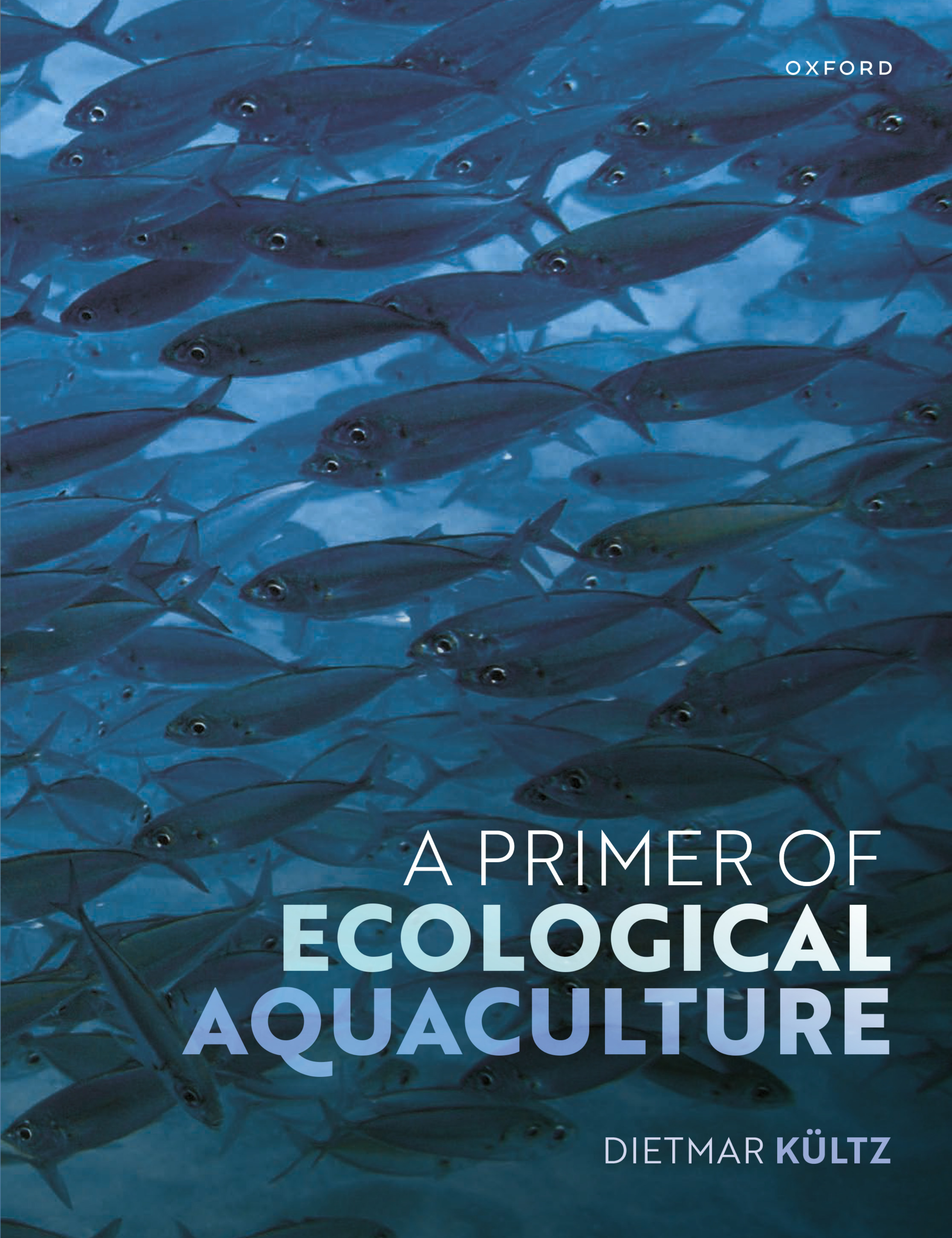

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A PRIMER OF ECOLOGICAL AQUACULTURE

DIETMAR **KÜLTZ**

A Primer of Ecological Aquaculture

Endorsements

"This important new volume on aquaculture presents a remarkable synthesis of all the key issues involved in the commercial culturing of freshwater and marine species. It provides a comprehensive overview of the basic biological elements of aquaculture, including new information on the use of genomic and genetic tools, and incorporates these analyses into a broader ecological, environmental, and sociological context. The emphasis on strategies for protecting water quality—a vital part of the aquaculture enterprise—is especially well-presented. The volume deserves wide readership among students and scientists who not only have interests in aquaculture, but also in sustaining robust aquatic ecosystems in freshwater and marine environments."

George N. Somero, David and Lucile Packard Emeritus
Professor of Marine Science, Hopkins Marine Station, Stanford University, USA

"Dietmar Kültz has distilled many years of teaching an undergraduate course in aquaculture into an engaging and accessible text. The book is a huge endeavour and presents an honest and rigorous assessment of aquaculture practices with clear, detailed descriptions of invertebrate and vertebrate aquatic culture, diseases, and water management. The 'Key Conclusions' at the end of every chapter are particularly useful for students."

Patricia A. Wright, Professor, Department of Integrative Biology,
University of Guelph, Canada

"A must-read primer for anyone considering aquaculture either as undergraduate and postgraduate students or aquaculture farmers. Dietmar Kültz takes readers on a fascinating journey into the world of ecological aquaculture to stimulate awareness of the need to reach a more sustainable future."

Silvia Gomez-Jimenez, Director of Accredited Aquaculture Diagnosis Laboratory,
Research Centre for Food and Development, Mexico

"*A Primer of Ecological Aquaculture* by Dietmar Kültz is the latest addition to the growing list of entry-level books on the topic of aquaculture. It differs from other books, however, on its emphasis on ecological aspects of aquaculture. As such, it is like a new tool that seems impossible to have lived without before it was acquired. The book succeeds by providing a holistic assessment of various aquaculture production systems including inputs, outputs and how they contrast and compare among various species groups. Most importantly, the book presents both problems and opportunities associated with aquaculture in a concise and balanced manner. Aquaculture production must increase to meet future seafood demand and this book provides solid information and guidance on how society can meet seafood demand by employing sustainable aquaculture practices."

Ronald Hardy, Professor Emeritus, Department of Animal,
Veterinary, and Food Sciences, University of Idaho, USA

"As the demand for wild caught seafood is continuing to increase while stock volumes are rapidly decreasing, our future food security will rely more heavily on ecologically sustainable aquaculture practices. Kültz presents a detailed exploration of its limitations and novel paths to diminish its ecological footprint, enriched with comprehensive analysis and clear graphics. This accessible primer systematically dissects the rationales behind current practices, from monocultures and polycultures to microcosms and mesocosms. It also provides clear signposts to sustainable practices aimed at minimizing the exploitation of natural ecosystems, while maximizing production efficiency and food security."

Gillian Renshaw, Professor, School of Allied Health Sciences,
Griffith University, Australia

A Primer of Ecological Aquaculture

Dietmar Kültz
Professor of Physiological Genomics, College of Agricultural and Environmental Sciences, University of California Davis, USA

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Cover image: High-density aquaculture of Bigeye scad (Selar crumenophthalmus)
is supported by their natural schooling behaviour. Photo by author.

About the Author

Dietmar Kültz is a Professor of Physiological Genomics at the College of Agricultural and Environmental Sciences, University of California Davis, USA. His laboratory focuses on investigating the mechanisms of stress-induced evolution in fish and marine invertebrates. His research spans molecular to organism levels of biological complexity and utilizes reductionist synthetic biology, biochemical, and holistic systems level approaches to dissect causality between environmental effects on cells and organisms, physiological responses, and complex adaptive phenotypes. He teaches a molecular genetics laboratory course, an introductory aquaculture course, and a stress physiology course at UC Davis. Professor Kültz received his BSc/MS and doctoral degrees from the University of Rostock in Germany. He was a DAAD postdoctoral fellow at Oregon State University, a Fogarty Visiting Fellow at the National Institutes of Health (Bethesda), and Assistant Professor at the University of Florida before joining the faculty at UC Davis.

Preface

Aquaculture exemplifies the ongoing global struggle to strike a sustainable balance between the conflicting needs of a large human world population, human health, ecosystem health, the welfare of wild and domesticated animals, and the economic principles of globalized economies. On the one hand, aquaculture has great potential for providing us with a healthy and nutritious food supply while alleviating pressure on capture fisheries and reducing fisheries-induced habitat destruction, overfishing, genetic modification of wild populations, and wholesale waste of bycatch. On the other hand, aquaculture relies heavily on clean water, an increasingly precious (and dwindling) resource that is subject to intense pressure through being used for many competing purposes. The multifaceted nature of aquaculture is most evident in the division of approaches between those that emphasize minimal reliance on ecosystem services (e.g. recirculating aquaculture systems, aquaponics) versus those aimed at maximizing profitability (e.g. open pond, cage, and raceway systems). Ecological considerations have received increasing attention in aquaculture since the turn of the millennium and their proper implementation promises to greatly accelerate the rate at which the field moves forward.

This book aims to introduce students to the basic concepts, opportunities, and challenges of aquaculture with an emphasis on ecological considerations. I contrast the many values and promises of aquaculture (including specific approaches and commodities) with their pitfalls, drawbacks, and challenges. My goal is to provide students with a broad understanding of the general state of aquaculture to equip them with the knowledge they need to contribute to future advances in the field. To achieve this goal, a critical assessment of current aquaculture practices from a broad, interdisciplinary perspective is necessary. The book carries out such an assessment from the standpoint of how best to align the two major (and often conflicting) goals of future aquaculture development: minimizing reliance on ecosystem services while maximizing productivity.

This book represents a broad snapshot assessment of the current state, past developments, and prospects of applying knowledge in aquatic animal biology and engineering to the captive culture of aquatic animals. My intent was to transcend traditional disciplinary boundaries whenever possible and present contrasting perspectives whenever applicable to stimulate critical assessment of aquaculture practices by students. There are many different opinions about the best way to further develop aquaculture. The perspective presented here should not be taken dogmatically, but rather should stimulate critical thinking in readers. To make the book more accessible, e.g. to students taking a semester- or quarter-long course on this subject, it presents the material concisely and provides select examples to illustrate pertinent points and key concepts, and it explains scientific and aquaculture-specific terminology when first used. It is not my intent to comprehensively review specific commodities or go into undue detail regarding specific aspects of aquaculture if such detail is unnecessary to support salient facts and arguments.

The motivation for writing this book arose from feedback provided by my students and colleagues. I have been teaching a general education (GE) class on aquaculture (ANS 18) at the University of California, Davis for more than a decade but a suitable text accompanying the class material was missing. Most students I have taught prefer single-author texts that require little prior knowledge of a subject and are written in a consistent style, rather than more specialized volumes comprised of chapters by different authors. Although there are many excellent books focusing on aquaculture, some of which are referenced in this volume, an integrated discussion of the ecological cornerstones of aquaculture in the form of a concise 'primer' was needed to help students learn pertinent concepts and principles. This book thus attempts to serve as such a 'primer' in a format that is accessible to readers from a broad range of academic backgrounds and experience. It is meant to consolidate and expand on my lecture notes to provide a study guide for students interested in both the natural biology and the culture of aquatic organisms, both marine and freshwater.

Although I majored in marine ecology when at university, my own research now focuses heavily on biochemical mechanisms of environmental tolerance and stress-induced evolution in fish and marine invertebrates using molecular, cellular, and systems biology approaches. It seems natural to investigate molecular phenomena at an increasing level of depth to explain how organisms function within their environment and how life works. However, at the same time it is important to integrate reductionist approaches with holistic approaches that explain the function of systems, e.g. ecosystems or aquaculture systems, that are more than just the sum of their parts. This book emphasizes the holistic view throughout.

This book could not have been completed without the support and encouragement from my family, friends, and colleagues. Many thanks go to my family, especially my wife, son, and parents for always supporting my pursuit of scientific research and enduring my spending long hours in the laboratory and at the desk pondering scientific questions. Their patience, encouragement, and feedback were invaluable for completing this book project, which took more effort and time than I had originally anticipated.

I am also particularly grateful to Professor George Somero (Stanford University), my postdoc mentor and long-term friend, who has read and commented on early drafts of all chapters. His knowledgeable feedback and constructive comments helped greatly in shaping the final draft of the book and pushing it over the finish line on time. I am also very grateful to other colleagues and friends who have read and made valuable suggestions for improving individual chapters of this book, including Professors Steve McCormick (University of Massachusetts), Ron Hardy (University of Idaho), Colin Brauner (University of British Columbia), Patricia Wright (University of Guelph), Brian Sardella (California State University Stanislaus), Wes Dowd (Washington State University), Jonathon Stillman (San Francisco State University), Silvia Gomez-Jimenez (CIAD and University of Sonora), Alison Gardell (University of Washington), Peter Allen (Mississippi State University), Frederick Silvestre (University of Namur), Jason Podrabsky (Portland State University), Katie Gilmour (University of Ottawa), Tyler Evans (California State University East Bay), Xiaodan Wang (East China Normal University Shanghai), and Esteban Soto and Jackson Gross (both University of California Davis). Many thanks also go to my graduate students Elizabeth Mojica, Meranda Corona, Larken Root, and Jens Hamar, who read chapter drafts and provided photos and valuable feedback that helped improve the book. I also thank my colleagues including Professors Avner Cnaani (Agricultural Research Organization, Beth Dagan), Delin Duan (Institute of Oceanology Chinese Academy of Sciences), Steve McCormick (University of Massachusetts), Olivier DeClerck (Ghent University) and Esteban Soto (University of California, Davis), and Miguel Sepulveda (Rio de Janeiro, Brazil), Christian Veterlaus (marinecultures.org), and Mark Zivojnovich (Hydromentia Technologies) who have kindly shared illustrations for the book. Their contributions are acknowledged in the corresponding figure legends.

Finally, I thank my editorial contacts at Oxford University Press, Ian Sherman, Charlie Bath and Sharmila Radha, who kept my writing on track with the planned schedule for publication and compatible with the projected size of this book. Ian and Charlie helped with all aspects of the book production process and in keeping the page number from increasing beyond a limit that we felt would diminish accessibility. The collective feedback and great advice I have received from many people helped substantially improve this book although, of course, I am solely responsible for any omission or errors that may remain.

Dietmar Kültz,
Davis, CA, November 10, 2021

Contents

PART 1

General Principles of Ecological Aquaculture

CHAPTER 1

Aquaculture terminology and basic concepts

'Science and engineering is meant to be questioned, tested and re-tested, but the road of true progress can be long, convoluted and tiresome.'

Adey and Loveland, *Dynamic aquaria: building living ecosystems* (2007)

This book introduces the basic concepts, opportunities, and challenges of aquaculture with an emphasis on ecological considerations. The road to progress in aquaculture has been followed for several millennia leading to a dramatic increase in its global productivity. We have arrived at a major, challenging junction on this road and future advancement of aquaculture depends on a thorough understanding of the ecological value of clean water as its main resource.

Therefore, this book outlines links between aquaculture, trophic cascades, nutrient cycles, and ecosystem services that determine water quality and ecosystem stability. A basic understanding of such links reveals opportunities for increasing the ecological sustainability of aquaculture and makes the diverse but interwoven facets of ecological aquaculture accessible to students entering this field.

I assess the prospects of various aquaculture practices for key species groups based on the premise of aligning two major (and often conflicting) development goals: minimizing reliance on ecosystem services while maximizing productivity.

The first part of the book builds a general understanding of terminology, the history, objectives, approaches, and ecological implications of aquaculture. It also emphasizes prospects for further development of ecologically sustainable aquaculture approaches. The discussion of aquaculture approaches focuses on their potential for meeting future demand in an economically feasible manner while minimizing the exploitation of common property resources and reliance on ecosystem services.

Although socio-economic aspects are critical for practical implementation of aquaculture solutions, they are not considered here in the interest of brevity and to maintain focus. They have been discussed extensively elsewhere and the reader is referred to recent works that highlight this important topic (Bunting, 2013; FAO, 2020).

Specific aquaculture practices are illustrated for a selection of economically important aquatic species in Part 2 of this book. These examples illustrate key concepts and contrast the values and promises of aquaculture with their pitfalls, drawbacks, and challenges to instil a broad understanding of the current state of aquaculture and prospects for increasing its ecological sustainability.

It was not my intent to comprehensively review specific aquaculture commodities or practices and omissions in this regard are unavoidable in this introductory overview. The reader is referred to excellent recent volumes that focus on particular aspects of aquaculture more comprehensively (e.g. Pillay and Kutty 2005; Bert, 2007; Davenport *et al.*, 2008; Costa-Pierce, 2014; Boyd and McNevin, 2015; Stickney, 2017; Lucas, Southgate, and Tucker, 2019).

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In addition, there are many volumes that cover aquaculture practices for a particular species or species group in great detail, e.g. oysters (Hanes, 2019), shrimp (Leung and Engle, 2010), and tilapia (El-Sayed, 2019).

Part 3 provides an overview of abiotic parameters and biotic factors that are critical for water quality management in aquaculture. Clean water is a common property resource that affects all. Aquaculture competes for this resource with other uses, including as drinking water, for sanitary purposes, for ecosystem health and species conservation, for agricultural irrigation, and for human recreational and cultural activities.

Most importantly, clean freshwater is limited and its value as a resource is increasing in parallel to the rising world population. Nevertheless, freshwater (FW, also referred to as land-based) aquaculture has greater prospects for future sustainable development than mariculture. Throughout this book I provide examples supporting this argument. Clean water, whether fresh or marine, can no longer be considered a free natural resource but must be valued by properly incentivizing its conservation.

1.1 What is aquaculture?

According to the Food and Agriculture Organization (FAO) of the United Nations (UN), 'Aquaculture is the farming of aquatic organisms in both coastal and inland areas involving interventions in the rearing process to enhance production.' (FAO, 2019). Farming is the rearing of organisms under (semi-)controlled conditions and implies ownership (by an individual or corporation) over the organisms that are being reared. In contrast to aquaculture, capture fisheries collect seafood from wild populations, i.e. from natural, unmanaged resources.

The organisms that are subject to capture fisheries are considered common property resources that can be exploited and are not owned by anyone, although fishing rights often apply. Capture fisheries yield has plateaued at approximately 90 million metric tons annually since the turn of the millennium while aquaculture yield continues to increase steadily (Figure 1.1). In fact, 52% of world marine fish stocks are already fully exploited, 17% are overexploited, and 8% are depleted (with 1% recovering), while 20% are moderately exploited and only 3% are underexploited by capture fisheries (FAO, 2011).

Aquaculture and capture fisheries play an essential role in ensuring food supply and security in the context of climate change, in particular in developing countries. These tasks are recognized in the 2030 UN Agenda for Sustainable Development that comprises seventeen sustainable development goals (SDGs) (United Nations, 2015). One of these goals (SDG 14) emphasizes the conservation and responsible use of the oceans and marine resources for sustainable development, which includes aquaculture development governed by proper ecological stewardship.

Aquaculture exemplifies the ongoing global struggle to strike a sustainable balance between the many (often conflicting) needs of a rapidly increasing world population. Such needs pertain to human health and nutrition, ecosystem health, the welfare of wild and domesticated animals, the cultural history of peoples, and the economic principles of globalized economies.

On the one hand, aquaculture has great potential for securing a healthy and nutritious food supply while alleviating pressure on capture fisheries and reducing fisheries-induced habitat destruction, overfishing, genetic modification of wild populations by fisheries-induced evolution, and wholesale waste of bycatch.

On the other hand, aquaculture relies heavily on clean water, an increasingly precious (and dwindling) resource that is subject to intense pressure of being used for many competing purposes. Although transitions between solid and liquid state water occur more rapidly because of climate change, the total amount of water on earth has not changed much.

The amount of available clean water is decreasing because water pollution has increased greatly over the past few centuries, which affects the utility of available water for many human needs. The rate of pollution of the world's inland water bodies mirrors the exponential growth of the human population, although environmental protection efforts have improved this trend in recent decades. Even the seemingly vast reservoir of ocean

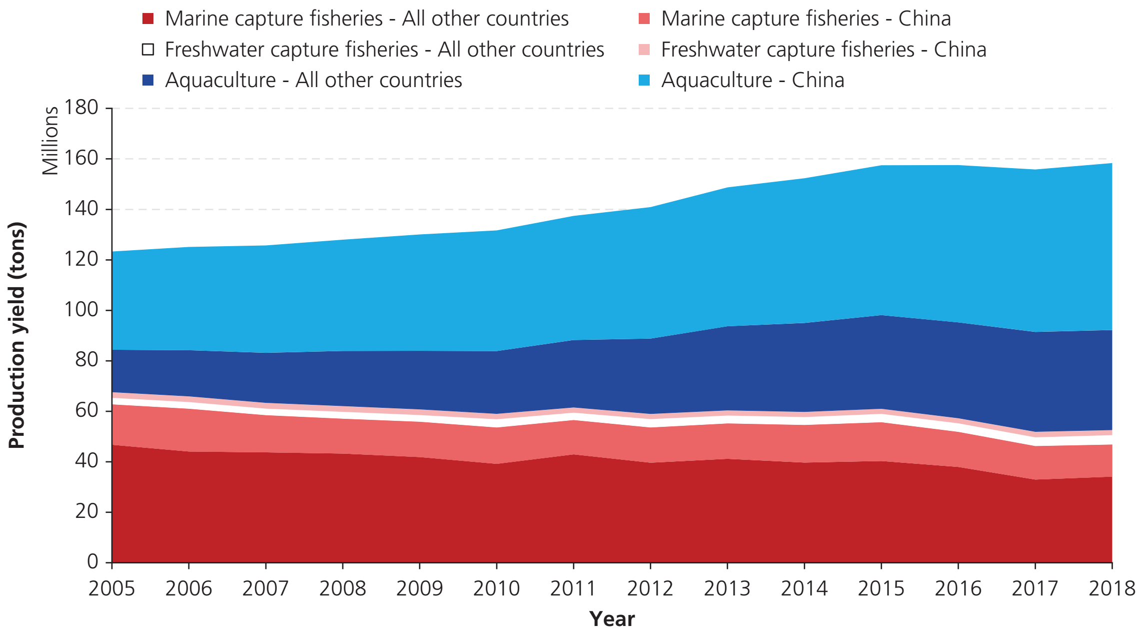

Figure 1.1 Yields of seafood production by aquaculture and capture fisheries from 2005 to 2018. Global yields excluding China and yields produced in China are shown separately. Data source: OECD.stat.

water is increasingly impacted by anthropogenic pollution.

A rising world population requires more FW for drinking, sanitary, agricultural, and other purposes. FW is also essential for maintaining the balance of inland ecosystems. Clean seawater (SW) is required to maintain ecosystem health and species diversity in the oceans, which is particularly critical in near-shore areas exploited by aquaculture, including coral reefs, kelp forests, and mangrove lagoons.

1.2 Sustainable aquaculture development

Ecological considerations have received increasing attention in aquaculture during the past few decades and their proper implementation promises to greatly accelerate the rate at which the field moves forward. As a result of the industrial revolution, clean water, in particular FW, became progressively precious as a resource and competition over water rights and access have resulted in fiercer rivalries as this resource became scarcer and its usage more prolific.

Although crucial for assessment of the ecological impact of aquaculture practices, 'comparatively little effort has been expended on documenting and analysing the range of methods used in exploitation of aquatic environments' (Beveridge and Little, 2014). Nonetheless, consumer awareness and interest in the sources of seafood is increasing.

Educational programmes, such as the SeaFood Watch programme of the Monterey Bay Aquarium, offer relevant knowledge and many markets now provide detailed information about seafood sources and methods of harvest such that this knowledge can be factored into consumer choices (Figure 1.2).

There is a growing public resentment against semi-intensive farming systems that rely heavily on common property resources and ecosystem service capacity (open systems). Another main concern with semi-intensive farming is animal welfare. To meet high seafood demand and address such concerns, aquaculture development goals should prioritize practices that maximize yields while also

Figure 1.2 Consumer information at a seafood market in Davis, California. Each seafood item is tagged with information about its origin and the method of catch if obtained by capture fisheries. This information educates consumers about their choice of seafood products and gives them the option to consider factors other than price (blacked out), appearance, and familiarity with the product for their selection. Tag information such as aquaculture farm-raised locally, aquaculture farm-raised imported, wild-caught by hook-and-line locally, wild-caught by bottom trawling imported, etc., expands the information available for educated consumer choices. Photo by author.

minimizing exploitation of ecosystem services and maximizing animal welfare.

Development of better wastewater treatment strategies should be accompanied by utilization of species that occupy low levels in trophic (nutrient) networks and are most amenable to high-density culture in captivity under high animal welfare standards.

Sustainable development was defined by the United Nations General Assembly in 1983 as 'development that meets the needs of the present without compromising the ability of future generations to meet their own needs' (Brundtland, 1987). This vague definition requires an assessment of present and future needs of humanity, which may be very subjective.

Prioritizing needs for political decision makers is the domain of lobbying efforts, which are highly polarized towards achieving specific objectives. For example, the need for access to clean water is prioritized differently by aquaculture producers, agricultural producers that depend on irrigation, metropolitan cities relying on water for sanitizing and drinking purposes, conservationists, or individuals requiring water for recreational and health activities.

Each of these needs has its own merits, but which is more important if the cumulative demand is higher than the supply? The answer to this question often depends on local elites with the strongest influence and their elitist priorities: 'the tendency for local elites to capture projects and programmes and use them for their own benefit should indeed be recognized as a fact of life' (Chambers, 2005).

Addressing increased seafood demand in a sustainable manner is not limited to increasing the sustainability and output of production. A key aspect for achieving this goal is to reduce food loss and waste, which has great potential to improve the efficiency of the whole food chain. Approximately one-third of food produced for human consumption (about 1.3 billion tons annually) is lost (Gustavsson, Cederberg, and Sonesson 2011). Reduction of this massive food waste must be a priority to sustain earth's limited natural resources.

Not only are we losing large amounts of the much-needed supply of safe and nutritious food, but a large part of the carbon footprint associated with food production is also generated in vain. Food loss occurs along all parts of the food chain, including the consumer level. It has been estimated that per capita food waste by consumers is highest (95–115 kg annually) in Europe and North America and lowest (6–11 kg annually) in sub-Saharan Africa (Gustavsson, Cederberg, and Sonesson, 2011).

Consumer behaviour, high food safety standards, and lack of coordination between producers and other commercial entities in the food supply chain are major causes of food waste in industrialized countries. In lower-income countries of the developing world the major causes of food loss are managerial and technical limitations in production, food preservation, and marketing systems.

Food loss can be reduced by raising awareness and coordination among food producers, retailers, and consumers in industrialized countries; by improving infrastructure, preservation, and management of the food supply chain in developing countries; and by globally increasing the ratio of food safety versus food waste. Aquaculture producers, commercial entities involved in the seafood supply chain, and seafood consumers need to enhance their efforts for reducing food waste as an integral and important part of sustainable development.

1.3 Cell-based seafood

Cell-based seafood is an emerging alternative to capture fisheries and conventional aquaculture. In this approach the seafood is produced from animal cells in tissue culture that yields tissue resembling muscles. Cells that make up muscle tissue in animals are used but these cells are grown in bioreactors and incubators rather than in the animal.

Ideally, no animals are required for cell-based seafood production, other than for taking initial tissue biopsies that are used to derive and immortalize cells. The immortalized cells grow and multiply in growth media inside bioreactors or cell culture incubators (in theory indefinitely). Part of the grown tissue is regularly harvested while the remainder is allowed to continue to grow to support regular harvests. This area of food technology represents undoubtedly a promising approach for ecologically sustainable food production systems.

The concept of cell-based foods is already well established for mammals (e.g. to produce burgers) or birds (e.g. to produce chicken breast substitutes). Many start-up companies are now exploring a similar strategy for a variety of different fish and invertebrates (e.g. shrimp) that are key aquaculture species.

There are advantages of cell-based seafood over cell-based foods derived from mammalian or avian cells. Fish cells and aquatic invertebrate cells can be grown at ambient CO_2 while mammalian and avian cells require CO_2 supplementation. Cells from cold-water fish and invertebrates do not require heated incubators or minimal energy for heating. Moreover, they naturally produce a higher level of healthy, polyunsaturated fatty acids to maintain an optimal fluidity of their plasma membranes and intracellular membranes at lower temperature (to counteract slower Brownian motion).

In theory, cell-based seafood could dramatically improve the ratio of seafood produced relative to the amount of nutrients used to grow it, while minimizing the amount of waste that is generated. Possibilities for optimizing and controlling a cell culture system in terms of inputs and outputs of matter and energy are much greater than for growing complex multicellular animals. Moreover, 100% of the cells or tissue produced would be utilized while generally less than 50% of the biomass of aquaculture animals is used for seafood production. In addition, given proper knowledge of the species, it is possible to direct the differentiation of cells in culture towards specific desirable cell types (e.g. myocytes or adipocytes).

In praxis, many challenges remain for reliable economical production of cell-based seafood. Generating cell lines from fish and aquatic invertebrates is anything but trivial, especially if differentiated adult tissues (e.g. muscle tissue) are used as the source of biopsies for establishing primary cultures. Immortalization is the process of preventing cellular senescence in culture to achieve indefinite mitotic cell division and growth in culture. This process is easier to achieve when embryonic, relatively undifferentiated cells are used as the source of primary cultures.

Although it is easier to create immortalized cell lines from embryonic tissues, the resulting cell lines will likely have a fibroblast or neuroepithelial cellular phenotype and need to be further manipulated to steer cell differentiation towards the desired phenotype of myocytes plus adipocytes. Manipulation of cell differentiation can be achieved via synthetic biology approaches, but such approaches may be unattractive to consumers because they are equivalent at the cellular level to producing genetically modified organisms (GMOs) at the animal level.

The alternative to synthetic biology approaches for directing cell differentiation are methods that employ stress-induced evolution and various supplements in cell culture media to steer cell differentiation towards the desired phenotype. Such media supplements may be tissue-specific growth factors, proteins, metabolites, or abiotic factors that control cell differentiation and pathways.

Another important consideration is that cellular phenotype may change with population doubling time while cell lines are being propagated continuously in incubators or bioreactors. For example, even if muscle biopsies are obtained and primary cultures are successfully immortalized, the resulting cell lines may dedifferentiate as they grow and multiply. Therefore, it is necessary to monitor the molecular phenotype (protein composition) of cells during the culture process. Such monitoring is possible using modern proteomics technologies, but costs are still relatively high.

There are very large differences in the propensity of cells from different species of fish and invertebrates to immortalize spontaneously in primary cell cultures. Obtaining immortalized cell lines from some species (few) is relatively easy while for (most) others this process is notoriously difficult. This difficulty applies especially when spontaneous cell immortalization approaches are pursued. Using very large amounts of starting biopsy material represents a possible remedy but is often impractical. An example of a spontaneously immortalized fish cell line from a major aquaculture species used for seafood production is the tilapia OmB cell line generated in the author's laboratory (Figure 1.3).

Spontaneous immortalization refers to a process during which primary cell cultures overcome cellular senescence and acquire the ability to grow and divide indefinitely without any invasive genetic manipulation. This process is based on natural selection of cells that can bypass senescence under culture conditions *in vitro*. It is comparable to traditional selective breeding or domestication at the level of whole animals. Selection of spontaneously generated genetic variants is generally preferred by consumers over synthetically creating specific genetic variants to promote cell immortalization. The latter approach is comparable, in principle, to producing GMOs (Chapter 6).

Another challenge for cell-based seafood is the development of appropriate edible matrices for cell attachment that mimic the three-dimensional structure of meat (muscle tissue), maximize the surface area for cell growth while ensuring proper media circulation, promote formation of an extracellular matrix (ECM consisting of secreted proteins and other components) that resemble ECM in muscle tissue, and minimize intercellular space to achieve a desirable texture.

Growing cell lines from fish and aquatic invertebrates in affordable, defined media is another task that requires careful consideration for commercial development of cell-based seafood. Animal serum such as foetal bovine serum (FBS) or fish serum is commonly used as a supplement in concentrations

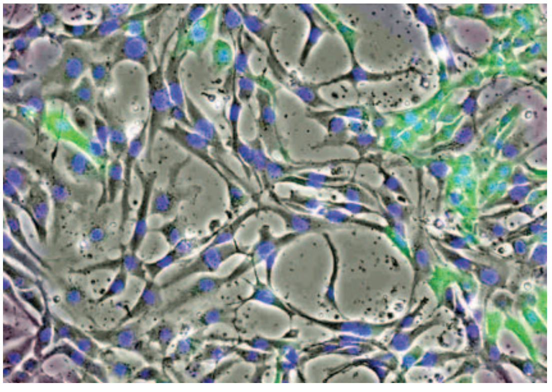

Figure 1.3 Immortalized tilapia OmB cell line that can be grown indefinitely *in vitro*. The cell line was produced in the author's laboratory (Gardell *et al*., 2014). The image was taken by a combination of phase contrast and fluorescence microscopy. For better visualization, cell nuclei in this batch of cells have been stained with a blue dye (NucBlue) and some cells express green fluorescent protein (GFP). The original OmB cell line was derived by stress-induced immortalization of primary cell cultures obtained from a tilapia biopsy without any genetic manipulation. Photo by Jens Hamar.

of up to 10% for cell culture media. If this is the case, then the argument that no animals are required to produce cell-based seafood no longer holds up.

Vertebrate serum contains many growth factors and metabolites that promote cell growth and differentiation. Finding specific combinations of these factors that can be used as defined media supplements in lieu of animal serum represents a highly active area of research. Associated with developing defined serum-free media is the development of methods for media recycling and for minimizing the retention of media hormones and growth factors in the final cell-based seafood product.

The technical challenges pointed out here are tricky but not unsurmountable, given the level of knowledge and technology that is currently available. However, other major obstacles to the adoption of cell-based seafood are consumer acceptance and consumer preference. Ecologically sustainable production of high quality, healthy food for seven billion or more people cannot be achieved for another century using current approaches. Novel and innovative solutions need to be implemented. Part of those solutions is education to influence consumer preference.

If, in fact, more or equally healthy and nutritious food can be produced by ecologically more sustainable cell-based systems, then it will be important that the look and feel of these new products mimics that of traditional food favourites as closely as possible. Research efforts for achieving such mimicry must consider regional differences in culinary cultures. They should be paralleled by education efforts for incentivizing a shift in consumer preference. The look and feel of current beef and chicken cell-based foods is already so much better than that of dietary supplement pills, but further improvements are necessary.

Although cell-based seafood represents a promising approach for sustainable food production it is still in its infancy and is not considered further in this book. Readers interested in cell-based seafood are directed to recent publications on this topic, including Rubio *et al.*, 2019 and Potter *et al.*, 2020.

1.4 Aquaculture concepts and terminology

In the remainder of this chapter, I briefly define key concepts and terms used often throughout the book.

Seafood is an umbrella term that describes edible products derived from aquatic organisms including FW, brackish, and marine organisms that are produced for the purpose of human consumption. Seafood is produced by aquaculture, capture fisheries, or most recently also by cell-based approaches. Methods of seafood production differ greatly in the extent to which they rely on common property ecosystem resources.

Ecosystems are 'diverse communities of organisms, supported and constrained by a given physical-chemical environment, interacting to capture and process energy and nutrients in food webs' (Adey and Loveland, 2007). Ecosystem services are defined as benefits provided by ecosystems to humankind for all purposes. Ecosystem services are critical for the provisioning of clean drinking water, the decomposition of organic wastes, and providing many other benefits. Because the capacity for ecosystem services is limited their provisioning must be monitored and, if necessary, regulated wisely.

Ecosystem services return the matter and energy exiting from aquaculture systems to the global nutrient cycle. This recycling capacity has limits that are different for each locality. Moreover, these limits are not static but are subject to dynamic changes over time. Spatiotemporal dynamics of ecosystem service capacity is impacted by anthropogenic pollution and acceleration of climate change, seasons, weather, and many other factors.

The dynamic nature of capacity limits and ecosystem succession must be considered in models aiming to predict the impacts of aquaculture systems that are open to the natural environment (flow-through pond, raceway, or cage cultures). The area of wild wetland habitat required to recycle wastewater produced by aquaculture depends on these dynamic limits of ecosystem service capacity.

Extensive aquaculture refers to the culture of aquatic species with a minimal level of control that requires little technology, no fertilization or feeding, and depends to a large extent on natural resources and ecosystem services.

In contrast, *intensive aquaculture* is defined as utilizing exclusively supplementary (including live) feeds and no feeds provided by surrounding ecosystems. In addition, intensive aquaculture accommodates the highest density of culture organisms. In this book, I refer to intensive systems only if, in addition to the points mentioned earlier, they also afford a high level of operator control, require elaborate management, and are highly dependent on technology such as aeration, pumps, wastewater treatment, and water quality monitoring systems.

Semi-intensive aquaculture is characterized by an intermediate level of human control and technology utilization. The reliance of semi-intensive aquaculture systems on natural resources such as clean water is very high when open systems such as flow-through earthen ponds, flow-through raceways, or cage culture systems are used that permit high stocking densities but are not very technology intensive. These systems rely to a great extent on ecosystem services.

Such reliance is considerably reduced when closed systems such as *recirculating aquaculture systems (RAS)* are being used. RAS are intensive systems that recycle wastewater produced by aquaculture using filters that remove solid waste and promote assimilation of soluble waste into bacterial and algal biomass, removal by chemical filters, or conversion to volatile gases (e.g. N_2).

The multifaceted nature of aquaculture is most evident by contrasting approaches that emphasize minimal reliance on ecosystem services versus those aimed at maximizing yield and profitability by fully exploiting common property resources. The former category is exemplified by indoor RAS and outdoor water reuse systems that include designated wastewater treatment ponds. The latter category is exemplified by open raceways and cage culture systems that are fully reliant on ecosystem services for providing clean water and treating disposed wastewater. Currently, the extent of using these different aquaculture systems is inversely proportional to their long-term ecological sustainability.

Mariculture is a special form of aquaculture that refers to the culture of organisms in SW or brackish water. Brackish water encompasses a wide range of salinity ranging from 0.5 g/kg (greater than FW) to 30 g/kg (less than SW). The majority of aquaculture utilizes FW or near-shore coastal systems. A minor fraction is contributed by animal mariculture.

The opposite applies to capture fisheries, which is dominated by marine offshore fisheries. Some modelling approaches have suggested that vast areas of the ocean can be used for mariculture (Gentry*et al.*, 2017). However, it is unclear how fragile marine ecosystems will be impacted by extensive aquaculture practices and irreversible, unintended consequences are possible and likely in the longer term.

An example for unintended consequences of once saluted aquaculture innovations are irreversible invasive species problems that arose from introducing aquaculture species to non-native habitat during the first half of the twentieth century. A recent review outlines links between mariculture and ecosystem services and emphasizes the importance of proper regulatory incentivization to improve the ecological sustainability of mariculture (*Alleway et al.*, 2019).

Sea ranching is a method of stocking aquatic animals in a natural aquatic ecosystem for grow out over extended periods of time without human interference before recapture (Bunting, 2013). It applies mostly to migratory species like salmonids, which use homing behaviour to return to the site of their release. This method is increasingly being adopted, although concerns about genetic dilution of wild stocks prevail (Section 6.5).

Such concerns also apply to *stock enhancement*, which refers to the culture of early developmental stages of a target species and the release of cultured juveniles to replenish wild populations. Stock enhancement has been practiced since the late nineteenth century, e.g. Atlantic cod (*Gadus morhua*) hatcheries have been operated for restocking since 1882 in Norway (Bunting, 2013).

The success of stock enhancement programmes is highly variable and depends on species, developmental state and size at release, time of release, and location of release. Released juveniles can be tagged with genetic markers that increasingly replace physical tags to afford more accurate assessment of stock enhancement impacts on wild populations. Sea ranching and stock enhancement are best practised with species and local populations that are native in the affected area.

Monoculture is the culture of a single species, which is more commonly practised but less ecologically sustainable than its counterpart, *polyculture*, which is the culture of multiple species. It is less commonly practised but more ecologically sustainable than monoculture. Historically, polyculture of different carp species has been practised for many centuries in China. However, most polyculture combinations of species have been explored only within the past fifty years.

Integrated MultiTrophic Aquaculture (IMTA) is a special form of polyculture that combines the farming of aquatic organisms belonging to different trophic levels. The goal of IMTA is to recycle waste from one trophic level by utilizing it as nutrients for another trophic level. IMTA can be extensive or intensive aquaculture.

Open IMTA systems often combine coastal cage mariculture of fish with the culture of filter feeders such as oysters, detritivores such as sea cucumbers, and primary producers such as seaweed. Some semi-intensive forms of IMTA are also referred to as integrated aquaculture-agriculture (IAA) when they combine waste from terrestrial animals (chickens, mammals) to fertilize aquaculture ponds and stimulate aquatic plant growth as a food source for herbivorous or omnivorous fishes (e.g. tilapia or certain carps).

Aquaponics is a form of IMTA that combines fish (e.g. tilapia) aquaculture and hydroponics, which is a method of growing macrophyte plants (e.g. lettuce, basil) without soil by direct submersion of roots in nutrient-containing water.

An overview of key aquaculture terminology would be incomplete without mentioning domestication. *Domestication* is the artificial (agent-driven as opposed to natural) selection of organisms for life in an environment that is controlled (to various extent) by humans. Artificial selection implies the human sorting out of genotypes according to their suitability for performing well in a human-controlled environment. This process can only be done over many generations and thus its duration depends on the generation time of animals being domesticated.

Domestication of terrestrial vertebrates (mammals, birds) has a longer history than domestication of aquatic animals. Carp domestication has been practised for centuries in Asia and Europe to yield koi (*Cyprinus carpio*) and goldfish (*Carassius auratus*), which are closely related to the Prussian carp (*Carassius gibelio*). These carps are arguably the longest domesticated aquatic species. Domestication of thousands of ornamental aquatic species started at the beginning of the twentieth century, including taxonomically diverse plants and animals.

Key conclusions

- Advancement of aquaculture depends on a thorough understanding of the ecological value of clean water as its main resource; Ecologically sustainable aquaculture must be properly incentivized.
- Aquaculture development goals are: 1) maximal production yield, 2) minimal reliance on ecosystem services, 3) maximal standards of animal welfare, and 4) maximal ratio of food safety vs. food waste.
- Seafood is produced by capture fisheries and aquaculture, but only aquaculture continues to increase to keep step with a growing human population and increased per capita consumption.
- Animal aquaculture development is now paralleled by the development of methods for growing cell-based seafood, which do not require animal husbandry but rely on aquatic animal cell lines.
- Most aquaculture is practised in FW while most capture fisheries take place in the oceans.
- Mariculture represents aquaculture in SW and brackish water.
- Aquaculture systems are diverse, including extensive, semi-intensive, intensive, open, closed, sea ranching, restocking, mono- and polyculture, and multi-trophic integrated approaches.
- Currently, the most common aquaculture systems are open semi-intensive ponds, cage, and flow-through systems, which rely heavily on common property ecosystem services.
- Domestication of many aquatic species has started at the beginning of the twentieth century although some carps (koi, goldfish) have been domesticated for much longer.

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CHAPTER 2

The historical origins of aquaculture

'The origins of aquaculture are lost in history and little evidence remains . . . '

Beveridge and Little, in *Ecological aquaculture: the evolution of the blue revolution* (2014)

Unambiguous archaeological evidence and written accounts that communicate clear evidence about the beginnings of aquaculture are scarce. Often, existing evidence is vague regarding whether it supports prehistoric capture fisheries (hunting) or aquaculture (farming) practices. However, the lack of records or archaeological evidence does not rule out the existence of ancient aquaculture practices. Consequently, the beginnings of aquaculture are hazy and can only be estimated.

Regardless of these uncertainties, there is general agreement that the historical time frame during which aquaculture activities have emerged can be traced back at least four millennia (Beveridge and Little, 2014; Nash, 2011). Despite this long history, the impact of aquaculture on the development of human society overall and its global ecological footprint remained very low until the dawn of the twentieth century.

2.1 The earliest records of aquaculture practices

Aquaculture is predated by agriculture, which originated after the last ice age at least eleven to twelve millennia ago (Larson *et al.*, 2014). Moreover, the domestication of aquatic animals started about 10,000 years later than that of terrestrial mammals (Balon, 2004). The marginal historical role of aquaculture contrasts starkly with the steady intensification and the major impact that terrestrial agriculture has had on the evolution of human society.

Multiple reasons for this discrepancy in the development and impact of food resource cultivation in terrestrial (agriculture) and aquatic (aquaculture) environments have been suggested. First, until the twentieth century the degree of resource-limitation was much greater for terrestrial than for aquatic resources, and second, aquatic habitats posed much greater challenges than terrestrial habitats regarding access and management and they instilled greater fear into ancestral peoples. Third, ancient civilizations had better opportunities to observe, and greater knowledge of, terrestrial than aquatic organisms (Beveridge and Little, 2014).

Notwithstanding the surmised overall miniscule impact of aquaculture on the development of ancient human societies, there are notable exceptions. For instance, ancient coastal societies may have been inspired by sustainable fisheries practices to manipulate crop plants and enter the 'era of agricultural domestication' (Malindine, 2019).

In particular the development of some island societies, such as the Polynesian cultures of Hawai'i (Section 2.7), was strongly influenced by aquaculture and integrated agriculture practices that reached a high level of sophistication almost 1000 years ago (Costa-Pierce, 2014). The unique mariculture and integrated agriculture practices and systems produced by the Hawai'ian Polynesians support the hypothesis that they have originated independently.

Archaeological evidence on early aquaculture practices in Africa, Asia, and Europe also supports multiple independent origins of aquaculture

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in these different geographic regions, although some geographic and chronological parallels are also apparent. Moreover, recent archaeological discoveries suggest an independent invention of floodplain aquaculture in the Amazon basin of South America long before the arrival of Spanish conquistadors (Nash, 2011).

Furthermore, in the Victoria region of Southeast Australia, the aboriginal Gunditjmara people sustainably managed wetland ecosystems primarily for Shortfin eel (*Anguilla australis*) production as early as 4000 years ago (Builth et al., 2008; Malindine, 2019). These ancient Australian eel farming systems utilized the same conceptual management innovation as the ancient mariculture systems of Hawai'i.

Despite their independent origins, both systems are based on the key observation that catadromous fishes (e.g. river eels, milkfish, and mullets) migrate from the ocean to nutrient-rich brackish or freshwater ecosystems where they grow and mature before returning to reproduce in the ocean. This observation prompted the construction of gated channels to control access from grow-out ponds and marshlands to the ocean. As a result of such management, these aquaculture systems facilitated a very convenient harvest of catadromous fishes when they arrived at the gates during their seaward migration.

Intriguingly, aquaculture of catadromous fishes has a much older and richer history than that of anadromous species. Nevertheless, the present aquaculture production of anadromous salmonids exceeds that of catadromous species. The main reason for this historical development is that technology-intensive freshwater hatcheries can be used for producing anadromous species while reproduction of catadromous fishes in captivity is economically more challenging and has only been implemented on a commercial scale for milkfish (*Chanos chanos*).

Although aquaculture originated independently in many parts of the world, the transition from capture fisheries (hunting) to aquaculture (farming) practices has been gradual in each case. It included intermediate stages that defy clear-cut classification as either hunting or farming. Primitive management of fisheries resources such as transplantation of fertilized eggs between different environments, entrapment of fish in suitable areas, and environmental enhancement to support reproduction and growth likely led to the development of management strategies that eventually culminated in more sophisticated aquaculture systems (Beveridge and Little, 2014).

Four theories—oxbow, catch-and-hold, concentration, and trap-and-crop—exist on how the transition from hunting to farming fish may have occurred (Rabanal, 1988).

The oxbow theory suggests that some oxbows formed by rivers winding through the landscape sometimes periodically became separated from the rivers (e.g. during floods followed by droughts or as result of the river changing its course). People discovered that it is much easier to catch more fish than immediately needed and keep them in these natural entrapments to let them grow larger until needed. Eventually, 'enterprising individuals' may have reinforced the embankments that enclose oxbow areas and started to manage fish in separated oxbows by stocking fry.

The catch-and-hold theory postulates that ponds and moats with a primary function that is unrelated to aquaculture (defending medieval castles in Europe or being a mill reservoir) have later been adopted in a multi-purpose capacity, that is, to hold and grow fish as a secondary function. Perhaps, during prime hunting season when fish supply was plentiful hunters disposed of excess fish in such artificial bodies of water, which turned out advantageous as some species grew well in these man-made habitats and were later available for harvest when hunting yields were low.

This theory would be applicable to the multi-purposing of dammed storage reservoirs for aquaculture, secondary to their primary purpose of controlling water flow for powering flour mills in medieval European monasteries (Nash, 2011). Similar multi-purposing of rice field floodplains may have sparked the origin of aquaculture in Asia (Beveridge and Little, 2014).

The concentration theory proposes that natural seasonal flooding of large plains and subsequent recession of floodwater from the plains left water holes of varying size in natural depressions on these plains. As the dry season progressed these water holes became progressively smaller, thus, concentrating fish they harboured. People inhabiting such floodplains may have taken advantage of this phenomenon as it greatly simplified the capture of fish. Eventually, this practice is thought to have led to active modification of water holes and construction of artificial ponds along with stocking fry and supplemental feeding.

The trap-and-crop theory differs from the other three theories by focusing on brackish and marine habitats. Coastal peoples of Southeast Asia and Oceania (e.g. Hawai'i) learned that fish, crustaceans, and molluscs regularly enter tide pools, lagoons, estuarine marshland, and other coastal ponds to feed in these nutrient-rich nursing grounds. These animals were much easier to catch in these shallow, protected bodies of water than on the open ocean. Over time, gradually increasing management of such coastal ponds and pools led to the development of sophisticated mariculture systems. One of the earliest forms of such management may have been the installation of gates to control the flow of water and prevent the escape of fish and aquatic invertebrates once they entered.

2.2 Religious drivers of aquaculture development in Africa and Assyria

The need for a stable food supply represented only one of the various incentives that promoted the development of aquaculture practices. Other important drivers included religious and cultural motives.

The high standing of fish as religious symbols in ancient Egypt is exemplified by naming entire large metropolitan areas after specific species of sacred fish. For instance, the city of Oxyrhynchus was named after the sharp-nosed Nile elephantfish (*Mormyrus kannume*) (Wallis Budge, 1904a).

During the time of pharaohs, Egyptians believed that Nile fish (e.g. tilapia) symbolize the concept of rebirth and virtues of the goddess of the West, who receives the deceased and can take on different forms (e.g. as Nut or Hathor) (Desroches-Noblecourt, 1954). *The Book of the Dead* mentions two sacred fishes of the river Nile—Abtu and Ant—that guide and protect the boat of the sun god Ra carrying the deceased to the underworld (Wallis Budge, 1904b, 1904a).

Another ancient Egyptian deity associated with fish is the goddess Hatmehit, who bears a fish head and represents the female counterpart to Ba-neb-Tettu (the personification of the souls of Ra, Osiris, and other gods) (Wallis Budge, 1904a). In ancient Egyptian mythology (e.g. in *The Book of the Dead*) the fish god Remi is mentioned as the personification of Ra's tears (Wallis Budge, 1904b).

The eel was worshipped in Upper Egypt and mummied eels were buried during religious rituals in sepulchral boxes:

> That the crocodile, ibis, dog-headed ape, and fish of various kinds were venerated in Egypt is true enough; they were not, however, venerated in dynastic times as animals, but as the abodes of gods . . . the Egyptians began to keep . . . fishes in sanctuaries, and to worship them as deities incarnate' (Wallis Budge, 1904b).

Such practices of keeping fish for worshipping purposes may have resulted in reproduction of tilapia and other readily reproducing species in artificial, man-made, and managed sanctuaries. The opportunity to closely observe life cycles of these fish in such sanctuaries likely improved their management and promoted aquaculture development.

Frescos in Egyptian Tombs illustrate that ecologically sustainable concepts of aquaculture, which are currently revelled by technocratic language such as integrated multi-trophic aquaculture (IMTA) and aquaponics, were embraced in ancient Egypt more than three millennia ago (Figure 2.1).

Interestingly, artificial (human-driven) selection for most efficient resource utilization and pollution resilience in human-made artificial ponds yielded herbivorous and omnivorous fish such as tilapia, goldfish, common carp, and milkfish as historically preferred aquaculture species. Aquaculture of herbivores and omnivores is generally more ecologically sustainable than that of carnivorous fish. Predatory carnivores such as salmonids, bass, or seabream occupy top positions in trophic networks and require more ecological resources per kg of body mass produced than herbivores or omnivores. In that regard, the history of aquaculture teaches us an important lesson about trophic ecology.

The roots of aquaculture in Northern Africa (Egypt) may be intertwined with those in Western Asia (the Middle East). Assyrians ruled much of the Middle East from about 5000 to 2500 years ago. During this time, they constructed many fish ponds that surrounded temples and other sacred places—not unlike the sacred ponds build in ancient

Figure 2.1 Part of a fresco from the Tomb of Nebamun at Thebes (1550–1229 BC), showing an artificial fishpond containing what looks like Nile tilapia among aquatic plants and waterfowl. This fresco suggests that ecological aquaculture has been practiced for more than 3000 years (perhaps unintentionally) by integrating fertilization from waterfowl manure with the production of water lilies and tilapia in a polyculture system. Photo reproduced under CC0 1.0 licence from Wikimedia Commons.

Egypt. Moreover, wealthy citizens of many Assyrian towns owned fish ponds within their estates that were used for religious/ornamental purposes. Evidence of such sacred Assyrian fish ponds appears in written documents that date back to 422 BC (Nash, 2011).

Moreover, these people, including the Sumerians and Babylonians, created freshwater reservoirs by damming the Tigris and Euphrates to manage crop irrigation. More than 2500 years ago, such reservoirs existed for grow-out of large numbers of fish, presumably for producing food (Nash, 2011). The Assyrians probably used different species of fish for food production and religious/ornamental use, but reliable documentation hasn't yet been found.

2.3 Origins of freshwater aquaculture and fish domestication in Asia

Some of the earliest known/documented origins of aquaculture are rooted in China and date back approximately four millennia. Fish rearing operations in China appear in 4000-year-old records. Around 2070 BC the emperor Si Wen Ming (Da Yu the Great) wrote about the practice of stocking fish ponds with larvae and the regulation of specific periods when harvests of fish were permitted (Nash, 2011).

The first written record devoted entirely to aquaculture was *The Chinese Fish Culture Classic*, a short book by Fan Lai (Fan Lee, Fan Li) from between 475 and 473 BC (Rabanal, 1988).

Slightly later (300 BC) in India, the philosopher Kautilya comments on the management of fish in freshwater reservoirs (Nash, 2011). The polyculture of fish and rice (and some other plant species) is documented in written publications that are at least 2000 years old. These early origins of aquaculture in China and India are all focused on the culture of freshwater fish (mostly carp species).

Although freshwater carp aquaculture is undoubtedly the earliest form of aquaculture documented in China, the particular carp species that was originally cultured is somewhat controversial. Many authors believe that common carp (*C. carpio*) was native to China and that it was the