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CHAPTER ONE

Nothing as Practical as a Good Theory

This book presents a mathematical theory of fish stocks and fish communities. The theory describes the demography of fish stocks, the structure of fish communities, and the evolutionary ecology of fish. Throughout, the theory is applied to relevant problems in fisheries science: impact of fishing on demography, fisheries reference points, evolutionary impact assessments, stock recovery, ecosystem-based fisheries management, and so on, as well as to basic ecological and evolutionary questions: population growth rate, density dependence, offspring size, and the like. Before going into the details of the theory, some context is needed: Why do we need a new theory? Which problems should it address? How do we formulate such a theory?

Fish are the dominant marine organisms in the body size range from about 1 g to 100 kg. They inhabit all the worlds' oceans, from the sunlit surface waters to the darkest depths, and in freshwater they are able to find niches in even in the smallest lakes and rivers. Their exceptional high productivity makes them an important source of food and wealth for humans. The Food and Agriculture Organization (FAO, 2016) estimates that fisheries provide about 10 percent of global human consumption of protein at a value of about $100 billion/yr. Despite fish being highly productive and fecund, modern fisheries have been capable of overexploiting fish stocks since the advent of modern trawler technology in the mid-twentieth century. To maintain high yields, fisheries therefore have to be managed. Because fish are hidden from plain sight beneath the surface of the oceans, fisheries management relies on mathematical models to assess the impact of fishing on fish stocks and develop efficient fishing and management strategies. The theoretical background for such models was developed in the first half of the twentieth century on the basis of age-structured matrix models and condensed into the *Beverton and Holt framework* from 1949 (fig. 1.1). Today, most advice for fisheries management is supported by the Beverton and Holt framework; however, its age is showing, and it is coming under increased pressure.

Fisheries management faces several challenges. First, it struggles to implement the "Ecosystem Approach to Fisheries Management," laid down in the Reykjavik

FIGURE 1.1. Ray Beverton (with pipe) and Sidney Holt (front) at work in 1949. Photo by Michael Graham. *Source:* Ramster (1996) ICES J. Mar. Sci., 53:1–9.

declaration from 2001. The ecosystem approach mandates that current single-stock-oriented management is extended toward managing the entire ecosystem. The Beverton and Holt framework is geared toward managing single stocks, and new model tools are needed to deal with multispecies aspects. Second, management faces new questions: What are the long-term evolutionary consequences of the selection imposed by fishing? How should it deal with the large fraction of "data poor" fish stocks, particularly in the developing world, where no or little biological information exists? How should it handle the many ecosystems that are very species diverse, where fisheries are largely indiscriminate toward species, making management on a stock-by-stock basis impractical?

An obvious place to look for help and inspiration would be general ecology. However, because of the need to specialize, fisheries science has become isolated and disjoint from ecology. After Beverton and Holt published their framework, fisheries science branched away from general ecology and concentrated its efforts on operationalizing the framework to practical application for management. Fisheries science developed its own conferences, published much important research in the gray literature of conference proceedings or working group reports, and created its own specialized journals. In the meantime, ecology sprouted new branches, particularly in limnology (inland aquatic ecosystems), food-web ecology, structured populations, and evolutionary ecology, all of which could be relevant for fisheries science.

Among fish ecologists, the main action is in limnology. Pure marine fish ecologists are rare, as most are engaged with the fisheries practice. An exception is the study of coral reef fish, which are a special case not much treated here. The advantage of working in lakes—in particular, small ones—is that their ecosystems are easier to observe and understand because of their low diversity and low habitat complexity. Within theoretical population ecology, a notable development is physiological structured models (Metz and Diekmann, 1986), which generalize classic consumer-resource models to structured populations, and are particularly applicable to fish. These advances in understanding lake ecosystems have had next to no impact on fisheries science in the seas. There have been some attempts at convincing fisheries scientists to adopt insights and techniques from freshwater fish (Persson et al., 2014), but with little success; fisheries scientists seem not to appreciate the advanced insights and theories, as they cannot be easily operationalized in practical fisheries management. To reach out to fisheries science, limnologists must face the difficulties of working in the seas and the messy business of implementing fisheries management.

Other novel branches of ecology that would be relevant for fisheries science are food-web ecology and evolutionary ecology. The advent of computers made it possible to generalize simple competition or predator-prey models to entire food webs, and an entire discipline emerged to study such complex food-web models. The discipline homed in on questions of structure and stability to identify general patterns in the topology of food webs (who eats whom) and which types of structures make a food web stable. The discussion was largely about identifying general rules or statistical patterns, and there has been little attention to developing models of specific food webs of particular ecosystems. Further, the question of how food webs responds to perturbations, such as fishing, was never central. A notable exception is the EcoPath type of models, which has indeed been occupied with setting up food-web models of specific systems, and such models are also increasingly used in fisheries science. However, overall fisheries science and management have not been able to assimilate the developments in theoretical food-web ecology.

Fish have had a special place in the hearts of evolutionary ecologists, and evolutionary ecologists probably see fish in the broadest context. The idea of “life history invariants” was born through observations of fish (Beverton, 1992) and later generalized by Charnov et al. (2001). Central evolutionary problems in fish ecology are to understand the diversity of offspring size strategies, reproductive strategies, and the evolution of indeterminate growth. While evolutionary ecology has been central to understanding fish life histories, it has found little application in fisheries science.

Against the backdrop of the challenges to fisheries management and the increasing interest from classic ecology and evolutionary ecology in fish and fisheries, this book introduces the size- and trait-based approach as a modern, coherent, and unifying framework to model fish populations and fish communities. The theory is woven from strands taken from newer developments in ecology and fisheries science that will make it applicable broadly to fisheries and ecological problems. By catering to both fisheries scientists and ecologists, I hope to contribute to the long overdue unification of thinking in fish ecology and fisheries science. I will now describe the basic elements of the theory, starting with those elements coming from classic fisheries science—in particular, with regard to applications—and then moving on to size-based theory as developed in marine ecology, physiologically structured population models, and trait-based ecology.

Fisheries science and management is the most important application of the theory. In the context of fisheries science, the theory can be seen as a reformulation of the traditional single-stock Beverton and Holt framework from scratch. It is tempting to repair the Beverton and Holt framework and add some missing pieces to make it applicable to the ecosystem approach to fisheries management. That would be like constructing a car by welding two bikes together and adding an engine. Repairing Beverton and Holt would make it impossible to achieve the degree of theoretical rigor that I strive for. I believe, as does Kurt Lewin, who coined the quote in this chapter's title, that practical applications, like fisheries advice, are best given from a solid theoretical basic understanding. Starting over with a new theory entails throwing out classic concepts like the treasured von Bertalanffy growth equation with the ubiquitous K and L_∞ parameters, doing away with spreadsheet-friendly life tables, and scrapping the concepts of adult mortality, M and $M2$, to mention just a few. Instead of von Bertalanffy, I use physiology; instead of life tables, I use differential equations; and instead of the constant adult mortality, I use a size-based mortality. The absence of well-known concepts may make the theory appear inaccessible and overly complicated to one well-versed in the classics of fisheries science, such as described by Hilborn and Walters (1992) or Quinn and Deriso (1999). The reward is a theory that is consistently built upon a few fundamental assumptions, from which it deals with classic single-stock impact assessment, but also estimates evolutionary rates and makes ecosystem impact assessments.

Others have reformulated the Beverton and Holt framework. In a nineteenth-century castle housing the Danish Institute for Fisheries and Marine Research, K. P. Andersen[1] and Erik Ursin were toiling away in the 1970s. They wanted to bring the Beverton and Holt single-species framework into the multispecies

[1] No relation!

reality of real marine ecosystems. And they succeeded. Unfortunately, the theory was too complex, and it fizzled out. The equations themselves fill several pages (Andersen and Ursin, 1977). Not only that, but the numerical implementation of a complex model was a major undertaking at the time—it had to be coded on punch cards! Along the way, Andersen and Ursin introduced several important novel ideas: everything is based on a description of the physiology of individual fish, accountance of all mass flows—including primary-secondary production and recycling—and size-based selection of prey. Most of their work is forgotten because it was published in obscure journals—for example, Ursin (1979) in *Symposia of the Zoological Society of London*, or the now folded Danish journal *Dana*.

I combine Andersen and Ursin's ideas with size-based theory. The importance of body size as a central structuring component of ecology and evolution has been recognized for at least a century. I rely upon the scaling of metabolism with body size, referred to as Kleiber's law (Kleiber, 1932), and the rule that big fish eat smaller fish. Sheldon and co-workers showed how these two rules combine to explain body-size distributions (Sheldon et al., 1977), and the ideas were later used to develop the building blocks of dynamic models (Silvert and Platt, 1978). The *metabolic theory* (Brown et al., 2004) made similar predictions; however, I go further that the dimensional arguments in metabolic theory and I provide a stronger mechanistic foundation for some of the metabolic scaling rules—in particular, mortality. I also predict the size structure within populations, and not just within communities. Much of the work on size-based population demography builds on the pioneering efforts by Jan Beyer (1989). A surprising result is that some of the metabolic scaling rules actually do not apply as expected for fish population, despite the reliance on metabolic scaling on the level of individual organisms. This is important, as such rules are widely used formally or implicitly.

While fisheries science was largely content with developing the Beverton and Holt framework toward practical applications, ecologists continued their fundamental inquiry into the dynamics of fish populations—in particular, in limnology. A crucial juncture is the review by Werner and Gilliam (1984). Just as Beverton and Holt did, Werner and Gilliam stressed the importance of describing the entire life cycle of fish, and not just the adults. However, they also realized how the age-based Beverton and Holt theory was unable to describe the complicated interactions of competition and predation between different stages of fish populations. Interactions occur mainly because of differences in body size, not age, and these interactions lead to density-dependent bottlenecks. They then sketched a new theoretical framework based on body size instead of age. Lennart Persson and André de Roos bought Werner and Gilliam's vision about density-dependent bottlenecks and managed to surpass the formidable analytical challenges to develop applications of physiologically structured populations (De Roos and Persson, 2013). To create a theory directed toward fisheries applications, I focus on another aspect of Werner and Gilliam's vision—namely, the development of size-structured population dynamics. A similar development is integral projection models (Easterling et al., 2000), which are essentially discrete versions of the continuous time- and size-based demography that I develop here.

With regard to life-history theory, there is a fascinating analogy between the life histories of plants and fish. Both groups share three notable characteristics: they (mostly) make very small offspring; they (mostly) do not have parental care; and they continue to grow after maturation. There are other reasons for looking for inspiration in plant ecology. Plant ecologists have developed trait-based approaches that cut through the complexity of dealing with the myriads of species making up a plant community. Instead of describing each species separately, they rather characterize the distribution of the main traits of species in a community. This approach turns out to be very powerful when dealing with entire fish communities. Trait-based approaches are controversial—how can you throw away species, when species are at the core of fisheries management and biology? After all, Darwin wrote about the origin of species, not about the origin of traits. This is a valid concern. I use the idea of traits to generalize across all species; however, much of the theory on the population level can equally well be applied to particular species.

I found the inspiration to develop the trait-based framework for fish in the work of John Pope and co-workers (2006). They related all species-specific parameters to the average maximum size that individuals in each species can obtain. That crucial insight made the asymptotic (maximum) size into a master trait. Characterizing differences between species just by their asymptotic size opens the door to making broad statements about all fish species just by sweeping over asymptotic sizes. Of course, using only one trait is a gross simplification, and the trait-based approach can be generalized by including more traits than just the asymptotic size. Nevertheless, the central idea is to characterize species by just a few fundamental traits, so the introduction of additional traits must be done with care. The trait-based approach is particularly important for developing a dynamic theory of the entire fish community because it circumvents the complexity of having to deal with a tangled food web of many interacting species. It is also the secret ingredient that makes the theory particularly relevant to data-poor situations, because no matter how little we know about a specific stock, we have a good idea of the maximum size of landed individuals. Last, the trait-based approach is a powerful tool to obtain insights that have broad validity. However, one should not be dogmatic about it—real ecosystems actually do consist of species, and practical fisheries management must care about specific stocks. Therefore, the single-species model I present can equally well be applied to specific stocks, and I show how the trait-based community model can be formulated as a species-based food-web model.

1.1 WHAT CHARACTERIZES A GOOD THEORY?

A good theory can be likened to a game of cards. A game of cards is defined by a few simple rules that can be explained quickly over a coffee table. If the rules are well chosen, they define a complex and entertaining game. Similarly, a theory is based upon a few fundamental axioms. The axioms must be generally accepted and have a solid empirical foundation or relations to other theory. A good theory makes nontrivial predictions of both qualitative and quantitative nature. For example, a good theory about fish stocks not only predicts that some level of exploitation extracts the maximum yield from the stock, but it also predicts the actual level of fishing mortality that maximizes yield.

Fish ecology is challenged by the difficulty of carrying out controlled experiments. Let's compare with an idealized version of physics. In physics, theory goes hand in hand with experiments: experiments makes discoveries, theory proposes an explanation and possibly additional hypotheses, and experimentalists go back to check the explanation and the new hypotheses. Things are not quite that straightforward in ecology because experiments are less accessible. Physicists can create idealized experimental conditions where most confounding effects are eliminated or accounted for. In ecology, such conditions may be obtained while describing the physiology of individual organisms—for example, the functional response may be measured through the feeding of organisms at different food concentrations, or the swimming speed and respiration may be measuring in a flow chamber. For experiments with entire communities, however, clean conditions are out of reach. And that is not even considering the issue of time scales—the time scales of change of ecological communities are longer than the longest-lived individuals in the community, typically on the order of decades. Because of these fundamental difficulties, experiments are rare and only possible in a few cases and at great effort, such as in lakes (for example, Carpenter et al., 1987; Persson et al., 2007). We do have one (unplanned) experiment at sea: large-scale fishing operations have fundamentally altered marine communities over the past half century. And even better: where observations exist, we can see how marine ecosystems have responded to the removal of biomass. While these two examples provide some experimental support, most theoretical predictions stand without direct observational support.

The lack of access to controlled experiments is not unique to ecology. That challenge is shared by much of earth science, and astronomers can hardly experiment with stars. Does the lack of an active dialectic between theory and experiments make theory moot? Not quite, but it places a heavier burden upon the development of theory. As I mentioned earlier, theory is built on axioms, fundamental assumptions on which the theory rests. Theoretical physics largely rests on an agreed-upon set of axioms—Newton's laws of motion, the laws of thermodynamics, and so on—and the role of theory is making predictions on the basis of these axioms. In the subdisciplines of physics where experiments are difficult—for example, astronomy and much of earth science—the existence of these well-established laws of nature provides a solid foundation. In ecology, very few such axioms exist, and where they exist their range of validity is much more limited than the fundamental laws describing the dead nature. Ecology does not have the equivalent of Newton's laws or a Schrödinger equation to build upon. A large part of any ecological theory is therefore establishing the axiomatic foundations for the theory.

The difficulty of making experiments and direct observations of marine fish communities means that models have a special status. Model output represents our best understanding of nature. For example, fisheries management relies upon assessments of stock biomass and recruitment that are not direct observations but output of statistical models. In a similar vein, the reference points used for fisheries management, F_{msy}, F_{lim}, and so on, are not observations but are based upon model calculations. Even observations of growth rates are not directly observed but are fits to a particular growth model. In practice, however, we use such model outputs as if they were direct observations. In this manner, the models transgress from being descriptions of reality to becoming the reality itself. The lack of direct observations to check the models puts a particular burden on building trust in the models' foundational assumptions.

1.2 HOW TO READ THIS BOOK

This books presents the size- and trait-based framework for fish populations and communities as a single coherent theoretical framework (fig. 1.2). The theory is a synthesis of work over more than a decade published in more than 25 journal papers. Some of these papers are riddled with typos (for example, Andersen and Beyer, 2006), and some (if not most) are hard to penetrate (see Andersen et al., 2015, for a good example). The dense writing partly reflects the challenges in communicating complex concepts but also that my understanding was not yet fully formed while the theory was still developing. Further, the notation and some

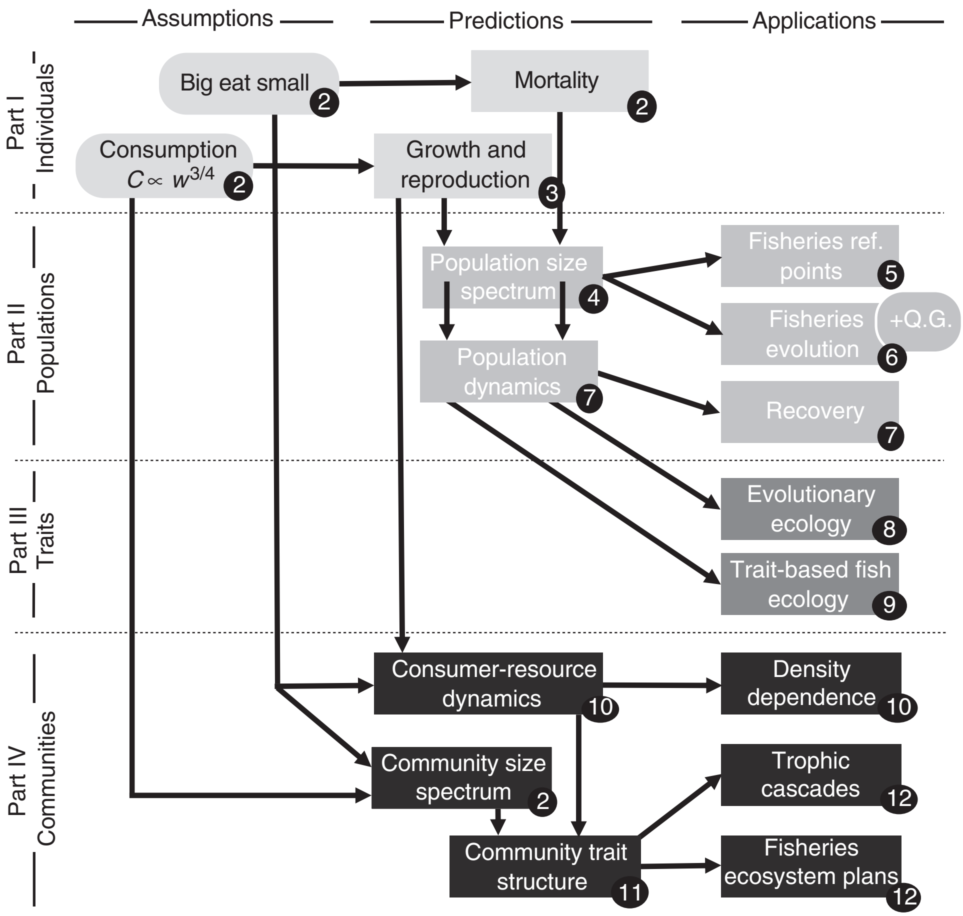

FIGURE 1.2. Sketch of the size- and trait-based theoretical framework. Boxes with rounded corners represent assumptions; chapter numbers are shown in the black circles. Fisheries-induced evolution, as addressed in chapter 6, needs further assumptions about quantitative genetics (Q.G.). Notice that the entire theory is based upon the two fundamental assumptions in the top-left corner, either directly or through concepts derived from those assumptions.

assumptions morphed throughout the process. Here, the theory is presented as a unified framework with consistent notation (summarized in table 0.1) and applied to fisheries problems, to evolutionary ecology, and to population ecology.

The size- and trait-based approach is appealing in its conceptual simplicity, but it comes at a cost of a mathematical formalism that is unfamiliar to most ecologists and fisheries scientists. I have tried to be accessible to biologists who know what an integral is but are not necessarily able to evaluate one. I do not expect prior familiarity with partial differential equations. I have focused the text on developing concepts, principles, and explaining results. Complicated mathematical derivations break the flow of reading and thinking, and consequently I have delegated them to boxes scattered throughout the text. The book can (and should) be read without going through the boxes in detail. The boxes are provided for reference and can be consulted whenever needed. All the code for the figures has been written in R. It is available at press.princeton.edu/titles/13516.html, including a Web application to simulate the impact of fishing on a stock.

The book is divided into four parts (as shown in fig. 1.2): “Individuals,” “Populations,” “Traits,” and “Communities.” Part I lays down the axiomatic foundations for the theory. The theory is rooted in assumptions at the level of individual organisms about their physiology, metabolism, clearance rate, and predator-prey interaction with smaller organisms. From that basis follows the size-structure of the entire marine ecosystem (chapter 2, “Size Spectrum Theory”). The assumptions are used to develop descriptions of how individuals grow and reproduce (chapter 3, “Individual Growth and Reproduction”).

In part II, “Populations,” I develop the demography of fish populations and with applications to single-stock fisheries management. By *demography*, I mean the distribution of small and large individuals within a population, which is described by the *population size spectrum* (chapter 4, “Demography”). The population size spectrum follows directly from the assumptions about growth and reproduction from chapter 3 and mortality from chapter 2. The derivation of the population size spectrum is followed up by descriptions of the ecological and evolutionary impacts of fishing (chapter 5, “Fishing”; and chapter 6, “Fisheries-Induced Evolution”). Well-established fisheries concepts such as maximum sustainable yield, yield-per-recruit, cohort biomass, and selectivity are recalculated to reveal insights hidden from classic age-based theory. The application of trait-based calculations provides broad predictions for fish stocks in general. Next, the theory is applied to population dynamics where the population changes over time, owing to environmental noise, fishing, or both (chapter 7, “Population Dynamics”).

Part III, “Traits,” turns away from fisheries demography and applies the theory to fundamental evolutionary problems relevant for fish (chapter 8, “Teleosts versus Elasmobranchs”). Traits represent a recurring theme, which resonates with increasing force throughout the book. The tension is released in chapter 9, “Trait-Based Approach to Fish Ecology,” where I outline the conceptual mechanistic trait-based framework and link it to classic life-history theory and evolutionary ecology.

Part IV, “Communities,” scales from single populations to entire communities. First, the focus is on a generalization of a classic consumer-resource model with a single population embedded in a community in chapter 10, “Consumer-Resource

Dynamics." Next, chapter 11, "Trait Structure of the Fish Community," derives the trait structure of the community. In chapter 12, "Community Effects of Fishing," I use the community model to repeat many of the classic impact calculations of a single stock on the entire community. Here, a focus is the appearance of trophic cascades. I discuss the relevance to the emerging ecosystem approach to fisheries management. Last, in chapter 13, "Opportunities and Challenges," I outline four future research questions where the theory could be applied: stochasticity, behavioral ecology, coupling to primary production, and thermal ecology and climate change.

This book does not have to be read from the start to the end. The chapters do follow a logical progression in complexity and build upon one another, but I have tried to make each chapter as self-contained as possible. This entails some repetition. I use references to previous chapters to provide links to the more fundamental chapters, like the arrows in fig. 1.2, but each chapter can be read independently. Which parts of the book you will focus on depends on your interests and background. If you are mostly interested in the fisheries applications, you might want to focus on parts II and IV, particularly the specific applications to fishery, chapters 5, 6, and 12. Perhaps you might want to consult chapter 10 for a deeper discussion of density dependence and a peek into the future of fisheries population modeling. If your interests are rather in population or community ecology, you might find the static demographic calculations in part II too altmodisch and will skip straight from part I to part IV and consult chapter 4 only for reference. However, to communicate with fisheries scientists, familiarity with the concepts in chapters 4 and 5 are essential. You might also want to read chapter 9 for inspiration about trait-based concepts in population and community ecology. In any case, I urge you to read at least the first part of chapter 2 to understand the basic assumptions of the theory, and perhaps also chapter 3. In short, follow your interest.

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