and Atlantic salmon (2 species sequenced in Norway); and the Antarctic bullhead notothen, Antarctic dragonfish, Antarctic-endemic copepod, and minke whale (4 species sequenced in South Korea), see Table 1. Most of these research institutions are located in North America or North Europe, which closely reflects their advantageous geographical proximity and long-term focus on polar research. However, it is worth noting that researchers from South Korea have sequenced the genomes of four polar animals, and thus, perhaps surprisingly, South Korea is currently the country that has contributed most to the sequencing of polar animal genomes (recognition of the contribution made to polar animal genome sequencing is based on the country where the first affiliation is located).

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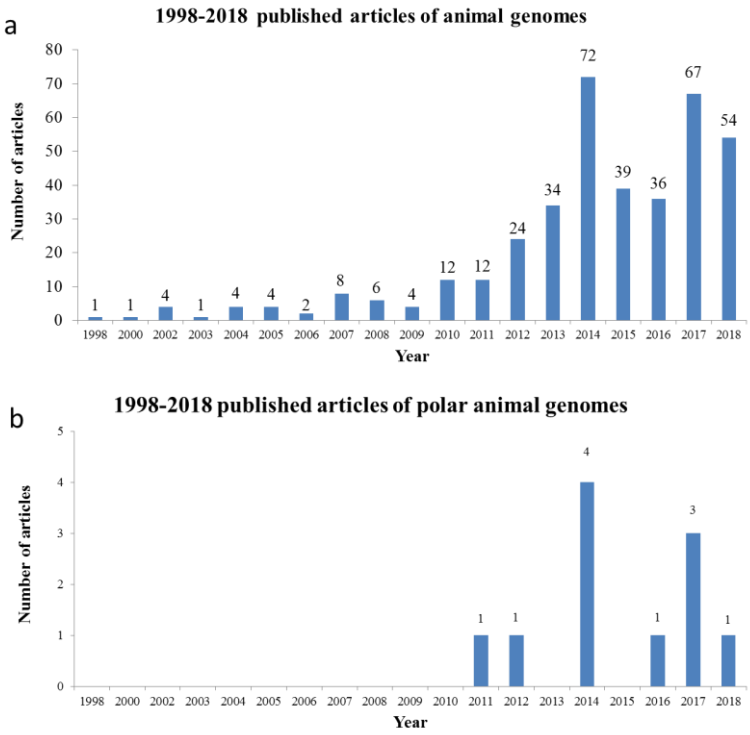

Fig. 1. The published articles on animal genomes (a) and polar animal genomes (b).

2.2 Current status of polar animal transcriptomic research

Many animals that inhabit the polar regions have unique biological characteristics. For example, the Antarctic icefish, which shows excellent tolerance to low temperature, lacks red blood cells and hemoglobin, whereas the bowhead whale, the cells of which appear to have a very low likelihood of becoming cancerous, is among the world's longest-lived animals. Transcriptome analysis is an important tool for the study of gene expression and function, and is of particular significance with respect to providing genetic resources for industrialization with potential for multiple applications. Studies on the transcriptomes of polar animal commenced in 2008, and to date, the transcriptomes of 31 polar animals (8 Arctic species and 23 Antarctic species) have been sequenced. The number of related published articles increased significantly from 2013, reaching a small peak in 2015. A majority of these studies have been conducted in North American and European institutions, with 45% of the articles being published by scientists from the UK and US. Similarly, the number of articles published by Korean workers has increased significantly since 2012 (Fig. 2).

2.2.1 Transcriptomic studies on biological adaptation to the polar environment

Given their typically extreme conditions, the polar regions have, not surprisingly, aroused interest in studying the survival mechanisms of those organisms that inhabit these seemingly inhospitable environments. Studies conducted to date have focused on the adaptation to low temperature, desiccation stress, oceanic acidification, and oceanic warming. From plants (e.g., *Chlamydomonas* sp. [13]) and invertebrates (e.g., the Antarctic nematode [14] and Antarctic copepod [15]), to fish (e.g., *Pagothenia borchgrevinki* [16], Antarctic notothenioid fish [17], Antarctic icefish [18], and *Lepidonotothen nudifrons* [19]), transcriptomes have been sequenced and assembled, and using these assembled sequences, signaling pathways have been analyzed in an effort to elucidate molecular mechanisms underlying the adaptation of these species to the cold environment. For example, based on cDNA library construction and sequencing, Cocca and colleagues discovered the loss of alpha-globin genes in Antarctic white-blooded icefishes [20]. Six species of Antarctic icefishes have also been found to lack myoglobin in ventricle of the heart, resulting in a blood that is virtually transparent and has only 10% of the oxygen-carrying capacity of the blood of red-blooded species [21]. The unique architecture of the oxidative muscles and large-bore vessels of icefishes facilitates the efficient diffusion of oxygen to tissues, and Xu et al. [22] further revealed a general trend of erythropoietic suppression in the cold-adapted notothenioids that lack oxygen-transporting hemoglobins.

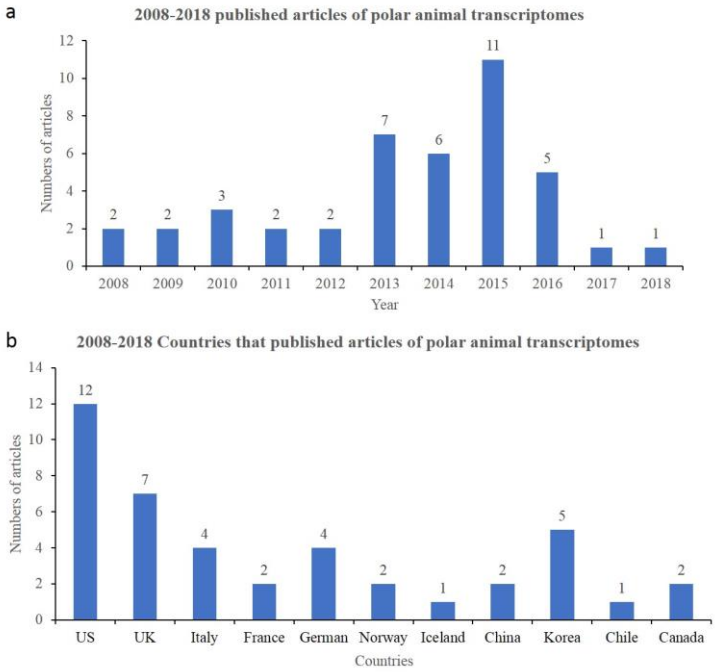

Fig. 2. Number of articles on polar animal transcriptomes (a) and the countries that published articles on polar animal transcriptomes (b).

Comparisons of the transcriptomes of the Antarctic fishes *Notothenia coriiceps*, *Chaenocephalus aceratus*, and *Pleuragramma antarcticum* with those of temperate fish, have revealed that a larger number of ubiquitin-conjugated proteins, which play important roles in maintaining proteins in their native state in the cold, are expressed in the Antarctic fish [23]. Analysis of the transcriptome of the high-latitude bald notothen *Pagothenia borchgrevinki* has revealed that genes related to ubiquitin-protein ligase activity and protein ubiquitination might be involved in the cold adaptation and thermal response of *P. borchgrevinki* [16]. During the reconstruction and annotation of the first skeletal muscle transcriptome of the icefish *Chionodraco hamatus*, active gene duplication and high mitochondrial densities in mitochondrial biogenesis and aerobic respiration were detected [24], which may contribute to enhancing oxygen diffusion and supplying energy to aerobic tissues for cold adaptation in this species.

In recent times, global climate change has raised concerns regarding the survival of polar animals and plants, and ocean acidification and climate warming are currently notably active areas of polar-related research. In this respect, HSP70, HSP90, ferritin, and GST have been shown to be over-expressed in the transcriptomes of Antarctic krill, which is conceivably associated with the mechanisms underlying environmental adaptation [25]. Similarly, Meyer et al. [26] have reported that metabolic pathways in Antarctic krill may have been affected by anthropogenic CO_2 emission and the adaptation of these crustaceans to ongoing environmental changes. Furthermore, changes at the transcriptional level have been detected in *Trematomus bernacchii* in response to rising temperatures [27]. Although there was little evidence of the upregulation of heat shock proteins, hundreds of other genes associated with cellular stress responses were found to be responsive to heat, thereby indicating the potential susceptibility of *T. bernacchii* to environmental variation. Moreover, under the combined stress of increasing temperatures and oceanic acidification, genes involved in metabolic shifts, DNA damage repair, immune system processes, activation of apoptotic pathways, and regulation of cell proliferation, were found to be over-expressed in *T. bernacchii* [28].

2.2.2 Transcriptome studies on stress responses to pollutants

Strong upregulation of the fibroblast growth factor 7 (FGF7) gene has been detected when polar cods are exposed to crude oil, which may protect the liver of these fish from the toxic effect of accumulated biliary compounds, and accordingly, the FGF7 gene could serve as a potential biomarker to assess exposure to oil pollutants [29]. In their transcriptome sequencing analysis of *Gondogeneia antarctica* exposed to three types of pollutant. Kang et al. [30] found that 658, 169, and 367 genes were screened out as potential biomarkers following exposure to polychlorinated biphenyls (PCBs), perfluorooctanesulfonic acid, and perfluorooctanoic acid,

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respectively [30]. Similarly, in a study of the Arctic sea urchin *Strongylocentrotus droebachiensis*, 11 genes were observed to respond to PCB treatment at the transcriptional level, and these genes could thus serve as novel indicator genes for assessing the condition of aquatic environments [31].

2.2.3 Transcriptome studies on different developmental stages and tissues

The growth and development of polar animals has also attracted considerable research interest. Since Pitta et al. first reported the transcriptomes of different tissues in Antarctic krill [32], a number of differentially expressed genes have been identified during the molt cycle of this species [33], and are speculated to be involved in the synthesis, degradation, and resorption of chitin. All brittle stars regenerate lost limbs, and it has been found that the Antarctic brittle star *Ophionotus victoriae* has one of the slowest rates of limb regeneration. Transcriptome analysis indicated that pathways, including the Wnt/β-catenin pathway and Hox gene, Sox gene, and TGF beta signaling pathways, were potentially related to these regenerative processes [34]. Furthermore, in their RNA-sequencing analysis conducted at four stages of development in charr embryos collected from different populations, Gudbrandsson et al. discovered that transcripts in several biological pathways were differentially expressed during charr development, whereas genes involved in energy metabolism and blood coagulation showed different patterns of expression in different populations [35]. Subsequent comparison of single-nucleotide polymorphism (SNP) frequencies indicated extensive genetic differentiation between these populations [35]. In a further study on charr, Magnanou et al. sequenced transcriptomes from different tissues, targeting multiple key pathways, including neuroendocrine, metabolic, and behavioral pathways [36].

2.2.4 Research status of functional genes in polar animals

A small number of functional genes from polar animals have been characterized based on homologous cloning and genome and transcriptome sequencing. These genes have been identified in more than 30 species, among which more than 20 are fish, and are associated with than 20 simultaneous life processes or functions (listed in Table 2) [37–50].

Certain fish inhabiting polar regions have the ability to synthesize antifreeze proteins for adaptation to low temperature. Among these is the Antarctic fish *Lycodichthys dearborni*, in which at least seven variants of the type III antifreeze protein were detected, which were translated into five protein isoforms [37]. The study confirmed that paralogs had diverged under positive selection, and the findings indicated that antifreeze protein diversity might be an important factor contributing to freezing point depression observed in this species [37]. Sequence alignment has revealed that the type IV antifreeze proteins found in *Pleuragramma antarcticum* and *Notothenia coriiceps* show 94% similarity. This protein, which is characterized by highly-conserved introns, is widely distributed amongst teleost fishes, and expression of recombinant proteins in these two species successfully resulted in the development ice crystals with thermal hysteresis values of 0.08°C, which confirmed their antifreeze activity [39].

Heat shock proteins (HSPs) are a widely distributed class of heat stress protein, the synthesis of which is triggered by thermal excitation to protect organisms when exposed to high temperature. The expression of HSP90 has been found to increase significantly when the Antarctic bivalve *Laternula elliptica* is exposed to a temperature of 10°C, indicating the important role of the HSP90 gene in the adaptation and thermal tolerance of this species [44]. Exposure to cold stress is typically associated with an increase in protein denaturation and misfolding, which in turn induces the over-expression of chaperon HSPs, thereby enabling organisms to survive, and in this regard, the constitutive upregulation of HSP70 transcripts in response to low temperature exposure has been reported in three Antarctic notothenioid fishes [45].

3 Problems and challenges

3.1 Polar animal genomic study is in the initial stages

Owing to limitations in sample acquisition technology, the genomes of only 13 polar animals have been sequenced to date, accounting for 3% of the total sequenced animals (more than 380 species). Although the polar region is characterized by rich animal resources, the genomic deciphering of polar animals has been carried out on a disproportionately small scale within only a few species, and predominantly in polar fish (6 species). Accordingly, given that the genomes of many polar animals (including the economically important Atlantic halibut and Antarctic krill) have yet to be sequenced, there would appear to be considerable potential for genome research on these animals.

Table 2. Functional genes that have been studied in polar animals (incomplete data).

Functional genes (proteins)	Latin name	Year of publication
Antifreeze proteins	*Lycodichthys dearborni*	2010 [37]
	Dissostichus mawsoni	2011 [38]
	Pleuragramma antarcticum	2011 [39]
	Notothenia coriiceps	2011 [39]
Zona pellucida proteins	*Notothenioids*	2016 [40]
Immunoglobulin	*Trematomus bernacchii*	2002 [41]
Tc1-like transposon	*Chionodraco hamatus*	2002 [42]
Myoglobin	*Chaenocephalus aceratus*	2007 [43]
Heat shock proteins	*Laternula elliptica*	2008 [44]
	Trematomus bernacchii	2005 [45]
	Pagothenia borchgrevinki	2005 [45]
	Harpagifer antarcticus	2008 [46]
Aryl hydrocarbon receptor	*Salvelinus alpinus*	2015 [47]
Glucocorticoid receptor	*Salvelinus alpinus*	2004 [48]
Red opsin gene	Five Antarctic notothenioid fish	2012 [49]
Hemoglobin	*Channichthyidae*	2011 [50]

3.2 Polar animal transcriptomic study is unsystematic

Although to date at least 31 types of polar animal have been sequenced at the transcriptomic level, owing to current limitations in sample acquisition and preservation technology, the transcriptomic research in polar animals has been characteristically fragmentary, which has accordingly hampered efforts to systematically dissect distinct traits in polar animals at the genetic level. Thus, the refinement of sample collection for the same species and massive transcriptome analysis of other species is pivotal for the large-scale exploitation of gene resources, as well as providing a basis for the genetic dissection of traits of interest in polar animals.

3.3 The functional analysis of genes is not intensive

At present, although preliminary studies have been conducted on some functional genes common to numerous polar animals, the methods employed have been relatively simple, and the primary focus has been on descriptive analysis (e.g., gene cloning and expression pattern analysis). Additionally, there is currently little progress being made with respect to the development of polar model organisms, owing to difficulty in mimicking the polar environment and the fact that there are no corresponding cell lines. Consequently, there is a lack of a platform for gene function analysis and further in-depth study.

3.4 Epigenetic studies on polar animals need to be launched

Although epigenetics plays an important role in animal adaptation to the external environment, such as to changes in temperature, there have been no published studies on epigenetic regulation of the phenotypes of polar animals in a cold climate.

3.5 The application potential of polar animal genes has rarely been realized

Owing to prevailing deficiencies in the acquisition, identification, and functional analysis of polar animal genes, as well as the lack of development of genetically engineered products, the application of polar animal genes is still limited, and thus such products are urgently required.

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4 Technical demands for the exploration and application of polar animal genetic resources

4.1 Systematic OMICs and genetic dissection of distinct traits in polar animals are required

It is necessary to initiate systematic OMICs studies and to develop sample acquisition and preservation techniques that can be applied to polar animals. In order to lay the theoretical foundations for determining the adaptive mechanisms of polar animals and their responses to global environmental change, sequencing of the genomes of polar fishery animals, particularly those inhabiting extreme environments, has particular significance and ideally should be an area of primary focus.

4.2 Research platforms need to be established for in-depth study of polar animal gene function

To investigate the genetics of distinct traits in polar animals, it is important to screen the key functional genes and establish relevant cell lines. Moreover, the development of laboratory culturing procedures and polar model organisms will provide a technical basis for the research that aims to determine gene function.

4.3 Mechanisms underlying adaptation to the polar environment need to be characterized

The adaptability of polar animals provides an ideal basis for studying the crosstalk between the environment and genes and the resultant phenotypes. In this regard, epigenetic research would facilitate elucidation of the mechanisms underlying the regulation of gene expression in an extremely cold environment. Although in general, polar fish are characterized by their slow growth and long life cycle, there are also certain polar species that have growth rates comparable to those of fish inhabiting warmer waters. For example, as a typical cold-water fish, the Atlantic halibut exhibits a rapid growth rate, increasing in weight from 0.25 kg to 2.5 kg in 2 years. The whole-genome sequencing and fine mapping of Atlantic halibut will contribute to accelerating our understanding the molecular mechanisms associated with the growth and metabolism of this fish, and may also provide novel insights with respect to the cultivation and genetic resources of other flatfish and marine fish.

4.4 Research on genetically engineered products and their application need to be strengthened

One of the primary goals of genomic research is to screen genes for application potential and generate genetically engineered products. As an example, antifreeze protein has been widely applied as a food additive and to confer cold resistance to crop plants. However, this protein is mainly obtained from natural sources, which substantially limits potential yields. Large-scale production of antifreeze protein would be achievable based on genetic engineering, and in this way, the industrial application of antifreeze protein could be realized in many fields, including cell and tissue cryopreservation, food, medicine, and cosmetics. Furthermore, it is of considerable significance and application potential to develop genetically engineered products of the low-temperature enzymes found in Antarctic fish, as detergent additives and disinfectants.

5 Countermeasures and suggestions

5.1 Developmental goals (year 2025 and 2035)

Here, we briefly summarize the goals that we anticipate to be achieved within the next 5 and 15 years.

By 2025, the whole-genome sequencing of 5 to 10 polar fish and other fishery animals, for example the Antarctic krill, will have been accomplished, which would hopefully make a significant contribution to elucidate molecular mechanisms underlying the adaptation of important polar fishery animals to the unique polar environment. In this regard, it will be important to verify the function of polar fish genes through gene editing technology in model fish or fish cell lines. The laboratory conditions for the temporary breeding of polar animals should also be explored, in order to establish a platform for research on polar animal gene function.

By 2035, we predict that a refined platform will have been established for polar animal gene resource exploration and that the genomes of 20 polar fishery animals will have been deciphered. Genetic dissection of three to five traits of particular interest will have been completed, with the identification of a series of key genes associated with adaptation to the polar environment. The technology for establishing polar animal cell lines will also have been improved. Temporary and long-term breeding of polar animals in the laboratory for the in-depth study of gene function will have been realized. Appropriate candidate genes will have been selected and one or

two genetically engineered products will have been developed for research transformation and industrial application.

5.2 Primary missions

5.2.1 Genetic dissection of distinct traits in polar fishery animals

As a priority area, genomic and transcriptomic research of important polar fishery animals needs to be strengthened, including sequencing the genomes of a larger number of polar species, and focusing on the genetic analysis of distinct traits. Furthermore, research should focus on the epigenetics of polar fishery animals, particularly the regulatory mechanisms associated with the cold adaption of these species. In this regard, genomic sequencing of those species with strategic ecosystem significance and food resource value, notably the Antarctic krill and Atlantic halibut, should be accorded with specific attention.

5.2.2. Functional confirmation of polar animal-specific genes

In-depth analysis of polar animal genomes and transcriptomes will be performed for the screening of polar animal-specific genes (or genes that have evolved to perform distinct functions). The function of these genes will be investigated in model fish or fish cell lines by employing gene editing, over-expression technology, and transgenic technology. In this regard, conditions suitable for the laboratory culture of polar animals should be explored with a view toward establishing a platform for gene function studies.

5.2.3. Development and application of genetically engineered products in polar fishery animals

With regards to the cold resistance, disease resistance, anti-cancer properties, rapid growth, and longevity of polar animals, functional genes will be screened and the corresponding products, such as antifreeze proteins, low-temperature enzymes, and products related to rapid growth promotion, will be produced through gene engineering technology. The application potential of functional gene products in food, medicine, household products, aquaculture, and other fields will be assessed, which will contribute to the transformation and utilization of gene resources, and increase the value-added effects in these fields.

5.3 Suggestions for key scientific and technological projects

As an initiative to advance studies on the genetic resources of polar animals, we propose the establishment of a national key R & D program for the exploration and application of genetic resources in polar fishery animals, which would mainly serve to promote the following developments: (1) the whole-genome sequencing and fine mapping of important polar fishery animals, including polar fish and Antarctic krill; (2) the genetic dissection of the distinct traits; (3) the establishment of cell cultures and cell lines; and (4) the development and application of genetically engineered products.

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