Chapter 1. Introduction

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As long as humans have exploited marine fish resources, fluctuations in availability and yields have been experienced. Nearly a century ago Hjort (1914, 1926) linked variation in yield to variability in recruitment. Today scientists still identify recruitment as a major driving force in stock fluctuations. This is reflected in the research focus on reproductive dynamics and recruitment over the past 30 years (see: http://www2.ncsu.edu/elhs/elhspubs.html) and in recent strategic plans as for the International Council for the Exploration of the Sea (ICES) (Anon. 2001). Most international research programmes focusing on reproductive biology and recruitment of marine fishes do so to improve the understanding of the underlying processes controlling survival and growth during the early life stages. Few are aimed primarily at directly linking these processes to the assessment and management of harvested stocks although progress in this area is evident. As exploited fish stocks decline, the demand for information on recruitment dynamics and for better prediction of recruitment typically increases. Furthermore, there is an increasing awareness of the importance of understanding these mechanisms for fisheries management.

The realisation that recruitment processes are of fundamental importance to the prosecution and management of fisheries has resulted in concerted efforts to monitor recruitment and to understand the factors controlling variability of marine fish populations. These efforts provide an unparalleled opportunity to study processes regulating fish populations and to understand and predict the impacts of harvesting on living marine resources. An extremely valuable compendium of estimates of adult biomass and recruitment has been assembled for exploited marine resources throughout the world ocean (http://www.mscs.dal.ca/~myers/welcome.html), offering opportunities to examine patterns of recruitment variability, compensatory dynamics, and current status of these stocks. The economic importance of fishes and their societal and cultural relevance provide powerful incentives for large-scale, sustained studies of their dynamics. Few other taxonomic groups –terrestrial or aquatic – offer such rich data bases for examination of these processes as those available for fishes.

1.1. Scope and Organization of the Book

The overall goal of this book is to give a picture of the present use of information on fish reproductive biology in assessment and management and its potential for improving management of these resources. We have partitioned this volume into three main sections. The first sets the stage by focusing on recruitment processes, reproductive biology, and the effects of fishing on exploited marine fishes. Here, we describe the critical role of recruitment in replenishing an exploited population, the importance of fundamental reproductive dynamics in this process, and how natural and anthropogenic forcing factors affect recruitment and sustainability. The second section explores the fundamental elements for any evaluation of fish population dynamics. These encompass issues related to identifying populations and stock units, estimation methods for obtaining abundance and demographic information at different life history stages, and the data requirements for more refined estimates of reproductive output and dynamics for inclusion in assessment and management. The final section describes both the current approach to management and ways in which a detailed understanding of reproductive processes can inform new approaches to management. Contributions to each of these sections are described in greater detail below. We also provide below references to key texts for further reading which complement the material presented in the individual chapters

1.1.1. Biology, Population Dynamics, and Recruitment

Consideration of the form of the relationship between the reproductive output of the population and the resulting recruitment lies at the very heart of any understanding of how a fish population will respond to sustained perturbations such as fishing (Chambers and Trippel 1997). This issue has been a focus of fisheries research for the last half century. Any such representation depends on an understanding of the life-cycle dynamics of the population from the production of viable eggs through the gauntlet of processes that affect the probability of survival to the age or size at recruitment. If we are to predict the likely effects of fishing on an exploited population we require conceptual and analytical models of this process. In Chapter 2, these considerations are used to introduce the principal themes recurring throughout this book including how a refined understanding of reproductive dynamics influences our perception of the status of the population, the relationship between the adult population and recruitment, and the choice of effective management strategies. The earliest recruitment models were cast in terms of total egg production. However, the general lack of time series of information on fecundity at the time necessitated the use of a proxy for this quantity – usually the total adult biomass of the population (Beverton and Holt 1957). The focus of these early efforts therefore was on the compensatory mechanisms that shape the relationship between spawning stock biomass and recruitment. There is now accumulating evidence that the spawning stock biomass alone is not always an adequate measure of the spawning potential of a fish stock. Maternal factors such as fecundity and egg quality are known to be affected by growth, condition, body size and spawning class. Further, sex ratios of many populations change with increasing fishing pressure in combination with selective harvesting practices. Collectively, these considerations argue for a return to the origins of recruitment theory with its recognition of the importance of the actual reproductive output of the population. Translated into a management setting, we see that ignoring the effective reproductive output of a population and status of the adult population in some cases can lead to an overly optimistic view of the condition of the population with attendant risks to sustainability.

The importance of gaining a detailed understanding of reproductive processes of fish in the context of recruitment studies has long been appreciated (Potts and Wooton 1984). Chapter 3 provides essential background on the reproductive biology of fishes with considerations spanning cellular development of primordial germ cells, individual fecundity, reproductive strategies, ontogenetic development, and factors affecting the quality of reproductive products. An understanding of the reproductive processes of fish at the cellular level is ultimately necessary to correctly determine and interpret the potential reproductive output of a population. An understanding of reproductive strategies and mating systems is no less important for some species. Semelparous life histories, in which adults spawn once and die, are notable among species such as capelin and Pacific salmon, while iteroparity involving multiple reproductive opportunities through the life span is common in most other fish taxa. Most fishes maintain separate sexes throughout the life span, but various forms of sequential hermaphroditism are also known among a number of important exploited species. Discrete seasonal patterns of spawning are common in temperate and boreal systems and are often linked to seasonal primary and secondary production cycle. In contrast, many tropical and subtropical species spawn throughout the year.

Factors underlying the characteristically large variation in recruitment of fishes, broadly classified into trophodynamic and physical/environmental components, are described in Chapter 4. The striking prevalence of highly variable recruitment patterns in marine fishes and the recognized underlying importance of stabilizing mechanisms has been called the stock-recruitment paradox (Rothschild 1986). Trophodynamic considerations such as prey availability during the pre-recruit stages and the risk of predation on the pre-recruits strongly influence survival. Physical processes such as turbulence can directly affect the probability of prey capture while other physical factors such as temperature affect activity levels and metabolic requirements. The role of transport, retention and loss has been linked to variation in survival during the early life stages of fish. Survival depends on successful transport to and/or retention within favourable habitats. Different early life stages exhibit different vulnerabilities to these environmentally-driven events. Although recruitment variability obviously is linked to processes in the local environment, there is evidence that these processes are driven by large-scale environmental variations. Thus, major climate and oceanic events have been shown to have effects on fish populations over a wide area. Fish populations respond to biotic and abiotic environmental forcing on both short (high frequency) and long (low frequency) time scales. The high levels of interannual variation in recruitment characteristically observed in fish stocks reflect high frequency forcing while long-term regime shifts in environmental factors are followed by changes in overall recruitment levels. High and low frequency changes in recruitment hold very different implications for the development and evaluation of management strategies. In the former case, stochasticity in recruitment should be taken into account in making short-term tactical management decisions, in the latter, adjustments of biological reference points used in management may be necessary to accommodate persistent shifts in productivity.

In Chapter 5, the direct and indirect effects of fishing on abundance and demographic structure of fish populations are described. Among the direct effects are a reduction in biomass of the adult population and truncation of the age structure. Changes in age composition, sex ratio, age or size at maturation, and other demographic characteristics may in turn be critical for recruitment. The potential indirect effects include the impact of fishing activities on the structure of ecological communities affecting the prey and predators of the species of interest, disruption of habitat, etc. (Hall 1998). These effects also have important implications for recruitment. An understanding of the mechanisms by which exploited populations can potentially compensate for changes in abundance or population structure induced by harvesting is crucial. Many life history traits of fishes have been assumed to be plastic, responding to environmental change. Currently, important efforts are underway in an attempt to separate environmental effects from potential evolutionary change induced by artificial selection due to fishing. Well documented changes in the age or size of maturation under size-selective harvesting for a number of fish species have been examined in both laboratory and field studies. The main concern is that fishing could lead to loss in genetic diversity and thereby produce non-reversible, or very slowly reversible, changes in the fish populations. Hence, rebuilding stocks that have collapsed can, as experience has shown, be a very slow process, and this means that overfishing poses a larger risk than previously expected.

1.1.2 Information Critical to Successful Assessment and Management: Methods and Data

The rationale and methods employed in scientific surveys of pre-recruit stages of fish is described in Chapter 6. Plankton surveys have been used to measure egg and larval abundance as well as other components of planktonic communities, including zooplankton species that are both predators and prey of fish larvae (Gunderson 1993). Stage-specific estimates of egg abundance are routinely used for some species to back-calculate the abundance of spawners based on knowledge of fecundity and estimates of egg mortality rates. Larval abundance estimates have also been used for this purpose and in some cases for making recruitment predictions. Estimates of juvenile abundance derived from net-based sampling, direct visual observation (e.g. in coral reef systems) and other approaches are used to provide forecasts of recruitment to the fishery. Mortality rates during the early life stages can be estimated based on serial sampling of successive life stages. Mortality estimates and their variability provide crucial information on expected recruitment variability and the probability distribution of recruitment. This can also give important insight into the timing of critical population events such as where in the life cycle density dependence is important, where the highest interannual variability in mortality occurs. The overall spatial scales on which sampling of the early life stages is conducted and the volume filtered by the sampling gear in relation to small scale patchiness of the organisms are important factors in the calculation of abundance indices for the early life stages. Consideration of small-scale distribution patterns is increasingly possible with new optical and acoustic sampling tools.

In Chapter 7, the critically important issue of defining population or stock units is addressed. Often stocks used as units in management are defined more from practical considerations, such as the spatial resolution of catch data or national borders, than biological considerations (Cadrin et al. 2004). This is clearly neither defensible nor desirable considering the importance of knowing the true dynamics of exploited populations in management, and scientific advice will attempt to address biological stocks whenever there is adequate data and the stock identity is known. Stock identification is complicated by the fact that fish stocks rarely are completely isolated from each other. Mixing may occur at all life stages, and in some cases individuals may transfer from one stock to another. Stocks are normally most clearly separated during the spawning periods when the fish tend to aggregate and it may then be possible to map the distribution of their eggs and larvae. If the distribution of later stages in the life cycle is also known, stock identity may not be a problem. However, there may be mixing of stocks even on the spawning grounds and recruits originating from different spawning grounds may produce mixed catches when they enter the fishery. Furthermore, adult fishes are usually distributed over a wide geographical area between spawning periods and mixing of individuals from different spawning populations on the fishing grounds is not uncommon. Such mixing of stocks requires mapping of the population structure to define the unit of analysis and a number of methods are being applied. The tools available to identify populations include examination of meristic characters, morphometric analysis, infestation rate of various parasites, analysis of nuclear and/or mitochondrial DNA, fatty acid profiles, otolith microstructure and otolith microchemistry. The methods are quantitative, but may give somewhat diverging results and the overall evaluation tends to be qualitative. Recently, consideration of metapopulation structure of fishes and the potential management implications have been explored with particular reference to issues such as the placement of marine protected areas.

As described in Chapter 8, fish stock assessments serve as vehicle for synthesis of diverse information on stock status, and prediction of the probable outcomes of alternative management outcomes (Quinn and Deriso 1999). The main purpose of stock assessment is to provide fisheries managers with the information needed to make effective management decisions. Fisheries management requires a determination of the current state of a stock, e.g. whether the exploitation rate is above a sustainable level or the biomass is low compared to earlier years. In addition, predictions of catch and biomass are needed for managers to know the most likely future effects of alternative management actions. Stock assessment is highly dependent on the available data and a number of different classes of models have been developed to meet different needs. The analyses depend on an evaluation of information derived from the fishery (catches, discards, fishing effort, age or size composition of the catch, etc.) and from fishery-independent sources, mainly research surveys. The simplest models do not include estimates of SSB (spawning stock biomass) and recruitment may be assumed to be constant, whereas more complex models typically include annual estimates of both. Recruitment is related to the abundance of the adult population, although the form of the stock-recruitment relationship may be obscure. It is typically masked by environmental influences and often apparent only when the stock has been driven to low levels. Considerations related to data availability have meant that the reproductive output of fish populations has traditionally been measured in terms of adult biomass as a proxy for total egg production. However, the fundamental models used to estimate population size by size or age classes in traditional stock assessments provide an important framework for extension to more refined estimates of reproductive output as information accrues on changes in sex ratios over time, female condition, and fecundity for an increasing number of species. Similarly, the models used to frame management advice can also be modified to incorporate more detailed considerations of reproductive biology.

Consideration of reproductive strategies and tactics and estimation of reproductive potential at the cellular and organismal levels are described in Chapter 9. Reproductive strategies encompass the range of expression of reproductive traits over the full spectrum of environmental conditions (Potts and Wooten 1984). Reproductive tactics refer to the manifestation of specific reproductive traits under particular environmental conditions. This distinction sets the stage for consideration of factors affecting the regulation of fecundity in marine fishes. The majority of marine fish species are highly fecund and produce a 'superabundance' of eggs. In these species the parental energetic investment per individual egg is relatively low and mortality during the pre-recruit stages is very high. Some species (notably the elasmobranchs) however produce relatively few young per spawning event, some exhibit parental care, and others are viviparous. The expression of factors such as fecundity and egg size under different environmental conditions is of course a critical element of stock reproductive potential. Fundamental reproductive characteristics such as whether a species exhibits determinate or indeterminate spawning have important implications for our ability to measure fecundity at the individual level. In turn, this affects our ability to estimate total egg production of a population. Further, emerging evidence suggests that a clear distinction between determinate and indeterminate fecundity for some species in some circumstances may not always be possible. Finally, the transition from estimates of potential egg production to realized egg production, including consideration of atresia and other mechanisms of down-regulation of fecundity, is critically important in estimating the reproductive dynamics of a population.

1.1.3. Incorporation of Reproductive Biology and Recruitment Considerations into Management Advice and Strategies

The forms of biological advice on management of fish stocks currently given on both international and national levels are described in Chapter 10. This advice is traditionally framed in terms of benchmarks related to fishing mortality rates or biomass levels relative to defined ‘optimum’ or ‘risk’ levels (Charles 2001). These benchmarks are called biological reference points. Management advice is mostly given only for the short term and often concerns a total allowable catch (TAC) for the next year, while national, regional and fleet quotas are decided by political processes. The advice may have the form of a clear recommendation of a TAC, or may present options within a biologically acceptable range of catch levels, describing the short-term effects of each option. Increasingly, however, advice is given for a management strategy which may aim at rebuilding the stock or stabilising catch and biomass levels over a specified time frame. It is now strongly recommended that management advice be based on the “Precautionary Approach”. The underlying philosophy is to avoid reduction of SSB to levels where recruitment will be impaired. The SSB and the fishing mortality rate, both which have a defined a set of reference points, are the most important elements of the advice. The basis for estimating biological reference points ranges from simple production models, models that consider only the effects of fishing on a cohort of fish (yield per recruit models), to full age-structured models that explicitly account for the stock-recruitment relationship. In all cases, an appropriate measure of the actual reproductive output of the population is critical. In the last decade, emphasis has been placed on limit reference points, serving as warning signs of overfishing and stock declines. If the problem of overexploitation can be overcome, target reference points aimed at optimising yield or economic returns will assume greater importance in management.

Chapter 11 explores new approaches to management, grounded in detailed information on environmental influences on recruitment, the oceanographic setting, reproductive biology, ecological interactions, and spatial dynamics. These points are crystallized in a detailed case study of cod population dynamics around the British Isles. This perspective is clearly in keeping with the move toward a more holistic ecosystem approach to management of fishery resources which has been increasingly advocated around the world (Jennings et al. 2001). Many of the concepts raised in previous chapters are highlighted and new dimensions considered. The importance of incorporating these more detailed biological and ecological considerations is made clear in this case study. The development of spatially-explicit simulation models incorporating information on patterns of spawning aggregation, advective transport of eggs and larvae, larval settlement, vital rates of juvenile and adult cod, and exploitation patterns as in this example, provides a powerful tool for synthesis, integration, and prediction.

Chapter 12 concludes this volume with a compelling argument for the need to move toward the use of total egg production and consideration of demographic characteristics in our evaluation of stock reproductive condition. Egg viability can be related to the age and reproductive history of the female. Truncating the age composition toward younger spawners can have a disproportionate effect on recruitment that is not reflected in simple measures of the adult population such as spawning stock biomass. Changes in sex ratio in response to harvesting in species with dimorphic growth can be very important in estimating the actual reproductive output of the population compared with estimates based on total adult biomass. Further, these changes can alter mating systems and other aspects of behaviour in some fishes with direct effects on spawning and recruitment.

Although constraints on the availability of time series of fecundity estimates have hindered progress, these limitations are beginning to ease. In the interim, recognition of the broader availability of sex ratio information over time has allowed estimation of female spawning biomass for an increasing number of stocks as a stepping stone to enhanced consideration of reproductive dynamics. In other cases, it has been possible to employ other measures based on female energetic reserves as a proxy for effective egg production. Inclusion of other factors such as the age diversity of female spawners has also proven useful in some circumstances in improving the predictability of recruitment.

1.2. Summary

A full appreciation of reproductive dynamics is critical for assessing the impacts of harvesting on fish populations and in devising appropriate management strategies.

Attempts to ascertain limits to exploitation and defining optimal harvesting strategies have typically been based on proxies of reproductive potential of stocks – most notably simple measures of the biomass of the adult population. However, we need measures of the actual reproductive capacity and output of the population. This will entail an understanding of reproduction biology, behaviour and demographic characteristics of the population to provide adequate measures of reproductive capacity. We further need to understand the factors that affect the survival through the early life stages before recruitment to the fishery. The confluence of factors affecting egg condition and environmental effects on survival is critical in this regard.

Accounting for these factors in management will place renewed emphasis on demographic and other characteristics of the stock. Attention to the age and size structure of the population, sex ratio, etc. will lead to new ways of measuring the reproductive capacity and replace simpler measures such as total spawning biomass. Management tools to specifically address these issues will also require a shift from simple considerations of total allowable catch to measures that are designed both to limit the catch and to control its demographic composition. This will entail strategies such as the use of marine protected areas to protect segments of the population, the development of more selective fishing gears, etc. Consideration of factors such as preserving multiple reproductive opportunities for individual females will become increasingly important. We anticipate a shift towards increased emphasis on long-term management strategies from the current focus on short and, in some cases, medium term management. A full understanding of the stock-recruitment relationship will be essential in this endeavour.

There is an emerging international acceptance of the need for an holistic ecosystem approach to management for marine systems with the objective of preserving ecosystem structure and function, biological diversity, and habitat. The ecosystem approach will involve consideration of the cumulative impacts of human activities in the sea and evaluation of tradeoffs among potentially competing uses of the marine environment. Within this broader context however, regulation of individual ocean use sectors will remain important. Fisheries exert a dominant influence in many marine ecosystems. It will remain necessary to determine the status of individual stocks and to predict the effect of alternative management actions on these stocks and on the ecosystem as a whole, The advances in understanding reproductive dynamics and recruitment outlined in this book serve as a benchmark against which to measure future progress in meeting the goal of incorporating greater biological and ecological realism in management of fishery resources within this broader context.

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