The development and application of a length-based method to estimate the spawning potential ratio in data-poor fish stocks

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This thesis is presented for the degree of Doctor of Philosophy of Murdoch University

2014
Declaration

I declare that this thesis is my own account of my research and contains as its main content work which has not been submitted for a degree at any tertiary education institution.

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Adrian Robert Hordyk
Abstract

Although they support many millions of people, the vast majority of the world’s fisheries are small-scale and data-poor, and without the resources or data systems needed for comprehensive stock assessments. There is strong evidence that unmanaged fisheries are a recipe for disaster, with over-exploitation of the stock almost inevitable. Additionally, it is increasingly recognised that the spatial scale of the stocks of many marine species is much smaller than previously thought, which adds another layer of cost to the stock assessment process, as the cost of collecting and analysing such fine-scale data is prohibitive. The overall aim of this thesis was to develop and test novel methods of stock assessment for data-poor and small-scale fisheries, based on the basic biological characteristics of the exploited species.

Knowledge of the basic biological parameters of fish stocks, such as the natural mortality rate ($M$), the growth parameters (commonly described by the von Bertalanffy equation, $L_\infty$ and $k$), and the length at maturity ($L_m$), is important for many stock assessment methodologies. However, collecting such information is costly, and usually requires sophisticated ageing studies. I conducted a meta-analysis of over 120 marine species, from a range of taxa including teleosts, chondrichthyans, mammals and invertebrates, and examined the variation and patterns in the life-history ratios, and the relationships between size and spawning potential (Chapter 2). These patterns were examined by standardising the age and size of each species so that the relationship between size and spawning-per-recruit for a large range of diverse species could be compared on the same scale. This meta-analysis demonstrated that species that are often considered to be quite different, essentially have the same life-history strategy when viewed on the same relative scale. For example, tuna can be considered as ‘larger, slower’, anchovies, while prawns are ‘smaller, faster’ versions of fish. Additionally, and somewhat surprisingly, a number of teleosts with low $M/k$ values of $\leq 0.5$ appear to have life-histories similar to marine mammals, and quite different from those expected of fish. The results of this study suggest that there is potential to establish a theoretical framework for ‘borrowing’ knowledge from well-studied species to apply to unstudied species and populations as an initial starting point for management.

The ratios of these parameters ($M/k$ and $L_m/L_\infty$) are less variable between individual stocks of the same species than the individual parameters, and certain values of these ratios ($M/k = 1.5$ and $L_m/L_\infty = 0.66$), known as the Beverton and Holt Life History Invariants (BH–LHI) have been used commonly to provide preliminary estimates of unknown parameters. However, many species have life-history ratios that vary considerably from the BH–LHI, and in this study I demonstrate the link between variation in the ratios ($M/k$ and $L_m/L_\infty$) and the life-history strategy of a species. For example, species with low $M/k$ (e.g., $M/k \leq 0.5$)
mature, and reach maximum size, early in life; i.e., have determinate growth and unfished populations dominated by large, mature, individuals. Conversely, species with higher $\frac{M}{k}$ (e.g., $\frac{M}{k} = 3.0$) mature at a smaller relative size, and have indeterminate growth. I developed analytical models to examine the relationship between these ratios and length structure, growth pattern, spawning-per-recruit, and the spawning potential ratio (SPR) for exploited stocks (Chapter 3). These analytical models were extended to include more realistic assumptions about maturity and selectivity-at-length, and a model that uses knowledge of the life-history ratios, and data on the length structure of the catch, was developed to calculate the SPR, an internationally recognised measure of stock status; the length-based SPR model (LB–SPR).

The key parameters of the LB–SPR model are: $\frac{M}{k}$, $L_\infty$, and the variation in length-at-age (CV$_{L_\infty}$), as well as information on the size of maturity ($L_m$). The utility of the LB–SPR model, and its sensitivity to violations of the main assumptions, was examined using Monte Carlo simulations (Chapter 4). Length data were generated for four different species, reflecting different life-history strategies, and the variation of the estimated SPR was examined in a number of scenarios, including: mis specification in the input parameters, the number of fish measured, presence of dome-shaped selectivity, and recruitment variability. The results demonstrate that the model returns unbiased estimates of SPR, and performs well when the biological parameters are well known and the stock is at, or near, equilibrium. However, the model is sensitive to mis specification in the input parameters, particularly to $L_\infty$, where SPR can be significantly under- or over-estimated if $L_\infty$ is not close to the true value. With high recruitment variability, the variation in estimates of SPR from the equilibrium-based LB–SPR model becomes greater, particularly when recruitment trends are auto-correlated. The results of the sensitivity tests indicate that the LB–SPR model has potential to provide a tool for rapid and cost-effective estimation of SPR for data-poor fisheries, which could be used for guiding management decisions and prioritising the direction of future research. Nevertheless, the results also showed that care must be taken to evaluate the validity of the assumptions of the LB–SPR model, and the precision of the biological parameters for the relevant stock, when interpreting the results of the model.

Fisheries managers usually make their decisions in response to estimates of the stock status. For example, if the stock is estimated to be below some target reference point, managers may choose to reduce catches or fishing effort to allow the stock to rebuild. The linking of the status of the stocks and the management decisions are often done by means of a harvest control rule (HCR), which defines a pre-determined agreed response to the estimated status of the stock. I developed a simulation model to perform a management strategy evaluation (MSE) to test a HCR that links the estimates of the SPR from the LB–SPR model to an appropriate management decision (Chapter 5). Three species, representing different life-history types, were investigated and the performance of the model was examined under a number of different scenarios, including: increased recruitment variability, dome-shaped selectivity, and time-varying natural mortality. The results indicate that
the LB–SPR HCR is capable of recovering an over-exploited stock within an acceptable time-frame. The results also demonstrate that care must be taken when setting SPR target reference points, especially when the biology of the species is not well known, and when recruitment is highly variable.

The developments of this thesis highlight the potential of applying a simple methodology to assessing and managing data-poor stocks, requiring only basic information on life-history and length composition of the catch. A framework was established for using knowledge from well-studied species to inform data-poor stocks, which allows initial estimates of the stock status to be made with only minimal data requirements. The methodology developed in this thesis thus provides a cost-effective, easily understood, and transparent method for estimating the SPR for data-poor and small-scale fisheries with only minimal data requirements, and thus allows managers and other stakeholders to begin making informed decisions without having to wait for the collection of additional data. In this respect, the LB–SPR model developed and demonstrated in this study provides a starting point for the assessment of data-poor and small-scale stocks, and assists in identifying important data gaps, prioritising research and collecting information to validate the unknown biological parameters, and beginning the process of gathering additional data to allow alternative assessment methods to be applied in the future (e.g., a time-series of total catches). Finally, this study has also identified areas for additional research, particularly further empirical testing of the LB–SPR model and the development of an integrated harvest strategy framework based on SPR reference points (Chapter 6).
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Acknowledgments

Working on my doctoral studies has been an incredible, but often overwhelming and challenging, experience, and it would not have been possible to complete this thesis without the help and support of many kind and generous people.

I was very fortunate to have had two wonderful supervisors for my PhD, Professors Neil Loneragan and Jeremy Prince. I am extremely grateful for their guidance and advice over the last four years. Jeremy never wavered in his belief of the significance of this work, and I’m thankful for his continued encouragement and patience, especially during the (many) times where I was lost confidence. Neil was tireless in his efforts to edit and improve my writing, always had time available for meetings and catch-ups, and provided much useful and appreciated advice throughout my entire time at Murdoch University. Thanks to you both for your training, advice, and encouragement throughout my PhD, especially for continuing to remind me of the bigger context of my work.

Funding for this project was provided by means of a research scholarship from Murdoch University. Thanks also to the Marine Stewardship Council and the David and Lucille Packard Foundation, who provided significant additional funding which allowed me to complete the final stages of this research. Thanks to David Agnew and Nicolas (Nico) Gutierrez, from the MSC, whose support, comments, and discussions were very helpful and much appreciated. Also thanks to Keith Sainsbury for his advice and assistance, especially with the theoretical development of my length-based model, and Tony Smith, who also provided useful advice and suggestions.

A big thank you to all the members of the Centre for Fish, Fisheries and Aquatic Ecosystems Research at Murdoch University. It’s great to have such a fantastic group of people to work with, and such a wonderful research centre to be a part of.

My PhD study has been quite an adventure, and included two extended trips to the University of Washington in Seattle, USA. I am grateful to Professors Ray Hilborn and André Punt for allowing me to audit their classes at the School of Aquatic and Fisheries Science, and also for providing me with space and resources in their labs. I am especially thankful for the time both Ray and André made to meet with me and discuss my work. I thoroughly enjoyed my time at SAFS and in Seattle. The coursework was challenging but extremely rewarding, and I would not have been able to complete my PhD without the training and advice I received there. Thank you to all the members of Ray’s lab for your kindness and generous hospitality. I will never forget my time there. Trudging around the Alaskan tundra on the lookout for sockeye salmon and grizzly bears was a special highlight!

One of the other highlights of spending time at SAFS was meeting Kotaro Ono: a fine
officemate, a great co-author, and a fantastic friend. Thanks to you and Marine for being such great friends. I miss sharing offices with you in Seattle, and am grateful for your discussions and help regarding my work. I’ll never cease to be amazed at your ability to spend a couple of seconds checking my equations that took me, quite literally, a week to work out!

Thanks also to Sarah Valencia, another great friend whom I met in the USA. I’ve very much enjoyed working together over the last few years, and look forward to continuing to work together into the future.

Also thanks to our other great friends from Seattle: Heather and Luke Rogers who were very generous and kind landlords during our first trip in 2011/2012, and Ryan and Alicia Hemphill with whom we stayed for 3 months in late 2012. Your kindness and hospitality are greatly appreciated.

During the course of my PhD I’ve had the fortune of traveling to a number of national and international conferences and workshops. Thanks to all the wonderful people I’ve met at these meetings and during my travels. In particular, I’d like to thank Pablo Pita, as well as Diana and their daughter, Ada, who showed me such generous hospitality during my recent trip to beautiful Galicia, Spain. What a fantastic way to celebrate the (almost) completion of my PhD!

I am especially thankful for all the support and encouragement from my family and friends. In particular, I am deeply indebted to my parents, Harry and Arly, for all that they have done for me throughout my life, and their support, advice and encouragement over the years, especially during my time of study. Dad, a special thanks for proof-reading my thesis, this was very much appreciated.

Life has a habit of presenting new and unexpected challenges, and the recent year was no exception. The news of Mum’s illness, and her passing several months later, was a difficult experience for us all, and I thank God that I have such a close and loving family and a network of friends that remained so supportive during this difficult time. Thank you all for your thoughts, words, prayers, and support during my entire PhD, but especially in this last year.

Finally, my thanks to my darling wife Candice. Candy, thanks so much for your patience and love. I am incredibly grateful and amazed at your patience and understanding, especially when I decided so many years ago to quit my perfectly good job, and chase my dream of becoming a marine scientist! Thank you. For everything. You know that this would have been impossible without you. Now it is your turn. I am so proud of you in your studies, and know that you are going to make an exceptionally wonderful nurse!
Dedication

In loving memory of my mother, Arly Hordyk (1953–2013)
for believing in me, and teaching me to believe
Publications resulting from this study

The following chapters of this thesis have been peer reviewed and accepted for publication:


Chapter 5 has been accepted for publication in the journal *Fisheries Research*. Hordyk, A.R., Loneragan, N. R., & Prince, J.D. An evaluation of a harvest strategy for data-poor fisheries using the length-based SPR assessment method. Submitted February 2014 to *Fisheries Research*. 
1 General Introduction

1.1 Introduction

Accounting for some 16% of the total animal protein consumed by global human population, fish are arguably one of the world’s most important natural resources (FAO, 2012). The successful management of the world’s fisheries is important to ensure food security from fish protein (Rice and Garcia, 2011). Although the annual global fish production from capture fisheries has stabilised at around 80 million tonnes for the past decade (FAO, 2012), it is predicted that an additional 75 million tonnes of fish will be required by 2050 to feed the increasing world population (Rice and Garcia, 2011). Aquaculture currently contributes over 40% of total fish production, and is expected to be an important source of fish production in the future (Duarte et al., 2009; Godfray et al., 2010; Merino et al., 2012; FAO, 2012). However, effective fisheries management is essential to maintaining or increasing world fish production (Merino et al., 2012).

There is increasing evidence that many marine species are comprised of numerous, relatively isolated, though genetically related, local populations exhibiting local population dynamics (Cowen et al., 2000; Warner and Cowen, 2002; Prince, 2003; Wilson, 2006). For example, local populations of the blacklip abalone, *Haliotis rubra*, widely distributed around Tasmania, have markedly different growth rates, which has consequences for the management of the species (Prince, 1989, 2005). The existence of micro-stock structure in fisheries provides significant challenges for researchers and managers to collect sufficient biological data to manage each stock separately. Many of the modern quantitative methods for stock assessment and management approaches, including harvest policies and quota systems, require a level of information simply beyond the capability of most fisheries; especially when the concept of micro-stocks is taken into account (Cochrane, 1999; Prince, 2010).

The problem of providing data for quantitative models is further compounded when small-scale fisheries are considered. According to some estimates, all except 500,000 of the approximately 50 million fishers in the world are involved in small-scale fisheries (Berkes, 2003). Small-scale fisheries are distributed around the world, but tend to be concentrated in tropical, less-developed, regions of the world, where the capacity for fisheries management is poorly developed or completely absent (Berkes et al., 2001; Gutiérrez et al., 2011; Worm and Branch, 2012; Pitcher and Cheung, 2013). Additionally, due to a number of reasons, small-scale stocks often lack sufficient information for assessment and management of the fishery, and are often considered data-poor (Berkes et al., 2001; Honey et al., 2010). However, data-poor fisheries are not restricted to small-scale fisheries in less-developed
regions, but are found in many more-developed nations, including the United States, Australia, and New Zealand (Bentley and Stokes, 2009b; Dichmont and Brown, 2010; Honey et al., 2010). These fisheries are often small-scale or lower value fisheries, where the economic return from the fishery has been too small to justify investment in research and stock assessments. Additionally, many species are targeted by recreational fishers, or caught as bycatch in larger fisheries, and their low economic value means that little information is available for quantitative assessments of the fisheries. The challenge to produce quantitative stock assessments for the world’s innumerable small-scale stocks, coupled with the fact that a large fraction of the world’s fisheries are data-poor, is overwhelming, and it is clear that alternative methods are required to solve this difficult problem. In this thesis, I develop an approach to address the issue of assessing small-scale and data-poor fisheries based on the biological characteristics of the species. In this Chapter, I summarise the current status of world fisheries, highlight the significance of data-poor and small-scale fisheries, and establish the need for alternative methods to assess and manage data-poor and small-scale fisheries. I then provide a brief overview of the currently available rules-of-thumb for data-poor fisheries, and the biological basis for these rules-of-thumb, particularly the Beverton and Holt Life History Invariants (BH–LHI). This information provides the basis for the approach for developing a new methodology for assessing data-poor fisheries. In the final section of this chapter, I present the structure of the thesis, and briefly outline the contents of each chapter.

1.2 The status of the world’s fisheries

In the late 1990s and early 2000s a number of papers were published in high profile journals, such as Science and Nature, that described an alarming trend of declining fish stocks around the world (e.g., Casey and Myers, 1998; Pauly et al., 1998, 2002; Myers and Worm, 2003). An alternative view, that these were “alarmist claims”, was also put forward. For example, Hilborn (2006) noted that several of the studies that purported to demonstrate examples of collapsed fisheries were based on flawed analyses or interpretation, and suggested that the sensationalist appeal of such “doom and gloom” stories may lead to a publication bias in their favour. However, a number of recent publications have demonstrated that generalising the status of global fisheries is a complex issue, and note many examples of successful fisheries management, particularly in developed countries, but also highlight regions for concern (Hilborn, 2007a; Worm et al., 2009; Worm and Branch, 2012; Pitcher and Cheung, 2013). Despite differing opinions on the overall status and trends in the world’s capture fisheries, researchers generally agree that there is little room for expansion in the world’s fisheries, and that, particularly in the developing world, many stocks are seriously depleted and over-exploited (Costello et al., 2012; Worm and Branch, 2012; Pitcher and Cheung, 2013).

In contrast to large fisheries in many developed countries (e.g., parts of Europe, North America, New Zealand, and Australia), most stocks around the world are effectively un-
managed (Hilborn, 2004). For example, although the annual fisheries production of Indonesia and the United States of America is similar (around 4–5 million tons), the capacity for fisheries management is much lower in Indonesia than in the USA (FAO, 2012; Worm and Branch, 2012). In addition, the lack of management capacity has a strong correlation with areas of high biodiversity, poverty, and the local importance of fish to food security (Worm and Branch, 2012; Pitcher and Cheung, 2013). Worm and Branch (2012) identify such areas as “fisheries-conservation hotspots”, and suggest that the future of fisheries science lies in developing effective management solutions for the data-poor fisheries in developing countries.

1.3 Small-scale and data-poor fisheries

A clear, universally accepted, definition of small-scale fisheries does not exist (Berkes et al., 2001), but the term is generally used to describe low technology, labour-intensive fishing, in contrast to capital-intensive commercial fisheries (Berkes et al., 2001; Sowman, 2006; Jacquet and Pauly, 2008). Small-scale fisheries tend to centre around village communities and consist of a large number of fishers using many small vessels, often consisting of several fleets fishing localised stocks, and, although they are not restricted to these areas, small-scale fisheries tend to occur most often in the coastal regions of developing countries (Berkes et al., 2001). In contrast, large-scale commercial fisheries commonly originate in developed countries, with a relatively small number of large vessels fishing a very large area (Berkes, 2003). Small-scale fisheries include traditional, artisanal, and subsistence fisheries, and often exploit many of the same stocks as commercial fisheries, but because of the use of unselective gear, small-scale fisheries typically harvest a greater variety of species than large-scale commercial fisheries (Berkes, 2003). Small-scale fisheries also play an important role in combating poverty in many developing countries, although fishers are still often ranked in the lowest group of people on the economic scale (Béné, 2003; Walmsley et al., 2006; Wagenaar and D’Haese, 2007; Andrew et al., 2007; Stanford et al., 2013, 2014). While the reasons that fisheries are often synonymous with poverty are still being debated, it is clear that a large proportion of the world’s population depends on fishing for their daily sustenance and survival (Kent, 1997; Berkes et al., 2001; Béné, 2003; Walmsley et al., 2006).

Despite their significant contribution to global yield, and their considerable importance to the social and economic well-being of many millions of people, small-scale fisheries have largely been overlooked in the development of conventional fisheries science (Mahon, 1997; Sowman, 2006). In theory, the formal stock assessment methods developed for large-scale fisheries (e.g., Hilborn and Walters, 1992) could be applied to small-scale fisheries. In reality, however, the multitude of small-scale fisheries, and the large amount of data required to assess each stock, makes the cost of assessment and management prohibitive (Mahon, 1997). In an effort to assess and manage fisheries, researchers have developed increasingly complex stock assessment models, often requiring large amounts of data and
that are only accessible to a limited group of highly trained people (Froese, 2004). In small-scale fisheries, the high grade quality and quantity of data required for such assessments is often lacking or only partially available, and research costs are amplified due to a lack of trained and competent researchers (Mahon, 1997; Andrew et al., 2007).

Similar to the issue of defining a small-scale fishery, it is difficult to provide a generally accepted definition of a data-poor fishery. Fisheries are complex and dynamic systems, and even the most studied fisheries are not fully understood. Furthermore, many fisheries are rich in data but remain information poor, i.e., even if large amounts of data have been collected for a fishery, the lack of technical expertise and suitable methods may mean that effective assessment and management is still not possible (Bentley and Stokes, 2009a). The definition of a data-poor fishery in this thesis follows that of Honey et al. (2010), who define “data-poor” as:

“A condition to describe a fishery that lacks sufficient information to conduct a conventional stock assessment; this includes fisheries with few available data, as well as fisheries with copious amounts of data but limited understanding of stock status due to poor data quality or lack of data analysis.”

1.4 The need for alternative methods

Numerous studies have demonstrated that, despite effective management leading to recovering stocks in many developed countries, the data-poor and small-scale fisheries in developing countries should be a primary focus for fisheries science. For example, Worm and Branch (2012) suggest that the next major challenge for fisheries science is to develop systems and approaches to obtain information on stock status in developing countries. The mismatch between the traditionally large-scale spatial management of commercial fisheries and the growing realisation that many marine species function on small spatial scales is receiving increasing recognition (Hilborn et al., 2005; Wilson, 2006; Prince, 2010), and researchers have highlighted the importance of matching the scale of data collection and assessment to the appropriate scale of the stock and fishery (Hilborn, 2004; Prince, 2005). Other researchers emphasise the need to develop simple, cheap procedures based on local indicators, collected directly from the catch, to make assessment and management feasible, especially for small-scale, cash-poor fisheries (Berkes et al., 2001; Prince, 2010; Hilborn, 2012; Pitcher and Cheung, 2013). By abandoning traditional management objectives such as maximum sustainable yield (MSY), sustainable fisheries management does not require perfect science (Johannes, 1998; Worm and Branch, 2012), and simple rules-of-thumb and methods based on life history characteristics have great potential to providing cost-effective methods to assess and manage fisheries in both developed and developing countries (Reynolds et al., 2001; Hilborn, 2004; Pitcher and Cheung, 2013). While the idea of MSY has been criticized in the past (e.g., Larkin, 1977), it is still regarded as a useful concept in fisheries science, particularly as a limited reference point (Punt and Smith, 2001), and the work presented in this thesis is based on the MSY paradigm.
Strong leadership, trust, and cooperation between stakeholders, including managers, scientists, industry and conservation groups, are crucial for successful fisheries management, and it is clear that the assessment and management process must be transparent in order for this to be achieved (Hilborn, 2002; Gutiérrez et al., 2011). Many assessment models require a times series of data from the fishery (e.g., total annual catches), knowledge of the biology of the target species and, depending on their complexity, a time series of fishery independent data (Hilborn and Walters, 1992). Conventional stock assessment methods often involve complex age-based statistical models that are difficult to understand by individuals without advanced mathematical training, and can appear opaque, or as a ‘black box’, to fishers and other stakeholders (Cotter et al., 2004). However, even simple fisheries assessment models still require considerable amounts of data. For example, surplus production models are one of the simplest analytical models for assessing fish stocks, but require a time-series of catch and effort data to calculate catch-per-unit-effort (CPUE) (Hilborn and Walters, 1992; Haddon, 2001); information which is not available for many of the world’s truly data-poor fisheries (Mahon, 1997; Honey et al., 2010). In most cases, only large, valuable fisheries, e.g., the Alaskan pollock fishery, worth annually over $US1 billion (Fissel et al., 2012), have enough resources to pay for expensive scientific surveys and stock assessments, as well as facilitate meetings, workshops, and training to foster sufficient understanding and clear communication between all stakeholders. However, the vast majority of the world’s fisheries are of much lower economic value and are often data-poor. Alternative assessment and management methodologies are needed in order to successfully manage these fisheries, which has become a focus for research in recent years (e.g., Wayte and Klaer, 2010; Prince et al., 2011; Dick and MacCall, 2011; Klaer et al., 2012).

Managers of data-poor and small-scale fisheries, especially in developing countries, are faced with the difficult task of conducting stock assessments without the necessary data or resources (Mahon, 1997; Honey et al., 2010). Faced with such a paucity of data, managers are often presented with three choices: 1) do nothing and wait for more data to be collected, i.e., no management at all; 2) rely solely on expert judgement, as is often used, for example, for risk assessment of vulnerable species (Hobday et al., 2011) and to inform Bayesian priors (Maunder and Punt, 2013); or 3) use whatever empirical data are available to make initial estimates of the status of the stock to inform management decisions, perhaps imprecise but demonstrably better than the first two options (Leung and Steele, 2013). Currently assessment methods are lacking for situations where very few data on the exploited stock are available, e.g., no time-series for the estimated total catch or the relative index of abundance. Under these circumstances, managers of data-poor and small-scale fisheries may be forced to take one of the first two options i.e., to do nothing or rely on expert judgement. The focus of this thesis is to develop methodologies for assessing such data-poor stocks, i.e., stocks for which there are no data on historical catch and effort, no fisheries independent surveys, and little or no biological information, and to provide a tool for managers to use the data that are available, e.g., the length structure of the catch, to make informed decisions for the sustainable management of the stock. Rather than waiting for more data
to be collected, managers can begin the assessment and management process, while simultaneously identifying and prioritising important areas for further research. Over time, the time series of data, e.g., catches and effort, that are collected, together with information on the biology of the stock, can be incorporated into more sophisticated stock assessment methods.

Even if the ubiquitous technical issues of assessing data-poor fish stocks was solved in a satisfactory manner, the existence of an adequate governance structure is still essential for successful fisheries management (Hilborn, 2007b; Gutiérrez et al., 2011). However, for numerous and varied reasons, such governance structures are often not in place for many small-scale and data-poor fish stocks (Berkes et al., 2001; Johannes, 1998; Pitcher and Cheung, 2013). This is an important aspect of managing data-poor fish stocks, and much work has been focused on the understanding of the governance requirements for successful fisheries management (Hilborn et al., 2005; Hilborn, 2007b; Andrew et al., 2007; Gutiérrez et al., 2011). The work described in this thesis focuses on the technical challenge of developing a new method to conduct assessments of data-poor fish stocks, and while acknowledging its importance, does not address the issue of the required changes to governance structures for data-poor stocks.

1.5 Empirical methods and rules-of-thumb for data-poor fisheries

A number of methods have been developed to provide effective ‘short-cuts’ to assess fish stocks without the large amount of data and expense associated with classical quantitative methods. For example, Thorson et al. (2012) used life history and landings information from assessed stocks to estimate the status of unassessed stocks. Dick and MacCall (2011) integrated MacCall’s (2009) Depletion-Corrected Average Catch method into the stock reduction framework to provide a method to estimate sustainable yields from a time-series of past catches, although this method requires estimates of historical annual catches since the beginning of exploitation. Other methods propose estimating biological reference points directly from biological parameters, and demonstrate that, assuming the existence of a reliable index of abundance, the status of the stock can be estimated without the need for a quantitative model or extensive fisheries data (Brooks et al., 2010).

While a large number of methods have been developed to address the problem of assessing the status of data-poor fisheries, it is not always clear exactly how the authors have defined “data-poor”. For example, many of the methods developed to address data-poor stocks on the west coast of the United States (e.g., Dick and MacCall, 2011) require data and historical records from the fishery that are not available to a large number of fisheries around the world. Indeed, researchers working in tropical reef systems have demonstrated that fisheries can be managed in, effectively, a data-less environment by using local fisher knowledge, e.g., to identify the location and timing of spawning aggregations (Johannes,
Despite the heavy reliance of fisheries science on formal methods of quantitative assessment, there has been a rich history of workers, with experience across a wide range of fisheries and species, developing valuable rules-of-thumb to provide reliable ‘guesstimates’ of the basic biological parameters needed to parameterise simple assessment models, from simple and commonly collected data. The most easily and commonly collected biological data in fisheries are commercial catch rates and size composition of the catch, and the simplest biological studies are those on weight-at-length, size-at-maturity, and size-at-age (Quinn and Deriso, 1999).

Numerous empirical methods have been developed to estimate biological parameters and stock status from these simple data. For example, the rate of natural mortality of fish populations ($M$) is an important parameter for most stock assessment models, but one of the most difficult to estimate reliably (Vetter, 1988; Kenchington, 2013). Consequently, many of the early empirical approaches were developed in an attempt to estimate this parameter. For example, Beverton and Holt (1959), in a study on the growth and life-spans of fishes, noticed a general relationship between the von Bertalanffy growth parameter ($k$) and the natural mortality rate, and stated:

“it seems that for a wide range of fish species the natural span of life is nicely adjusted to the time needed to complete or nearly to complete, the growth pattern.”

This relationship has been investigated further (Cushing, 1981; Griffiths and Harrod, 2007; Gislason et al., 2010), and it is the main principal behind the widely cited empirical equation to estimate $M$ of Pauly (1980), which related $M$ to the von Bertalanffy growth parameter ($k$), asymptotic size ($L_\infty$) and the ambient environmental temperature. A second widely cited method to estimate $M$ was developed by Hoenig (1983), who investigated the relationship between $M$ and the maximum observed age for a range of species. Assuming a uniform $M$ across all age classes of a species, Hoenig (1983) calculated separate regressions of maximum age against estimates of $M$ for a range of molluscs, fish and cetaceans. He suggested that preliminary estimates of $M$ could be obtained by ageing a few of the largest fish. However, he also noted that this method was subject to bias through the estimation of oldest fish, which will vary with sample size, recruitment variability and the level of fishing that has occurred before the age samples are attained.

The mean length at which a population becomes sexually mature ($L_m$) is another important metric that is often used in fisheries science. The ratio between $L_m$ and the mean asymptotic length ($L_\infty$) of the population, referred to as “reproductive load” (Cushing, 1981), is relatively consistent within taxa of similar size and generally falls between 0.4 and 0.9 (Beverton and Holt, 1959; Pauly, 1984; Charnov, 1993; Stamps et al., 1998). Froese and Binohlan (2000) developed empirical relationships to estimate $L_m$, $L_\infty$, and the length at which the yield-per-recruit is maximised ($L_{opt}$), and demonstrated how these rules-of-thumb could be useful in determining the status of exploited stocks.
Knowledge of the biological parameters is important for the successful assessment and management of fish stocks. Because of the difficulty and expense associated with obtaining these estimates, especially for data-poor stocks, the use of these rules-of-thumb has become popular in fisheries science, and research continues into developing and refining these empirical relationships (Gislason et al., 2010; Charnov et al., 2013).

1.6 Life-history invariants

The consistency of patterns in the ratios of some of the life history parameters of fish was first recognised by Beverton and Holt (Beverton and Holt, 1959; Holt, 1962; Beverton, 1992) and these relationships have been further explored by other researchers (Charnov and Berrigan, 1990, 1991; Charnov, 1993). Three such relationships are:

\[
\frac{M}{k} \quad \text{The ratio of the natural mortality rate (M) to the von Bertalanffy growth rate (k)}
\]

\[
A_m M \quad \text{The age at maturity (A_m) multiplied by the natural mortality rate}
\]

\[
\frac{L_m}{L_\infty} \quad \text{The ratio of the length at maturity (L_m) to the asymptotic length (L_\infty)}
\]

These relationships have been given a theoretical foundation through life-history optimisation theory (Roff, 1984; Jensen, 1996; Charnov et al., 2001) and using size-spectrum theory in community ecology (Andersen et al., 2009; Andersen and Beyer, 2013). Holt (1962) recognised that these special relationships could be useful for estimating difficult parameters from more easily obtainable data. As described above, Pauly (1980) and others have used these life history patterns to produce empirical equations to estimate \( M \) (see Kenchington (2013), for a review of these empirical methods).

The ratio of the rate of natural mortality (M) and the von Bertalanffy growth coefficient (k) is one of the most important and well-known life-history invariants. Charnov (1993) examined this relationship for the data from 175 fish stocks, and found that the mean relationship was \( \frac{M}{k} \approx 1.65 \). Jensen (1996) demonstrated that, assuming age at maturity coincides with the inflection point in the von Bertalanffy growth curve, the optimal value, from a bio-energetic perspective, of \( \frac{M}{k} \) was 1.50. This ratio has become known as one of the Beverton–Holt life history invariants (BH–LHI) and have been used extensively in fisheries science, to estimate the notoriously difficult parameter \( M \) (e.g., see many papers citing Jensen, 1996) and for setting biological reference points (Williams and Shertzer, 2003; Beddington and Kirkwood, 2005).
However, the apparent invariance in the life histories ratios has been debated, with some authors claiming that it is a statistical illusion caused by a fundamental methodological error (de Jong, 2005; Nee et al., 2005; Cipriani and Collin, 2005). The term ‘invariant’ appears to have fueled the debate, and it might be better to refer to these relationships as ‘dimensionless numbers’ (Mangel, 2005; Savage et al., 2006). Both proponents and detractors of life history invariance theory agree that ‘invariance’ does not mean that there is no variation at all (Charnov, 1993; Nee et al., 2006), and Charnov (1993, pg 5), one of the original advocates of life history invariance, states:

“The invariance holds only in a statistical or probabilistic sense. Most life history variables estimated for field populations are noisy. How constant is constant enough to be considered invariant is worthy of much thought, considering that noisy field parameters are our stock in trade and will be forever.”

Despite the debate on whether the apparent life history invariants describe any real constraints on evolution or not (Nee et al., 2005; Savage et al., 2006), these relationships have the potential to be used to make preliminary estimates of the life history parameters of a data-poor fish populations.

Estimates of natural mortality, and age and size at maturity, are important for the sustainable management of an exploited fish stock, and when little or no biological data are available for a particular population, initial estimates of \( M \) or \( L_m \) may be made by using empirical methods based on the BH–LHI (e.g., Pauly, 1980; Froese and Binohlan, 2000). Although the empirical methods are very useful to estimate difficult parameters, a number of species are clearly exceptions to the rule. For example, a study of multiple populations of walleye (\textit{Sander vitreus}) in Canada found a general invariance between \( L_m \) and \( L_\infty \), but no invariant relationship between \( M \) and \( k \), or \( A_m \) and \( M \) (Purchase et al., 2006). Likewise, while Pauly’s (1980) empirical method to estimate \( M \) is widely cited, and appears valid in many cases, the estimates from this method deviate greatly from the estimates of \( M \) for many fish species (Pascual and Iribarne, 1993; Kenchington, 2013). The variability around the BH–LHI has not been explored comprehensively across a wide range of species, and this topic is examined in detail in this thesis through a meta-analysis (Chapter 2).

1.7 Research and structure of the thesis

The BH–LHI have become well established in the fisheries science and marine ecology literature (Jennings and Dulvy, 2009), despite the recognition that the life-history invariants do not adequately describe many species (Beverton, 1992; Mangel, 1996). While the life history ratios have been intensively studied in the context of life histories strategies (e.g., Charnov et al., 2001), their use in fisheries assessment has been limited largely to estimating \( M \) to parameterise stock assessment models, or to estimate fishing mortality \((F)\) from estimates of total mortality \((Z)\) and \( k \) by assuming that \( \frac{M}{k} = 1.5 \) (e.g., Beddington and Kirkwood, 2005). While in many cases \( \frac{M}{k} \) does vary significantly from the BH–LHI
value of 1.5, within closely related species or stocks the ratio is often less variable than the individual parameters for $M$ and $k$ (Beverton, 1992). Accurate and unbiased estimates of both $M$ and $k$ are difficult to obtain in exploited fisheries because most methods to estimate these parameters require samples of the oldest and largest fish which are usually the first removed by fishing (Kenchington, 2013). However, estimates of the ratios $\frac{M}{k}$ and $L_{\infty}$ for an exploited stock may be more readily obtained by studies of other nearby stocks or meta-analysis with closely related species.

The main research question addressed in this thesis is: is it possible to use basic information on the life history parameters to assess data-poor stocks? More specifically, this study aims to explore and develop a length-based assessment methodology that relies on the apparent consistent ratios of these life history parameters to estimate the spawning potential ratio for data-poor and small-scale stocks.

The thesis addresses the overall question by exploring the patterns in variation in the life-history ratios for a range of marine species (Chapter 2), developing and exploring the theoretical underpinnings for the new assessment method (Chapter 3), examining the sensitivity of the new model to variation in the main assumptions (Chapter 4), and developing a harvest control rule for the new assessment model, and incorporating the model into an assessment and management framework (Chapter 5). Finally, the main findings of this study are summarised and important areas for further research are identified in the general conclusion (Chapter 6).

Chapter 2 presents a meta-analysis that explores patterns in the life history ratios for a wide range of marine taxa, and demonstrates how standardising by asymptotic size ($L_{\infty}$) allows previously unrecognised patterns to emerge when comparing the life-history strategies across species. Furthermore, it examines the variability in the life history ratios across a wide range of marine species and taxa (fish, crustaceans, molluscs, chondrichthyans, and cetaceans), and explores the potential for prediction of the life history ratios for stocks for which the basic biological information is unknown.

Chapter 3 explores the life history ratios by introducing a number of analytical models that relate the life-history ratios to the expected length composition, the spawning-per-recruit, and the spawning potential ratio of exploited stocks. These models are then further extended to include more realistic assumptions about growth and selectivity, and the theoretical framework for using the life history ratios to estimate the spawning potential ratio (SPR) using the length frequency composition of the catch is introduced.

The fourth chapter formalises the analytical models developed in Chapter 3, and introduces the length-based SPR method (LB–SPR). Simulation modelling is used to test the performance and robustness of the LB–SPR method, and the sensitivity of the model to the various assumptions is explored in detail. The utility of the model is also examined by applying it to four species with different life-history strategies (life-history ratios), and comparing the results of the LB–SPR method with the estimates from a conventional biological study.

Chapter 5 develops a SPR-based harvest control rule, and uses simulation modelling
to test the sensitivity of the LB–SPR method in a dynamic setting for three species with different life-history strategies. This work provides a framework for incorporating the LB–SPR methodology into the assessment and management of data-poor fisheries, and also highlights the limitations of the method.

The final chapter, Chapter 6, summarises the major findings from the thesis, and discusses the general applicability of the LB–SPR method as a tool for assessment and management of data-poor stocks. Finally, key areas for future research are identified, and several suggestions are made regarding the general applicability of the LB–SPR method to addressing the issue of assessing and managing the world’s data-poor and small-scale stocks.
2 Revisiting the concept of Beverton–Holt Life History Invariants with the aim of informing data-poor fisheries assessment

Abstract

The complexity and cost of existing fishery assessment techniques prohibits their application to 90% of fisheries globally. Simple, cost-effective, generic approaches are needed for small-scale and data-poor fisheries that support the majority of the world’s fishing communities but cannot currently be assessed quantitatively. This meta-analysis of the relationship between spawning potential and the normalized size and age of 123 marine species suggests that the so-called Beverton–Holt Life History Invariants \((BH\text{--}LHI; \frac{L_m}{L_\infty}, \frac{M}{K}, A_m M)\) actually vary together in relation to life history strategy, determining the relationship between size, age and reproductive potential for each species. Although little realized, the common assumption of unique values for the BH–LHI also implies that all species share the same relationship between size, age, and reproductive potential. This implicit assumption is not supported by this meta-analysis, which instead suggests there is considerable, but predictable, natural variation in the BH–LHI ratios, and the relationships between size, age and reproductive potential that they determine. This re-conceptualization of the BH–LHI has potential to provide a theoretical framework for ‘borrowing’ knowledge from well-studied species to apply to related, unstudied species and populations and, when applied together with the assessment technique developed in Chapter 3 and tested in Chapter 4, could make simple forms of size based assessment possible for many data-poor fish stocks that are currently considered unassessable.

2.1 Introduction

A persistent challenge for sustainable fisheries is the scale, complexity and cost of fishery assessment (Walters and Pearse, 1996; Beddington and Kirkwood, 2005; Hilborn et al., 2005; Mullon et al., 2005). Current assessment techniques require technical expertise, detailed biological knowledge and time-series data on catch, effort and/or surveyed abundance (Walters and Martell, 2004) resulting in an annual cost of $US50,000 to millions
of dollars per stock (Pauly et al., 2013). This represents a substantial impediment to assessing small-scale, spatially complex and developing world fisheries (Mahon, 1997). By some estimates, 90% of the world’s fisheries, which directly support 14–40 million fishers and indirectly support approximately 200 million people, are unassessable using current methods (Andrew et al., 2007).

Considerable uncertainty surrounds the status of unassessed stocks (Costello et al., 2012; Pauly et al., 2013) so that overfishing may go unrecognized until stocks collapse. Even where fishing communities want to change fishing practices, the technical difficulty and expense of current assessment techniques can prevent science-based harvest strategies from being developed and implemented for these fisheries. A new methodology is needed for small-scale and data-poor fisheries (Andrew et al., 2007; Pauly et al., 2013) along with theoretical frameworks for informing the assessment of unstudied species with biological knowledge about related species (Punt et al., 2011).

The correlation between biological parameters across species has been widely used to provide generic parameter estimates necessary for assessment modeling (Charnov, 1993) and were first described in fisheries by Beverton and Holt (1959) for the clupeid and engraulid (herring and anchovy-like bony fishes) stocks of the North Sea (Beverton, 1963). They observed correlations between: 1) the instantaneous natural mortality rate ($M$) and the von Bertalanffy (1938) growth rate constant ($k$), 2) length at maturity ($L_m$) and asymptotic length ($L_\infty$), and 3) $M$ and the age of maturity ($A_m$).

Beverton and Holt’s primary interest was in estimating $M$, a parameter that is notoriously difficult to measure, from studies of $k$, $L_m$ and $A_m$, which by comparison, are easily estimated. Although neither Beverton nor Holt used the term, these three life history ratios ($\frac{M}{k}$, $\frac{L_m}{L_\infty}$, and $A_mM$) are now commonly referred to as the Beverton–Holt Life History Invariants (BH–LHI). Widely considered to be environmentally influenced constants (Pauly, 1980), the BH–LHI have been used extensively to parameterize fisheries models (Charnov, 1993; Beddington and Kirkwood, 2005; Gislason et al., 2010). In this chapter I use Jensen’s (1996) definition of the three BH–LHI: $\frac{M}{k} = 1.5$, $\frac{L_m}{L_\infty} = 0.66$, and $A_mM = 1.65$.

The spawning potential ratio, or spawning per recruit (SPR), is a commonly used index of the relative rate of reproduction (Mace and Sissenwine, 1993; Walters and Martell, 2004) in an exploited stock. Brooks et al. (2010) recommend its utility for applying to stocks in data limited fisheries. The SPR is defined as the proportion of the unfished reproductive potential left by any given fishing pressure. It can be conceptualized as the total reproductive potential of all the cohorts in a population at equilibrium, or the life-time reproductive potential of an average individual passing through a population at equilibrium. By definition, unfished stocks and individuals in an unfished stock, have an SPR of 100% (SPR$_{100\%}$) and fishing mortality reduces SPR$_{100\%}$ from the unfished level to SPR$_{X\%}$. Generic SPR-based reference points have been developed theoretically and through the meta-analysis of quantitatively assessed fisheries, and have been recognized in international fisheries law (Restrepo and Powers, 1999; Australian Government, 2007). For example SPR$_{40\%}$ is generally considered a conservative proxy for maximum sustainable yield (Mace and...
Sissenwine, 1993; Clark, 2002; Walters and Martell, 2004). Typically, estimating SPR requires unique population models to be parameterised for each stock using estimates of natural mortality, growth, reproduction, and a time series of abundance, or age composition data (e.g., Ault et al., 1998; Walters and Martell, 2004).

Inspired by previous work that used size data to assess and manage fish stocks (Prince et al., 2008, 2011), the aim of this chapter was to investigate the possibility to develop a simple generalised approach for using size composition data to evaluate the SPR of exploited populations. The study began by addressing the question: do all species exhibit the same relationship between size of maturity, relative size composition, and SPR?

This question was first approached by an extensive literature search, where estimates of the biological parameters (e.g., age and size at maturity, natural mortality, and information on the growth curve) were collated for a wide range of marine species, including teleosts, chondrichthyans, invertebrates and marine mammals. A spawning-per-recruit model was used to investigate how SPR relates to size of maturity, relative body size and age for the 123 species included in the meta-analysis. The results presented here suggest that there are predictable patterns in the life history ratios $M_k$ and $L_m/L_{\infty}$ which are related to each species’ life history strategy, unfished size compositions, and the distribution of spawning potential by size, and provide support for the development of a generalised method to estimate the SPR from size composition data. The patterns observed in this study form the basis for the size-based technique for estimating the SPR that is developed in the rest of this thesis.

2.2 Methods

2.2.1 Selection of parameter sets

For the meta-analysis I collected studies of marine and estuarine species for which I could find robust estimates of growth, natural mortality, reproduction, and length-weight relationships. Strict selection criteria, based on criteria developed by Gislason et al. (2010), were applied in order to control the quality of the parameter sets. Gislason et al. (2010) define the six criteria as: “

1. Estimates were rejected if they had been derived from empirical relationships (e.g., Beverton and Holt, 1959; Pauly, 1980) or ‘borrowed’ from studies of similar species.

2. Estimates by size or age were rejected if they had been derived from multi–species modeling.

3. Parameters were rejected if they were based on an insufficient amount of data, if the authors expressed concern that they could be biased or uncertain, or if the sampling gears and/or procedures for working up the samples were likely to have biased the estimates.

4. Estimates of total mortality based on catch–at–length, or catch–at–age were accepted as estimates of $M$, only if the data had been collected from an unexploited or lightly
exploited stock over a sufficiently long time period to ensure that they reflected mortality and not simply differences in year class strength, and if growth parameters or ageing methods were considered appropriate.

5. Estimates derived from tagging data were included only if the following factors had been considered: mortality associated with the tagging operation, tag loss, differences in mortality experienced by tagged and untagged fish, migration out of the study area and uncertainty regarding tag recovery.

6. Estimates derived from regressions of total mortality and effort were included, only if it was credible that total fishing mortality would be proportional to the measure of fishing effort considered, and if extrapolation did not result in excessively large confidence intervals.”

While Gislason et al.’s focus was solely on ensuring the quality of natural mortality estimates, these criteria also ensured the quality of estimates for the broader list of parameters of interest to this study (i.e., growth, reproduction, and length-weight relationships).

To ensure that each species’ parameter set described a single population and a similar population density an additional seventh criterion was also applied, defined as:

7. All parameter estimates for a species should be from the same geographic population, and from the same time period.

Species were only included if they met all seven criteria and all the necessary parameters could be estimated. While this limited the number of studies available to the meta-analysis, the criteria were important to minimise the error when comparing patterns in the parameters across the species, and to avoid circular reasoning, e.g., where some parameters (such as $M$) were estimated by methods based on empirical relationships with the other parameters. A total of 123 species, including representatives from teleosts, invertebrates, chondrichthyans, and marine mammals, were included in the meta-analysis. A complete list of species, parameter values and source references are provided in Appendix A. It should be noted that these criteria biased the selection process towards well-studied populations prior to, or during the early phase of exploitation. Thus almost all the studies included in the meta-analysis are of lightly exploited populations. The meta-analysis is not exhaustive or representative of all, or even groups of, marine species. For this reason there was no attempt to apply statistical techniques of analysis, as there is no expectation that the samples are distributed normally or are representative of any mean condition, parameter value or relationships. As discussed below, such statistical concepts are not applicable to a study such as this. The aim of this study was entirely qualitative; to look for, and to describe patterns of variation that exist in nature. The theoretical understanding of the patterns observed in this study are examined in detail in Chapter 3.
2.2.2 Spawning potential ratio (SPR) model for the meta-analysis

The SPR achieved at any given age was modelled for the 123 species to examine patterns in the relationships between age, length, weight and reproductive output. The SPR is usually calculated by summing the total reproductive output of all age classes and dividing by the number of recruits in order to obtain a general measure of current rate of reproductive output in relation to the maximum potential output, i.e., the unfished, level. However, the interest of this study is in calculating the cumulative proportion of total lifetime reproductive output achieved when an individual reaches each age/size, and how that varies across the widest possible range of marine species. For this purpose, an age-based equilibrium SPR model was developed and applied to each species. The number of survivors, average individual length and weight, and percentage of total reproductive output achieved for both individuals and cohorts at each successive time step was calculated. To enable comparisons across species age, length, weight and reproduction were normalized with respect to their maximum value. The maximum age class \( t_{\text{max}} \) was determined to be the first age class with an abundance of \( \leq 1\% \) of the initial cohort size (i.e., \( \leq 10 \) individuals with an initial population size of 1,000). This is consistent with the results of empirical studies of Hewitt and Hoenig (2005) who note that a range of 1–5% has generally been used for the purpose of estimating \( M \), and who conclude that 1.5% is most appropriate.

For each parameter set, the cohort declined with constant natural mortality:

\[
N_{t+1} = N_t e^{-M}
\]  
(2.1)

where \( N_t \) is the number of age \( t \) individuals, and \( N_0 \) is 1,000. Reproductive output (EP) was estimated at each age \( t \) as:

\[
\text{EP}_t = N_t f_t
\]  
(2.2)

where \( f_t \) is mean fecundity at age \( t \). The cumulative spawning potential ratio (SPR) was calculated for each age class \( t \):

\[
\text{SPR}_t = \sum_{t=0}^{t_{\text{max}}} \frac{\text{EP}_t}{\sum_{t=0}^{t_{\text{max}}} \text{EP}_t}
\]  
(2.3)

where \( \text{SPR}_t \) is the proportion of potential lifetime reproductive output achieved at age \( t \). When no fecundity data were available, the reproductive output of a mature age class was assumed proportional to biomass:

\[
\text{EP}_t = N_t W_t m_t
\]  
(2.4)

where \( W_t \) is mean weight at age \( t \), and \( m_t \) is the probability of being mature at age \( t \).

This study used the simplifying assumption that \( M \) remains constant over all age and size classes in a population. This is unlikely to be true in nature, as juvenile mortality rates are
generally observed to be greater than adult mortality rates, and mortality rates maybe size-dependent throughout a species’ life cycle (Gislason et al., 2010; Charnov et al., 2013). However as noted by Charnov et al. (2013) juvenile mortality rates do not influence the estimation of life-time reproductive output in a species, and adult mortality rates tend to be more constant than juvenile rates, and so more likely to be compatible with this simplifying assumption.

A broad range of formulations to describe growth, fecundity, mortality and relationships between age, length and weight were found in the literature, and these are described below. The formulation of the SPR model was adapted for each species to the formulations and units used in the source literature. If < 15 age classes were present, the unit of time was converted to the next lowest unit (i.e., years to months, or months to weeks) to smooth the functions being modelled.

Five growth models were used by the collated literature to describe the growth of the 123 selected species. The three–parameter von Bertalanffy growth function (VBGF) was used to describe the growth of 117 species:

\[ L_t = L_\infty \left( 1 - e^{-k(t-t_0)} \right) \]  

(2.5)

where \( L_t \) is mean length at age \( t \), \( L_\infty \) is asymptotic length, \( k \) the growth coefficient, and \( t_0 \) is the theoretical age at zero length. The Schnute growth function was used for three species:

\[ L_t = \left[ \left( y_1^B + \left( y_2^B - y_1^B \right) \frac{1 - e^{-A(t-T_1)}}{1 - e^{-A(T_2-T_1)}} \right) \right]^\frac{1}{B} \]  

(2.6)

where \( T_1 \) and \( T_2 \) are reference ages, \( y_1 \) and \( y_2 \) length at each reference age respectively, and \( A \) and \( B \) are constants \( \neq 0 \). The Gompertz growth function was used for one species:

\[ L_t = \omega_0 e^{G \left( 1 - e^{-g t} \right)} \]  

(2.7)

where \( G, \omega_0 \) & \( g \) are constants. Two generic length models were used for two species:

\[ L_t = L_\infty + \alpha \beta^t \]  

(2.8)

\[ L_t = L_{t-1} + \frac{\alpha}{1 + e^{t_{t-1}-\phi}} \]  

(2.9)

where \( \alpha, \beta \) and \( \phi \) are constants.

Length-weight relationships were described in the literature for all except two species by:

\[ W_t = a L_t^b \]  

(2.10)

where \( a \) and \( b \) are constants. Polynomial regressions were reported for the length-weight relationships for two species:

\[ W_t = a - b L_t + c L_t^2 \]  

(2.11)
where \(a, b\) and \(c\) are constants.

When fecundity at length, weight, or age was not available, reproductive output was assumed proportional to the biomass of an individual or cohort, based on the reported maturity ogive for each species (Equation 2.4). When no maturity ogive was available, whichever available estimate of length at maturity (e.g., \(L_0, L_{50}, L_{100}\)) was used to delinate between juvenile and adult size classes, and maturity was assumed to be knife-edge at that size. Size-fecundity relationships were available for 24 species. For the remaining 99 species, reproductive output was assumed proportional to individual weight for teleosts (75 species) and some crustaceans (4 species) and molluscs (7 species), and size-independent for elasmobranches (8 species) and mammals (5 species).

Where sexual dimorphism was recorded only female parameters were used in the SPR model developed for the species. The database includes several hermaphroditic species, for these species the maturity ogive was defined as female maturation ogive, and if occurring after the female stage (which is generally the case), the male stage was considered to contribute to the reproductive potential of the population, and for the purpose of SPR modeling treated as a continuation of the female phase.

### 2.2.3 Simulation of length composition

To assist with understanding of the observed patterns, an age-based model was developed to simulate the length frequency composition of the theoretical unfished populations across the range of \(M_k\) observed in the meta-analysis. To achieve the desired ratios of \(M_k\) for each simulation \(M\) was fixed at 0.2 and solved for the appropriate value of \(k\). Size compositions were simulated using nine values of \(M_k\) (4.0, 1.65, 1.0, 0.8, 0.6, 0.4, 0.3, 0.2, & 0.1). Growth was assumed to be described the the von Bertalanffy equation (mean \(L_\infty = 1, CV_{L_\infty} = 0.1, t_0 = 0\)) in arbitrary units, with \(L_\infty\) distributed normally among individuals, and with the variance in mean length a function of mean cohort length (Sainsbury, 1980). Because of the variation associated with length-at-age, some individuals have lengths greater than mean \(L_\infty\) (1.0); thus the length composition was calculated for lengths between 0 and 1.4. The size of maturity for these simulated size compositions was calculated using the Beverton (1992) equation derived for teleosts:

\[
\frac{L_m}{L_\infty} = \frac{3}{3 + \frac{M}{k}}
\]  

### 2.3 Results

Figure 2.1a–d shows the modeled SPR for every species in the meta-analysis as functions of (a) normalized weight \(\left(\frac{W}{W_{\text{max}}}\right)\), (b) normalized length \(\left(\frac{L}{L_{\text{max}}}\right)\) and (c) normalized age \(\left(\frac{A}{A_{\text{max}}}\right)\). As described in the methods, \(W_{\text{max}}, L_{\text{max}}\) and \(A_{\text{max}}\) are defined as the value attained when modeled cohort abundance declines to \(\leq 1\%\) of initial abundance. In Figure 2.1d the SPR–at–weight trajectories are standardised with respect to both weight-at-maturity and
maximum weight \( \left( \frac{W_{\max} - W_m}{W_{\max} - W_m} \right) \) making it evident that much of the crossing of trajectories observed in Figure 2.1a & b is due to variation in size of maturity. The spectrum of curves observed in Figure 2.1a–d appears to be determined by the range of \( \frac{M}{k} \) ratios observed in the meta-analysis; species with the greatest ratio \( \left( \frac{M}{k} = 3.5 \right) \) have trajectories in the upper left of Figure 2.1a & b and, while those with the lowest ratios \( \left( \frac{M}{k} = 0.1 \right) \) have trajectories in the bottom right.

Also plotted in Figure 2.1a–d (black lines) are the relationships expected for species with biological parameters conforming to Jensen’s (1996) estimates of the three BH–LHI \( \left( \frac{M}{k} = 1.5, \frac{L_m}{L_{\infty}} = 0.66, \text{ and } A_mM = 1.65 \right) \), and the assumption that reproductive output is proportional to mature weight, which in turn is a cubic function of length. It is clear from this result that the three BH–LHI proscribe a unique relationship between normalized size, age and SPR. However, the BH–LHI relationship is apparently some form of ‘median’ form of the relationship observed across all 123 species in the meta-analysis, rather than an invariant relationship that is applicable to many species as originally expected might be the case.

Figure 2.2 illustrates that the \( \frac{M}{k} \) ratio determines the relative shape of a population’s unfished size composition. Note again the use of the simplifying assumption that \( M \) remains constant over the all age and size classes in a population, and the influence that this assumption has on the shape of these simulated size compositions. However, using the rationale of Charnov et al. (2013) that adult mortality rates are more likely to tend towards a level of consistency, and determine life–time reproductive output, these results demonstrate that unfished populations with \( \frac{M}{k} > 1.0 \) do not tend to exhibit an adult modal size (Figure 2.2). This is because the fish grow relatively slowly and die too rapidly to accumulate around a species asymptotic size (see derivations in Chapter 3). This contrasts with unfished populations of species with \( \frac{M}{k} < 1.0 \) in which the fish grow relatively quickly and persist long enough to accumulate around an asymptotic size so that a modal adult size becomes observable, and increasingly prominent as \( \frac{M}{k} \) declines (Figure 2.2). To assist in the description of the variation observed around the BH–LHI relationship between normalized size, age and SPR, the species in the meta-analysis were categorised with respect to \( \frac{M}{k} = 1.0 \), and whether their growth is determinate or indeterminate. Species with indeterminate growth continue growing throughout adult life, although slowing to some extent with increasing size, while species with determinate growth do not grow as adults. These two criteria defined three broad groups or ‘Types’ of species in the meta-analysis; Type I – \( \frac{M}{k} > 1.0 \) and indeterminate growth, Type II – \( \frac{M}{k} < 1.0 \) and indeterminate growth, Type III – \( \frac{M}{k} < 1.0 \) and determinate growth (Figure 2.1). No species with \( \frac{M}{k} > 1.0 \) and determinate growth were observed in the meta-analysis.

A total of 49 Type I species (green lines) were identified, including 34 teleosts, 10 chondrichthyes, 3 crustaceans and 2 molluscs. Their trajectories occupy the upper left hand side of Figure 2.1a, b and d and the lower right of Figure 2.1c. Type I species conform to the general shape of the BH–LHI trajectories, and have a slightly higher average \( \frac{M}{k} \) (1.95, cf. 1.5; Table 2.1) but slightly lower average \( \frac{L_m}{L_{\infty}} \) (0.55, cf. 0.65; Table 2.1) than those for the
Figure 2.1: Observed relationships for 123 selected marine species between spawning potential ratio (SPR) and (a) standardised weight ($W_{\text{max}} = 1.0$), (b) standardised length ($L_{\text{max}} = 1.0$), (c) standardised age ($A_{\text{max}} = 1.0$), and (d) weight standardized for size of maturity ($W_{m} = 0$) and maximum weight ($W_{\text{max}} = 1.0$). Green lines denote species with indeterminate growth and $\frac{M}{k} > 1.0$; blue lines denote species with indeterminate growth and $\frac{M}{k} < 1.0$; red lines denote species with determinate growth and $\frac{M}{k} < 1.0$; black lines show the relationship for species conforming with BH–LHI; $\frac{M}{k} = 1.5$, $\frac{L_{m}}{L_{\infty}} = 0.66$ and $A_{m}M=1.65$. 
**Figure 2.2:** Simulated length frequency histograms illustrating how the size compositions of unfished populations are determined by the $\frac{M}{k}$ ratio for a species'. The range of $\frac{M}{k}$ ratios (0.1 to 4.0) chosen for simulating these histograms was based on the range of ratios observed in the meta-analysis of 123 species. Top row: $\frac{M}{k} = 4.0, 1.65, 1.0$. Middle row: $\frac{M}{k} = 0.8, 0.6, 0.4$. Bottom row: $\frac{M}{k} = 0.3, 0.2, 0.1$. Shading indicates the proportion of the mature, adults in the population, assuming $\frac{L_m}{L_{\infty}} = \frac{3}{3+\frac{M}{k}}$, as derived from Beverton (1992).
BH–LHI. They begin reproduction at relatively small sizes (Figure 2.1a and b) but at a relatively later stage of their life cycle (Figure 2.1c) than Types II and III. Unfished Type I populations are numerically dominated by juvenile length classes and do not exhibit an adult modal size (Figure 2.2; top panel). Most (60–80%) of the reproductive potential in these populations comes from smaller individuals that are <80% of their asymptotic size (Figure 2.1a and b).

A diverse range of species comprise the Type I category, including coastal bivalves *Gari solida*, *Semele solida*, a crab *Callinectes sapidus*, two spiny lobsters *Panulirus argus*, *P. ornatus*, several carcharhinid *Carcharhinus obscurus*, *C. plumbeus* and triakid sharks, *Mustelus antarcticus*, *Prionace glauca*, and teleosts ranging from low tropic level species such as *Scomber japonicus*, *Cololabis saira* and the clupeid *Brevoortia patronus* to higher trophic level species, such as the rockfish *Sebastes chlorostictus*, *S. melanostomus* and two apex piscivores, the scombrid tunas *Thunnus alalunga*, and *T. tonggol*.

Type II species (blue curves on Figure 2.1) are shifted to the right of Type I species in Figure 2.1a and b, and to the left in Figure 2.1c. They share the indeterminate growth pattern of Type I species. Type III species (red) grow to a determinant asymptotic adult size, and reproduce without further growth. Their trajectories are shifted to the extreme right in Figure 2.1a and b, and the extreme left in Figure 2.1c. In contrast to Type I species, Type II and III species do not reproduce until growth is almost complete; Type II species produce approximately 70% of their SPR at sizes >80% of the asymptotic size, while Type III species produce 90% of SPR at sizes >80% of asymptotic size (Figure 2.1). Unfished populations of Type II and III species are dominated by adult size classes, and exhibit distinct adult modes that become more pronounced with lower $\frac{M}{L}$ ratios (Figure 2.2; mid and lower panels).

The Type II species (blue) form a middle group of 59 species (45 teleosts, 1 elasmobranch, 5 crustaceans, and 8 molluscs) with average $\frac{L}{L_\infty}$ similar to the BH–LHI ratio (0.69, cf. 0.66; Table 2.1), but a lower average $\frac{M}{L}$ than the BH–LHI ratio (0.62, cf. 1.5; Table 2.1). Type II species include crustaceans, *Nephrops norvegicus*, and all of the prawns (shrimp) in the analysis *Penaeus indicus*, *P. latisulcatus*, *P. merguiensis*, all three haliotid gastropods *Haliothis rubra*, *H. laevigata*, *H. iris*, a carcharhinid shark *Rhizoprionodon tayloiri*, and a range of teleosts including flat-forms *Pleuronectes platessa*, *Psettichthys melanostictus*, tropical snappers *Lutjanus malabaricus*, *L. carponotatus*, *L. argentimaculatus* and the long-lived orange roughy *Hoplostethus atlanticus*.

The 15 Type III species (red) exhibit trajectories that balloon into the bottom right of Figure 2.1a and b. These species reach maturity (Figure 2.1c) and a determinant asymptotic size (Figure 2.1a and b) relatively early in life. Type III species have the largest average $\frac{L}{L_\infty}$ ratio (0.88; Table 2.1) and lowest average $\frac{M}{L}$ ratio (0.57; Table 2.1). Besides the five marine mammals in the database, Type III species include two triakid sharks *Galeorhinus galeus*, *Furgaleus macki*, eight teleosts, including the long-lived *Scorpis aequipinnis*, and two relatively short-lived Lethrinidae species.

In Figure 2.3a the $\frac{L}{L_\infty}$ of each species in the analysis is plotted as a function of $\frac{M}{L}$. The
Table 2.1: A synopsis of the taxa and species in this meta-analysis summarizing the range of parameters used for each species group. Appendix A contains a table listing the parameters used for each species and supporting sources.

<table>
<thead>
<tr>
<th>Taxa</th>
<th># Families</th>
<th># Species</th>
<th>Maximum age (yrs)</th>
<th>Maximum length (m)</th>
<th>$\frac{M}{k}$ mean (range)</th>
<th>$\frac{t}{L}$ mean (range)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Type I</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chondrichthyes</td>
<td>8</td>
<td>10</td>
<td>10–49</td>
<td>0.57–3.19</td>
<td>2.07 (1.03-3.16)</td>
<td>0.64 (0.50-0.79)</td>
</tr>
<tr>
<td>Crustacean</td>
<td>2</td>
<td>3</td>
<td>&lt;1–14</td>
<td>0.15–0.25</td>
<td>1.55 (1.20-1.90)</td>
<td>0.52 (0.46-0.56)</td>
</tr>
<tr>
<td>Mollusc</td>
<td>2</td>
<td>2</td>
<td>5</td>
<td>0.06–0.07</td>
<td>2.92 (2.74-3.10)</td>
<td>0.35 (0.32-0.39)</td>
</tr>
<tr>
<td>Teleost</td>
<td>22</td>
<td>34</td>
<td>&lt;1–102</td>
<td>0.04–1.49</td>
<td>1.88 (1.00-3.52)</td>
<td>0.55 (0.32-0.71)</td>
</tr>
<tr>
<td><strong>Type II</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chondrichthyes</td>
<td>1</td>
<td>1</td>
<td>8</td>
<td>0.073</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Crustacean</td>
<td>3</td>
<td>5</td>
<td>&lt;1–15</td>
<td>0.03–0.08</td>
<td>0.74 (0.62-0.94)</td>
<td>0.55 (0.30-0.74)</td>
</tr>
<tr>
<td>Mollusc</td>
<td>5</td>
<td>8</td>
<td>3–154</td>
<td>0.07–0.14</td>
<td>0.53 (0.14-0.84)</td>
<td>0.55 (0.34-0.80)</td>
</tr>
<tr>
<td>Teleost</td>
<td>23</td>
<td>45</td>
<td>5–96</td>
<td>0.12–1.83</td>
<td>0.63 (0.21-0.98)</td>
<td>0.72 (0.32-0.84)</td>
</tr>
<tr>
<td><strong>Type III</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chondrichthyes</td>
<td>2</td>
<td>2</td>
<td>17–46</td>
<td>1.21–1.62</td>
<td>0.68 (0.63-0.73)</td>
<td>0.92 (0.91-0.93)</td>
</tr>
<tr>
<td>Mammal</td>
<td>3</td>
<td>5</td>
<td>58–115</td>
<td>2.67–21.49</td>
<td>0.46 (0.20-0.75)</td>
<td>0.88 (0.87-0.91)</td>
</tr>
<tr>
<td>Teleost</td>
<td>6</td>
<td>8</td>
<td>5–77</td>
<td>0.21–0.69</td>
<td>0.61 (0.12-0.83)</td>
<td>0.87 (0.85-0.89)</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>77</td>
<td>123</td>
<td>&lt;1–154</td>
<td>0.03–21.49</td>
<td>1.17 (0.12–3.52)</td>
<td>0.66 (0.30–0.93)</td>
</tr>
</tbody>
</table>
Figure 2.3: The relationship between relative length of maturity ($\frac{L_m}{L_\infty}$) in (a) the 123 marine species selected for this meta-analysis; and (b) nine teleost families with more than three species plotted against the $\frac{M}{k}$ for each species. In a), green points denote species with indeterminate growth and $\frac{M}{k} > 1.0$; blue points indeterminate growth and $\frac{M}{k} < 1.0$; red points determinate growth and $\frac{M}{k} < 1.0$. The solid black lines plot the Beverton (1992) relationship; $\frac{L_m}{L_\infty} = 3$ + $\frac{M}{k}$. The dashed and dotted lines, respectively show the relationships $\frac{L_m}{L_\infty} = 2.5$ + $\frac{M}{k}$ and $\frac{L_m}{L_\infty} = 3.5$ + $\frac{M}{k}$.

solid black line ($\frac{L_m}{L_\infty} = 3$ + $\frac{M}{k}$) is derived from Beverton (1992), but is originally from Holt (1958) who used this equation to demonstrate that size at maximum biomass ($L_{opt}$) can be estimated from the ratio of $\frac{M}{k}$ (see Chapter 3 for more detailed examination of this relationship). Numerous empirical studies observe that length at maturity ($L_m$) coincides with $L_{opt}$, and various theoretical studies postulate that this is because the evolutionary fitness of a species is maximized by this coincidence (Fryer and Iles, 1972; Roff, 1984; Beverton, 1992). The factor of ‘3’ used in this equation comes from the assumption that weight is proportional to $L^3$. The dashed and dotted lines plotted in Figure 2.3 indicate alternative relationships obtained by substituting factors of 2.5 or 3.5 into this equation, which would be equivalent to assuming weight and fecundity are proportional to $L^{2.5}$ and $L^{3.5}$ respectively, and covers the range generally observed for this parameter (Hilborn and Walters, 1992). These alternative relationships are plotted to provide some scaling of likely variance around the relationship.

Very few of the species in the meta-analysis fall above the Beverton (1992) curve for the relationship between $\frac{M}{k}$ and $\frac{L_m}{L_\infty}$; most of the outliers are below (Figure 2.3a). This is primarily because the meta-analysis encompasses all marine species, some of which have fixed rates of reproduction, while Beverton (1992) worked almost entirely with teleosts for which fecundity is normally more closely related to adult body size. In Figure 2.3b the relationship between $\frac{M}{k}$ and $\frac{L_m}{L_\infty}$ is plotted for the 9 teleost families with three or more species in the database and these conform much more closely to the Beverton (1992) relationship.

In Figure 2.3b there is the suggestion that species within families tend to group together on the $\frac{M}{k}$ and $\frac{L_m}{L_\infty}$ spectrum, which in Figure 2.4 is shown with the three most numerous
Figure 2.4: Observed relationships between the spawning potential ratio (SPR) and (a) standardised weight \((W_{\text{max}} = 1.0)\), (b) standardised length \((L_{\text{max}} = 1.0)\), (c) standardised age \((A_{\text{max}} = 1.0)\) for the three most numerous teleost families in the meta-analysis; Gobiidae, \(n=5\), green; Lethrinidae, \(n=10\), red; Acanthuridae, \(n=7\), blue. The broken black line show the BH–LHI relationships: \(M = 1.5\), \(L_{\infty} = 0.66\), and \(A_{m}M = 1.65\).

teleost families to result in their SPR at size and age trajectories grouping into distinctive family bands. Comparison to the plotted BH–LHI trajectories (Figure 2.4 – broken black line) shows that to some extent the BH–LHI relationship describes the weight and length trajectories of the Gobiidae in the study (Figure 2.4 – solid black line), but not their SPR at age relationship. The BH–LHI relationship over-estimates the productivity of the Lethrinidae (Figure 2.4 – solid red line) and Acanthuridae (Figure 2.4 – solid blue line), by suggesting higher than observed SPR at lower sizes for those families, while describing a relationship between SPR and relative age that is intermediate between the Lethrinidae and Acanthuridae relationships in the analysis.

Figure 2.5 shows an examination of the predictive power of Pauly’s (1980) equation for estimating \(M\) empirically, by comparing the \(M_{k}\) and \(L_{\infty}\) ratios of species in the meta-analysis with those derived from Pauly’s (1980) equation for estimating \(M\) empirically. The relationship between \(M_{k}\) and \(L_{\infty}\) is plotted for the 109 species in the meta-analysis with \(L_{\infty} \leq 200\) cm, which excludes marine mammals and large sharks (Figure 2.5a). The solid lines indicate the estimates of \(M_{k}\) that would be derived using the Pauly equation across the range of \(k\) values observed in this meta-analysis. The Pauly equation requires an assumption about ambient temperature. For simplicity, temperature was assumed to be 15°C, but sensitivity analyses showed that increasing the assumed temperature only raised the plotted lines minimally. The Pauly equation generally produces estimates of \(M_{k} > 1\), especially for species with \(L_{\infty} < 50\) cm. This database includes a considerable number of teleosts with \(L_{\infty} < 50\) cm and \(M_{k} < 1\), for which the Pauly equation over-estimates \(M\). This pattern is maintained even when the analysis is restricted to the teleost families with three or more species (Figure 2.5b).

2.4 Discussion

In fisheries science, the three Beverton Holt–Life History Invariants (BH–LHI) are most commonly used separately to estimate individual parameters for population modeling;
The relationship between asymptotic length \((L_\infty)\) and \(\frac{M}{k}\) for a) 109 marine species in the database with \(L_\infty \leq 200\) cm and b) nine teleost families with more than three species, for those species with asymptotic size \(\leq 200\) cm. Coloured lines show the relationships estimated from Pauly’s (1980) equation assuming the range of \(k\) observed in this meta-analysis (0.1–1.0) and an ambient temperature of 15°C.

Generally they are only linked within studies seeking to relate evolutionary fitness and metabolic parameters to the optimization of life histories (e.g., Jensen, 1996; Charnov et al., 2013). However, the novel result of this study demonstrates that the combination of the three life history relationships imply a unique generalized relationship between normalized size, age and SPR. The meta-analysis suggests that rather than approximating some unique relationship between size, age and reproductive potential that is broadly applicable across species, the BH–LHI estimate some form of ‘median’ relationship for the 123 species in the meta-analysis (Figure 2.1) that is not necessarily found in any species.

The first formulations of BH–LHI (Beverton and Holt, 1959; Beverton, 1963) were based on North Sea teleosts (clupeids and engraulids) that this analysis has classed as Type I species. Since that time, fisheries biology has tended to accept, seemingly by default, that the values derived from those initial studies are relatively constant across much broader suites of species, particularly the ratio of \(\frac{M}{k} \sim 1.5\). This was, however, not an assumption ever made by Holt (1958) nor Beverton (1992), who both conceptualized species as displaying a range of \(\frac{M}{k}\) values co–varying with \(\frac{L_m}{L_\infty}\) (Figure 2.3), nor by Pauly (1980), who correlated ambient temperature and adult body size with the \(\frac{M}{k}\) ratio for each species.

Apparently confirming earlier studies, the descriptive meta-analysis presented here illustrates the natural variability observed across marine species. This study defined three broad types of marine species with characteristic relationship between size, age and reproductive potential, and ratios of \(\frac{M}{k}\) and \(\frac{L_m}{L_\infty}\). The intent in doing so is not to imply fundamental differences or strong ‘significantly different’ boundaries between categories, but to provide an initial indicative categorization to aid the discussion of the observed phenomena. The aim here is to 1) illustrate that predictable patterns in size, age and SPR appear to exist in
nature, and 2) to postulate that these predictable patterns might provide an alternative theoretical framework for deriving knowledge about unstudied species from studies of related species.

A number of authors have developed classification systems to categorise species by their life history. For example, Pianka (1970) characterizes life history strategies as either 1) ‘r–strategists’ with high population turn-over rates, a tendency for boom and bust dynamics, and invasive ‘weed-like’ characteristics, or 2) ‘K–strategists’ with relatively stable population dynamics, lower turnover and adults that reproduce over many breeding cycles. Building on work by Winemiller and Rose (1992), King and McFarlane (2003) examined a wider range of fish species, and defined five groups: ‘Opportunistic’, ‘Intermediate’, ‘Periodic’, ‘Equilibrium’, and ‘Salmonic’ strategists. The results of this study suggest that the Type I species which mature at relatively small sizes, reproduce for a relatively short and late part of their life cycle, continue growing relatively rapidly as they reproduce, have unfished populations that are dominated by juvenile size classes, and do not exhibit a modal adult size, are ‘Opportunist’ and ‘Intermediate Strategists’ (King and Mcfarlane, 2003), and tend towards being ‘r–strategists’ (Pianka, 1970). While Type II and III species which mature at relatively high sizes, reproduce for a relatively extended part of their life cycle, growing slowly, or not at all, as they reproduce, and have unfished populations that exhibit a modal adult size, are typically ‘Periodic’ and ‘Equilibrium Strategists’ (King and Mcfarlane, 2003), and ‘K–strategists’ (Pianka, 1970). In the case of an unstudied stock, general knowledge of a species’ typical life-history strategy might be used to estimate a likely set of life history ratios and the likely relationships between size, age and SPR that these ratios proscribe. Furthermore, this suggests that the estimations developed in this way for a relatively unstudied stock will be more accurate than existing standard methods for applying the concept of BH–LHI to data-poor stock assessment.

Currently the BH–LHI are widely assumed to be ‘invariant’ and individual parameters are commonly estimated for data-poor assessments on that basis, but as illustrated here (Figure 2.1) this implies all species share the same BH–LHI relationships between size, age and reproductive output. Rather, the so-called ‘invariants’ vary together, matching patterns of growth and reproduction to different life history strategies, presumably ensuring that for each life-history strategy, length at maturity \(L_m\) and a cohort’s maximum biomass \(L_{opt}\) coincide, optimizing each species’ evolutionary fitness (Fryer and Iles, 1972; Roff, 1984; Beverton, 1992). It appears that the BH–LHI only tend towards relative invariance within groups of species sharing similar life-history strategies, reflecting the stage at which each life-history strategy transfers energy from allometric growth to reproduction (Charnov, 2008; Charnov et al., 2013). In this conceptualization, tuna can be considered as ‘larger, slower’ anchovies which rarely reach asymptotic sizes, while some prawns are ‘smaller, faster’ versions of the fish, lobsters and gastropods that breed multiple times close to asymptotic sizes.

The obvious question at this point is: where do phenotypic plasticity, and density dependent responses to fishing pressure fit into this conceptualization? Do they invalidate this
conceptualization of BH–LHI? The short answer is not at all, and although not studied in enough detail at the present time, these two phenomena are likely to provide the broader context, which will in time fully validate and extend this concept’s application. Implicitly because of the selection criteria used, this meta-analysis is basically a study of unfished, or lightly fished, populations and this limits what can be demonstrated here. In each of the cases, it would be expected that the individual parameter estimates will have changed as the stocks for which they were estimated have been fished down, just as it is expected that the individual parameters vary between geographically isolated populations of each species. A notable example is the case of *Cheilodactylus spectabilis*, where it is known that this occurred as the population was fished down (Ziegler et al., 2007). However, this study is not proposing a new alternative form of invariance within families, species or stocks. Rather, the emphasis is on returning to the spirit of the original formulation of this concept by Holt (1958), which was that the physiological constraints of species and families imply that the life history ratios will remain more stable across geographical distributions and density ranges, than the individual life history parameters, and so for the purpose of data-poor stock assessment the life history ratios are expected to be more informative and useful than the more variable individual parameters (S.J. Holt, Personal Communication). There is a growing body of literature to support this supposition, and in this context the body of work by Howard Choat on coral reef fish deserves to be highlighted and should be referred to (e.g., Choat and Robertson, 2002; Gust et al., 2002). Because the precedence set by fisheries science, and the selection criteria used in this study, place a strong emphasis on the quality of component estimates of natural mortality, the sampling of the literature has been strongly biased towards using lightly fished populations for this analysis. However, exploited marine species do not distinguish between whether a seal or a human eats them, and thus it would be expected that further study would reach similar conclusions if it were to broadened to use the ratio of \( \frac{Z}{k} \) rather than \( \frac{M}{k} \). On this basis, the results of this study suggest that for metabolic and evolutionary reasons, species respond to changes in total mortality by minimizing changes in their life history ratios, rather than the parameters themselves, and that this conceptualization of BH–LHI maybe useful for predicting how stocks are likely respond to fishing pressure, and thus the likely form and magnitude of density dependence mechanisms for each species.

The data in this meta-analysis are as yet too few to properly extend these aspects of the analysis. However, with the addition of further species it is expected that the sharing of similar life-history ratios and bands of SPR trajectories by closely related species will become more evident amongst both teleost and non-teleost families, and it may be possible to define a typical band of SPR at size and age trajectories for many marine families. From Figure 2.4a and b it can be seen already that assuming an average or median family value for an unstudied species of Lethrinid or Acanthuridae would produce a more accurate assessment of size data than the standard BH–LHI assumption of \( \frac{M}{k} \sim 1.5 \). Precautionary life history ratios and SPR trajectories might also be estimated for an unstudied species by taking the extreme bottom right hand and least productive of the SPR at size trajectories
observed for a family (Figure 2.4a and b).

The observation that the commonly assumed values of the BH–LHIs define a unique ‘median’ form of the SPR–at–size and age relationships observed in nature also has significant implications. Firstly, the results of empirical studies to more accurately derive single estimates of the BH–LHIs and to develop correlative techniques for estimating individual life history parameters (Pauly, 1980; Gislason et al., 2010), will be strongly influenced by the sample of species included in those studies. It is suspected that many of these studies are implicitly (and unintentionally) biased against the inclusion of low $M_k$ species. Noting the inherently lower productivity of low $M_k$ species, these species are expected to be more prone to early depletion in poorly managed systems, and less likely to sustain large, valuable fisheries (and thus research programs) in well managed systems. This could well have resulted in low $M_k$ species being under–represented in meta–analyses, especially if those studies have an implicit (and perhaps unavoidable) focus on research from regions with long histories of heavy exploitation, such as the North Sea, Atlantic and South-East Asia (Costello et al., 2012). This might explain the apparent conflict between the Pauly (1980) technique and this meta-analysis (Figure 2.5). Being based in Australia which has a relatively recent history of fishing and a strong history of research, there was ready access to recent research conducted in lightly exploited regions of Australia, and this study includes numerous studies documenting small bodied low $M_k$ teleost species, which were, apparently, not as well represented in Pauly’s (1980) analysis. In this context, the quest to more accurately estimate unique values for the BH–LHI looks somewhat misguided, unless narrowed carefully on taxonomic grounds, as were the original studies of Beverton and Holt (1959) and Beverton (1963).

Another significant implication of the observation that the BH–LHI define a unique ‘median’ form of the relationships between size, age and SPR observed in nature, is that existing stock assessments, using some derivation of the assumption that $M_k \sim 1.5$, are implicitly over-estimating the productivity of stocks with $M_k < 1.5$. This could amount to a serious systematic bias for the field, as such techniques are commonly used with long-lived species where the depletion of the older age classes through fishing is thought to have rendered the estimation of $M$ with aging studies unreliable. Species with $M_k < 1.0$ are most prone to having the older adult classes depleted through fishing, and are consequently, more likely to have had a technique based on $M_k \sim 1.5$ applied to them. Even without extending this meta-analysis rigorously down to the level of families, assessments that have used the assumption of $M_k \sim 1.5$ could be improved using the three Types of species defined here on the basis of life-history strategies and forms of growth.

### 2.5 Conclusions

The meta-analysis of this chapter suggests that the so-called Beverton–Holt Life History Invariants are actually co–variants, varying together in relation to life history strategies and defining a range of relationships between size, age and reproductive output. It appears
that the BH–LHI only tend towards relative invariance within groups of species sharing similar life-history strategies, reflecting the stage at which differing life-history strategy transfers energy from allometric growth to reproduction (Charnov, 2008; Charnov et al., 2013). This conceptualization of BH–LHI has potential to provide a theoretical framework for ‘borrowing’ knowledge from well-studied species for application to related unstudied stocks, and that together with the models developed in Chapter 3 and tested in Chapter 4 and Chapter 5, this may make it possible to assess many otherwise data-poor species from simple size studies.
3 Some explorations of the life history ratios to describe length composition, spawning-per-recruit, and the spawning potential ratio of fished species

Abstract

Evaluating the status of data-poor fish stocks is often severely limited by incomplete knowledge of the basic life history parameters: the natural mortality rate \( (M) \), the von Bertalanffy growth parameters \( (L_\infty \text{ and } k) \), and the length at maturity \( (L_m) \). A common approach to estimate these individual parameters has been to use the Beverton–Holt life history invariants (BH–LHI), the ratios \( \frac{M}{k} \) and \( \frac{L_m}{L_\infty} \), especially for estimating \( M \). In this chapter, I assume no knowledge of the individual parameters, and explore how the information on life history strategy contained in these ratios can be applied to assessing data-poor stocks, with \( \frac{M}{k} \) values ranging from 0.3 to 2.3, spanning the BH–LHI value of 1.5. I develop analytical models to develop a relationship between \( \frac{M}{k} \) and the von Bertalanffy growth curve, and demonstrate the link between the life history ratios and yield- and spawning-per-recruit. I further develop the previously recognised relationship between \( \frac{M}{k} \) and yield- and spawning-per-recruit (Beverton and Holt, 1964) by using information on \( \frac{L_m}{L_\infty} \), knife-edge selectivity \( \left( \frac{L_c}{L_\infty} \right) \) and the ratio of fishing to natural mortality \( \left( \frac{F}{M} \right) \), to demonstrate the link between an exploited stock’s expected length composition, and its spawning potential ratio (SPR), an internationally recognised measurement of stock status. Variation in length-at-age, and logistic selectivity patterns are incorporated in the model to demonstrate how SPR can be calculated from the observed size composition of the catch; an advance which has potential as a cost-effective method for assessing data-poor stocks. The effects of deviations in the assumptions of equilibrium, and imperfect knowledge of the life history parameters, on the application of the analytical models developed in this chapter as a cost-effective method for stock assessment are examined in detail in Chapter 4.

3.1 Introduction

Studies of the life history information on the growth, mortality and maturity schedules of fish stocks form the basis of fisheries science, and such information is important for
the effective management of exploited populations (Beverton and Holt, 1957; Hilborn and Walters, 1992). However, this information is only available for about 1,200 of the 7,000 or so exploited fish species, and it is not always available for all regions where the species are fished (Froese and Binohlan, 2000). Patterns of variation between life history parameters, particularly between natural mortality ($M$), and the von Bertalanffy growth rate and asymptotic size ($k$ and $L_\infty$), have long been observed for many fish populations, and a large amount of work has been done to document and understand these relationships, often with the aim of providing cost-effective ‘short-cuts’ to estimate the parameters, such as natural mortality, that are difficult or expensive to obtain (Beverton and Holt, 1959; Pauly, 1980; Roff, 1984; Beverton, 1992; Charnov, 1993). Typically, these studies have explored the relationships between single variables, such as $M$ or $k$, that are commonly used in stock assessments.

The $\frac{M}{k}$ ratio is one of the life history ratios that is known to be relatively consistent between closely related stocks (Beverton, 1992). The results of bio-energetic modelling by Jensen (1996) suggest that an optimal value for $\frac{M}{k}$ is 1.5. Assuming von Bertalanffy growth, the relationship between the biomass and mean length of a cohort can be derived from the $\frac{M}{k}$ ratio (Beverton, 1992; Jensen, 1996). Using this relationship, life history theory predicts that length at maturity ($L_m$) will be found at the length of maximum biomass in the population. This theoretical relationship provides the basis for the second life history ratio $\frac{L_m}{L_\infty}$, with an optimal value of 0.66 (Jensen, 1996). Supported by other empirical work (Charnov, 1993; Pauly, 1980), these value for the ratios of $\frac{M}{k}$ and $\frac{L_m}{L_\infty}$ have become known as the Beverton–Holt life history invariants (BH–LHI), and are often used as proxies for estimates of $\frac{M}{k}$ (1.5) and $\frac{L_m}{L_\infty}$ (0.66) in data-poor stocks. For example, it is not uncommon for studies to estimate the notoriously difficult parameter $M$ by simply using the Beverton–Holt invariant $M = 1.5k$ (e.g., see many papers citing Jensen, 1996), or by estimating the fishing mortality rate $F$ when the total mortality ($Z = F + M$) and $k$ are known, by assuming that $\frac{M}{k} = 1.5$ (Beddington and Kirkwood, 2005).

Extending their earlier seminal work (Beverton and Holt, 1957), Beverton and Holt (1964) were the first to show that yield and biomass equations could be restated using the dimensionless ratios $\frac{M}{k}$ and $\frac{L_m}{L_\infty}$. Since then, others have built on their work to incorporate the dimensionless numbers into fisheries science (Jensen, 1996; Mangel, 1996; Williams and Shertzer, 2003; Beddington and Kirkwood, 2005). However, it has often been assumed that these ratios are invariant, which is evidently not the case. For example, a recent study of the Kyphosid Scorpius aequipinnis, in south-west Australia, has found that the $\frac{M}{k}$ for the species is 0.33 (Coulson et al., 2012), much lower than the BH–LHI of 1.5, and reminiscent of a life history more commonly associated with marine mammals (see Chapter 2). Furthermore, the meta-analysis of 123 marine species of teleosts, chondrichthyes, invertebrates and marine mammals described in Chapter 2, found that the ratio of $\frac{M}{k}$ ranged from 0.12–3.52, indicating that the life history ratios often vary considerably from the BH–LHI. Others have also acknowledged this variability in $\frac{M}{k}$. For example, the widely used multivariate regression of Pauly (1980) implicitly correlated temperature and adult body size
with $\frac{M}{k}$ for each species, and Frisk et al. (2001) noted that $\frac{M}{k}$ for elasmobranches typically differs from that of bony fishes. Although some studies have explicitly accounted for variability in the $\frac{M}{k}$ ratio (e.g., Williams and Shertzer, 2003, 2005), the ratio is often assumed to be invariant and the variability of the ratios of $\frac{M}{k}$ and $\frac{L_m}{L_\infty}$ in fish stocks has not been explored comprehensively.

This chapter develops simple analytical models to explore the influence of changing the ratios of $\frac{M}{k}$, $\frac{F_M}{k}$, and $\frac{L_m}{L_\infty}$ on the von Bertalanffy growth curve, the length composition of the stock, and as a consequence the yield and spawning-per-recruit, under the assumption of equilibrium. It uses the data collated in the meta-analysis of Chapter 2 to provide the basis for the range of values investigated in this study. The initial models are extended to include more complex assumptions about growth and selectivity, and investigate the relationship between the three ratios and the spawning potential ratio (SPR). By developing the link between the life history ratios, the expected equilibrium size composition, and SPR, this study provides the potential to develop a cost-effective technique to assess data-poor fisheries using length frequency data; an idea that is further developed in Chapter 4.

3.2 Analytical models

3.2.1 Redefining the von Bertalanffy equation in terms of $\frac{M}{k}$

The von Bertalanffy equation is commonly used to model fish growth, and is given as:

$$L_t = L_\infty \left(1 - e^{-k(t-t_0)}\right)$$

(3.1)

where $L_t$ is length at age $t$, $L_\infty$ is theoretical length at infinite age, $k$ is the growth coefficient, and $t_0$ is the hypothetical age when length equals zero. The von Bertalanffy equation can be simplified by assuming $t_0 = 0$, and standardising length to the asymptotic length:

$$\bar{L}_t = \frac{L_t}{L_\infty} = 1 - e^{-kt}$$

(3.2)

The natural mortality rate ($M$) of fish is extremely difficult to estimate, especially for stocks that have been exploited for some time. A number of methods exist to estimate $M$ from empirical data, including methods where $M$ is assumed to be inversely correlated to longevity (Hoenig, 1983; Hewitt and Hoenig, 2005). A simple rule-of-thumb to estimate $M$ involves the assumption that a certain proportion ($P$) of animals survive to some maximum age $t_{\text{max}}$ (Quinn and Deriso, 1999):

$$M = \frac{-\ln(P)}{t_{\text{max}}}$$

(3.3)

Naturally, the accuracy of this rule-of-thumb is dependent on the appropriate value for the proportion $P$, and this has typically been assumed to be between 1% and 5% (Hewitt and
Hoenig, 2005). The choice of $P=5\%$ is somewhat arbitrary, and appears to over-estimate $M$ for a large range of species, with empirical work suggesting that $P=1.5\%$ is more appropriate (Hoenig, 1983; Hewitt and Hoenig, 2005). The accuracy of this rule-of-thumb is also highly dependent on a good estimate of $t_{\text{max}}$, which is often taken as the maximum observed age, and depends on both the sampling method and how heavily the stock has been exploited prior to sampling. For simplicity, this study assumes that $P = 1\%$, and so $t_{\text{max}}$ can be calculated from $M$ as:

$$t_{\text{max}} = -\frac{\ln 0.01}{M}$$

(3.4)

If age is standardised to $t_{\text{max}}$ then $x$ can be defined as $\frac{t}{t_{\text{max}}}$. From Equation 3.2, $\tilde{L}_t = 1 - e^{-kt}$ with $t = xt_{\text{max}} = -\frac{x\ln 0.01}{M}$, then:

$$\tilde{L}_x = 1 - e^{\left(-k\frac{x\ln 0.01}{M}\right)} = 1 - 0.01\left(\frac{x}{M}\right)$$

(3.5)

This demonstrates that the shape of the standardised von Bertalanffy growth curve is solely determined by the ratio $\frac{M}{k}$, and does not depend on the absolute value of either the $k$ or $M$ parameters (Figure 3.1). The biological significance of $L_\infty$ becomes increasingly vague as $\frac{M}{k}$ increases (Figure 3.1). For a species that conforms to the Beverton–Holt invariant $\frac{M}{k} = 1.5$, the maximum size ($L_{\text{max}}$; i.e., the length at $t_{\text{max}}$) is approximately $0.95L_\infty$. However, a species with $\frac{M}{k} = 2.3$ would only be expected to reach about $0.8L_\infty$ at $t_{\text{max}}$ (bottom curve on Figure 3.1). In contrast, a species with $\frac{M}{k} = 0.3$, like S. aequipinnis, would reach asymptotic size relatively early in life and then continue to live for a relatively long time without any further growth (top curve on Figure 3.1). The difference between $L_{\text{max}}$ and $L_\infty$ is more pronounced if $P$ is larger. For example, if $P$ was 0.05, $L_{\text{max}}$ would be $0.86L_\infty$ and $0.73L_\infty$ for $\frac{M}{k}$ values of 1.5 and 2.3 respectively. In reality the length-at-age of fish is usually variable and the von Bertalanffy equation is used to describe the average growth curve of the stock, with the $L_\infty$ parameter estimated as the average asymptotic size. This means that, in practice, some fish may have observed lengths greater than $L_\infty$ (i.e., $L_{\text{max}} > L_\infty$), even for species with higher $\frac{M}{k}$. However, Figure 3.1 demonstrates that it is important to distinguish between the biological parameter $L_{\text{max}}$ and the mathematical parameter $L_\infty$, and any assumptions regarding the relationship between the two parameters must be carefully interpreted in the light of other knowledge of the species (i.e., the $\frac{M}{k}$ ratio and the variability in length-at-age).
Figure 3.1: The standardised von Bertalanffy growth curves for fish at standardised length \( \left( \frac{L_t}{L_\infty} \right) \) and standardised age \( \left( \frac{t}{t_{\text{max}}} \right) \) from Equation 3.5 for \( \frac{M}{k} \) ranging from 0.3 to 2.3. The Beverton-Holt life history invariant (BH–LHI) of \( \frac{M}{k} = 1.5 \) is shown in bold.

### 3.2.2 Number of animals at age in terms of \( \frac{M}{k} \)

Assuming that growth is deterministic, it is possible to demonstrate that the number of animals at each age can be described by \( \frac{M}{k} \) ratio. Fish populations are often modelled with the assumption that the number of individuals in an unfished cohort decrease with constant natural mortality:

\[
N_t = N_0 e^{-Mt} \tag{3.6}
\]

where \( N_t \) is the number of individuals at age \( t \), and \( N_0 \) is the number of recruits (age 0). When working in terms of numbers per recruit, Equation 3.6 becomes the following:

\[
\tilde{N}_t = e^{-Mt} \tag{3.7}
\]

where \( \tilde{N}_t \) is number per recruit. The number of animals alive at standardised age \( x \) can be expressed in terms of \( \frac{M}{k} \) by re-arranging Equation 3.5 to find \( x \) at \( \tilde{L}_x \),

\[
x = \frac{M \ln(1 - \tilde{L}_x)}{k \ln(0.01)} \tag{3.8}
\]

Substituting \( xt_{\text{max}} \) for \( t \) in Equation 3.7 gives:

\[
\tilde{N}_x = e^{-Mx_{t_{\text{max}}}} \tag{3.9}
\]
Substituting \( M = -\frac{\ln 0.01}{t_{\text{max}}} \) and \( x = \frac{M \ln(1 - \tilde{L}_x)}{\ln(0.01)} \) and simplifying (see Appendix B) gives \( \tilde{N}_x \) in terms of \( \tilde{L}_x \) and \( \frac{M}{\tilde{\kappa}} \):

\[
\tilde{N}_x = (1 - \tilde{L}_x) \frac{M}{\tilde{\kappa}} \tag{3.10}
\]

It is of note that the proportion \( P \) drops out of Equation 3.10, so that the result is independent of \( P \) which is typically unknown and difficult to estimate. Equation 3.10 is effectively a survival function, which shows that the probability of a fish in the unfished state surviving to greater than standardised length \( \tilde{l} \) is determined by \( \frac{M}{\tilde{\kappa}} \):

\[
\Pr\{\tilde{L} \geq \tilde{l}\} = (1 - \tilde{l}) \frac{M}{\tilde{\kappa}} \tag{3.11}
\]

Figure 3.2 demonstrates Equation 3.11 for a range of \( \frac{M}{\tilde{\kappa}} \), and reiterates what is shown in Figure 3.1: a species with a high \( \frac{M}{\tilde{\kappa}} \) has a low probability of reaching large size (lowest curve on Figure 3.2), with the probability of reaching larger size increasing as the \( \frac{M}{\tilde{\kappa}} \) ratio decreases (upper curves on Figure 3.2). It follows from Equation 3.11 that the cumulative probability distribution is:

\[
G(\tilde{l}) = \Pr\{\tilde{L} \leq \tilde{l}\} = 1 - (1 - \tilde{l}) \frac{M}{\tilde{\kappa}} \tag{3.12}
\]

and therefore, in the unfished state, the probability that an individual is in length class \( i \) can be calculated from:

\[
P_{i \text{Unfished}} = \begin{cases} 
1 - (1 - \tilde{l}^{lo}_{i+1}) \frac{M}{\tilde{\kappa}} & \text{if } i = 1 \\
(1 - \tilde{l}^{lo}_{i}) \frac{M}{\tilde{\kappa}} - (1 - \tilde{l}^{lo}_{i+1}) \frac{M}{\tilde{\kappa}} & \text{if } 1 < i < I \\
(1 - \tilde{l}^{lo}_{i}) \frac{M}{\tilde{\kappa}} & \text{if } i = I 
\end{cases} \tag{3.13}
\]

where \( I \) is the number of length classes, and \( \tilde{l}^{lo}_i \) is the lower bound of length class \( i \). These equations can be used to simulate the expected unfished length composition for a given \( \frac{M}{\tilde{\kappa}} \), and Figure 3.3 shows that the equilibrium unfished length composition of species with low \( \frac{M}{\tilde{\kappa}} \) (e.g., 0.6) would be expected to be dominated by large animals, with relatively few animals of smaller size. On the other hand, the equilibrium size structure of species with higher \( \frac{M}{\tilde{\kappa}} \) (e.g., 3.0) would be expected made up predominantly of small individuals, and large animals (i.e., near asymptotic size) would be rare, even in the unfished state.
Figure 3.2: The probability of a fish in the unfished state surviving to standardised length from Equation 3.10 for a range of $\frac{M}{k}$ (0.3–2.3). The Beverton-Holt life history invariant (BH–LHI) of $\frac{M}{k} = 1.5$ is shown in bold.

3.2.3 Changing the scale of $M$ and $k$

By convention the rate parameters $M$ and $k$ are typically given as instantaneous annual rates, e.g. $M = 0.2$ year$^{-1}$ or $k = 0.15$ year$^{-1}$. Discrete age-structured population dynamics models implicitly assume that mortality and growth occurs once a year. Usually this assumption is of little consequence in modelling the dynamics of fish populations. However, for short-lived species the temporal resolution of annual parameters is too coarse to effectively model population dynamics. For example, suppose a species had $t_{\text{max}} = 1$ year (e.g. some penaeid prawn species), then, from Equation 3.4, $M = 4.6$ year$^{-1}$. It is obvious that such a temporal resolution would be far too coarse to use in an age-structured model, as only 2 age classes would be represented: $t = 0, 1$. Clearly, an annual time scale is too coarse and it makes sense to model growth at a higher temporal resolution. To ensure a sufficient number of age classes, such short-lived species are usually modelled in a finer temporal resolution of months, weeks or even days. Converting between time scales is straightforward: $M = 4.6$ year$^{-1}$ can be converted to a monthly rate $M = \frac{4.6}{12} = 0.38$ month$^{-1}$, where $t_{\text{max}} = 12$ months, or a weekly rate $M = \frac{4.6}{52} = 0.088$ week$^{-1}$, where $t_{\text{max}} = 52$ weeks. The $k$ parameter can be scaled in the same way to ensure it is in the same units as $M$. Obviously scaling to different units of time for the purpose of adequate resolution in age-structured models does not change the underlying biology of the animal, and the expected age and length composition of the species remains unchanged regardless of the units of time used.
Figure 3.3: The probability distribution of length for an unfished stock for four values of the ratio $\frac{M}{k}$: 0.6, 0.9, 1.5 & 3.0. Low $\frac{M}{k}$ means that large fish are most common in the population. As $\frac{M}{k}$ increases the probability of large fish in the population decreases, while the probability of small fish increases.
for the modelling. However, the true length composition of a stock is a continuous distribution, and any discretisation is an approximation. In general, a finer resolution of the discrete model will result in better approximation, and, especially for short-lived species, the modelled age and length composition is expected to better approximate the “true” composition when modelled with increasingly finer time scales, i.e., smaller units of time for $M$. For example, it is clear that the modelled length composition of the short-lived species mentioned above will better represent the “true” length composition when modelled in monthly or weekly units of time, rather than annual time-steps. Long-lived species can also be modelled in different units of time, although there is a trade-off between increased temporal resolution and computational requirements, and annual units of time are usually sufficient for these species. Additionally, with real data there is a trade-off between the resolution of the model and the variance of estimates caused by small sample sizes in each size or age class, and the resolution of the model is usually determined by the resolution of the observed data.

### 3.2.4 Relative biomass at age and length in terms of $\frac{M}{k}$

Holt (1958) was the first to identify that the $\frac{M}{k}$ ratio determined the relationship between the size and the relative biomass of a cohort, and he used this information to determine the size of first capture that would result in the maximum yield-per-recruit. The relationship between relative age (and size) and the biomass of a cohort can be demonstrated by manipulating the previously derived equations. If the standardised weight at standardised age $x$ is given as:

$$\tilde{W}_x = \tilde{L}_x^b$$  \hspace{1cm} (3.14)

where the exponent $b$ is usually close to 3 for most species (Hilborn and Walters, 1992), then the relative biomass at standardised age $x$ can be described by:

$$B_x = \frac{N_x}{\tilde{N}_x} \tilde{W}_x = (1 - \tilde{L}_x)^{\frac{M}{k}} \tilde{L}_x^b$$  \hspace{1cm} (3.15)

The shape of the relative biomass function is determined by a trade-off in growth and mortality (Figure 3.4). For example, species with a low $\frac{M}{k}$ obtain maximum length (and weight) at a relatively young age, while the number of individuals in the cohort is still high, (Figure 3.1), and hence biomass peaks at an early age and then rapidly declines as mortality reduces the number of fully grown individuals (Figure 3.4a). For example, the average female $S. aequipinnis$ reaches asymptotic size around age 15, but then lives for another 50 years without further growth (Coulson et al., 2012). As the average individual spends most of its lifetime at or near asymptotic size, the majority of the biomass is comprised of large individuals (Figure 3.4b). The reverse pattern is observed for species with high $\frac{M}{k}$, where the continual, albeit relatively slower, growth means that older, and relatively smaller (Fig-
Figure 3.4: The relative biomass as a function of a) standardised age and, b) standardised length for a range of $M/k$ (0.3–2.3). The area under each curve sums to 1. It is clear that as $M/k$ decreases, the unfished biomass is increasingly comprised of a greater proportion of younger and larger individuals. The Beverton-Holt life history invariant (BH–LHI) of $M/k = 1.5$ is shown in bold.

ure 3.1), individuals contribute more to the total unfished biomass (Figure 3.4a & b). For these species, the combination of relatively slower growth and higher natural mortality reduces the number of large individuals in the population, and smaller individuals contribute more to the total unfished biomass.

The influence of the $M/k$ ratio on the relationship between the relative size and biomass of a cohort is recognised as an important extension of Beverton and Holt’s work with the dimensionless numbers (Beverton, 1992; Beverton and Holt, 1964; Holt, 1958). For example, Jennings and Dulvy (2009) show the relationship between the relative weight and biomass of a cohort for three different $M/k$ ratios. However, by standardising age to $t_{\text{max}}$, this study further demonstrates that the relative age at which a cohort reaches maximum biomass will be the same for different species with the same $M/k$ ratio (Figure 3.4a). Determining $t_{\text{max}}$ is often difficult, and so in practice standardised age may be less useful than standardised length. However, Figure 3.4 shows that, when examined at the appropriate scale, species with vastly different life-spans (e.g., $M = 0.06$ and $M = 1.2$) but the same $M/k$ ratio have similar life-history.

An analytical solution to calculate the standardised length that maximises the biomass ($\tilde{L}_{\text{opt}}$) can be found by differentiating Equation 3.15 with respect to $\tilde{L}$, and solving for $\tilde{L}$ (see Appendix B for derivation):

$$\tilde{L}_{\text{opt}} = \frac{b}{M/k + b}$$ (3.16)

and:

$$L_{\text{opt}} = L_{\infty} \frac{b}{M/k + b}$$ (3.17)

which, although derived differently, is identical to Beverton’s (1992) equation for $L_{\text{opt}}$. Nu-
merous theoretical and empirical studies have suggested that evolutionary fitness is maximised if maturation coincides with $L_{\text{opt}}$ (Fryer and Iles, 1972; Roff, 1984; Beverton, 1992), which suggests that, assuming knife-edge maturity, length at maturity ($L_m$) occurs at $L_{\text{opt}}$, and, assuming that egg production is proportional to biomass, a theoretical relationship can be derived between $\frac{M}{k}$ and $\frac{L_m}{L_\infty}$:

\begin{align*}
\frac{L_m}{L_\infty} &= \frac{b}{\frac{M}{k} + b} \\
\frac{M}{k} &= \frac{b}{\frac{L_m}{L_\infty} - b}
\end{align*} \hspace{1cm} (3.18), (3.19)

The $L_m$ of a stock is often approximated at $L_{50}$, i.e., the length at which 50% of the individuals are mature, because of the variability in individual growth and maturity rates.

### 3.2.5 Estimating SPR from $\frac{M}{k}$, $F \frac{M}{M}$ and $\frac{L_m}{L_\infty}$ with simple assumptions

The spawning potential ratio (SPR) is defined as:

$$\text{SPR} = \frac{\text{Total Egg Production}_{\text{Fished}}}{\text{Total Egg Production}_{\text{Unfished}}}$$ \hspace{1cm} (3.20)

and is commonly used to set limit and target reference points for fisheries (Restrepo and Powers, 1999; Clark, 2002). Typically, the calculation of SPR requires estimates of the current fishing mortality ($F$), as well as estimates of natural mortality ($M$) and fecundity-and selectivity-at-age (Walters and Martell, 2004). The estimation of these parameters is often data intensive and difficult to obtain, especially for data-poor fisheries. However, with several simplifying assumptions, SPR can be calculated from the ratios $\frac{M}{k}$, $F \frac{M}{M}$ and $\frac{L_m}{L_\infty}$, without knowledge of the individual parameters.

Assuming that maturity is knife-edge at $L_m$, then the relative length at maturity is $\tilde{L}_m = \frac{L_m}{L_\infty}$ and $x_m$ is the standardised age that corresponds to $\tilde{L}_m$. Let $f$ be fecundity per unit of body weight for animals above $x_m$, then:

$$\text{Total Egg Production}_{\text{Unfished}} = f \sum B_x = f \sum \tilde{N}_x \tilde{W}_x = f \sum (1 - \tilde{L}_x)^{\frac{M}{k}} \tilde{L}_x^b \quad \text{for} \quad x_m \leq x \leq 1$$ \hspace{1cm} (3.21)

If all size classes are fully selected by the fishery, then the number of individuals at each standardised age $x$ and length $\tilde{L}_x$ in the fished state can be calculated by simply replacing $\frac{M}{k}$ in Equation 3.21 with $\frac{F}{k}$ (where $Z = M + F$) and expressing in terms of $\frac{M}{k}$ and $\frac{F}{M}$ (see Appendix B for full derivation), which gives:

$$\text{Total Egg Production}_{\text{Fished}} = f \sum (1 - \tilde{L}_x)^{\left(\frac{M}{k} \left[ \frac{F}{M} + 1 \right] \right)} \tilde{L}_x^b \quad \text{for} \quad x_m \leq x \leq 1$$

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Figure 3.5: The spawning potential ratio (SPR) for a range of $\frac{F}{M}$ (0–3) and $\frac{M}{k}$ (0.3–2.3). Maturity is assumed to be knife-edge with $L_m$ defined from Equation 3.18 and selectivity is assumed to be a) full selectivity (all size classes fully selected) and b) knife-edge selectivity at $L_m$ (only mature fish are selected).

SPR can then be calculated in terms of $\frac{M}{k}$ and $\frac{F}{M}$ as:

$$\text{SPR} = \frac{\sum (1 - L_x) \left( \frac{M}{k} [F + 1] \right) L^{b}}{\sum (1 - L_x) \frac{M}{k} L^{b}} \quad \text{for} \quad x_m \leq x \leq 1 \quad (3.22)$$

This demonstrates that, with the simple assumptions of knife-edge maturation, full selectivity, and no variation of length-at-age, SPR is determined by the ratios $\frac{M}{k}$, $\frac{F}{M}$ and $\frac{L_m}{L_\infty}$, and does not depend on the absolute values of the individual parameters. In other words, species with the same ratios of $\frac{M}{k}$, $\frac{F}{M}$ and $\frac{L_m}{L_\infty}$ will have the same SPR, regardless of their absolute values of $M$ and $k$ (Figure 3.5a).

### 3.2.6 Estimating SPR from $\frac{M}{k}$, $\frac{F}{M}$ and $\frac{L_m}{L_\infty}$ with knife-edge selectivity

Usually, not all length/age classes of a stock are vulnerable to fishing, and only a part of the stock is selected by the fishing gear. The simplest assumption is that selectivity is knife-edge at some standardised length $\tilde{L}_c$, i.e., all fish smaller than $\tilde{L}_c$ are not vulnerable to fishing mortality and only experience natural mortality, while all fish larger than $\tilde{L}_c$ are fully vulnerable to fishing mortality $F$. Accounting for knife-edge selectivity adds some complexity to the calculation of numbers of individuals alive at age, and hence the calculation of SPR. Simply replacing $\frac{M}{k}$ in Equation 3.21 with $\frac{Z}{k}$ assumes that the animals have experienced total mortality $Z$ for their entire lives. However, with knife-edge selectivity this is not the case, and the equation must be modified to account for the period of time
when the fish were only experiencing natural mortality:

\[ \tilde{N}_x = \begin{cases} 
(1 - \tilde{L}_x)^{\frac{M}{\tau}} & \text{for } 0 \leq x < x_c \\
(1 - \tilde{L}_x)^{\frac{M}{\tau}} (1 - \tilde{L}_c)^{-\frac{F}{\tau}} & \text{for } x_c \leq x \leq 1
\end{cases} 
\]

\[ = \begin{cases} 
(1 - \tilde{L}_x)^{\frac{M}{\tau}} & \text{for } 0 \leq x < x_c \\
(1 - \tilde{L}_x)^{\frac{M}{\tau}} \frac{M F}{\tau M} (1 - \tilde{L}_c)^{-\frac{M F}{\tau M}} & \text{for } x_c \leq x \leq 1
\end{cases} \tag{3.23}
\]

where \( x_c \) is the standardised age that corresponds to \( \tilde{L}_c \). It is important to note that \( \tilde{L}_x \) has the same meaning as defined in Equation 3.2, i.e., it refers to the expected (standardised) length at age \( x \) in the unfished state. These derivations assume that there is a direct relationship between length-specific and age-specific selectivity patterns. In reality, this is not the case, and the observed mean length-at-age in the fished state is likely to be less than \( \tilde{L}_x \) due to size selective fishing mortality removing the larger individuals from the population (i.e., the length-at-age distribution is unlikely to be normally distributed with size-specific selectivity). Total egg production in the fished state can then be given as:

\[ \text{Total Egg Production}_{\text{Fished}} = f \sum_x \left\{ (1 - \tilde{L}_x)^{\frac{M}{\tau}} \frac{M^3}{\tau^3} \right\} \frac{M F}{\tau M} (1 - \tilde{L}_c)^{-\frac{M F}{\tau M}} \frac{M^3}{\tau^3} \tag{3.24} \]

which can be substituted into Equation 3.22 to calculate SPR with knife-edge selectivity (Figure 3.5b). Figure 3.5 shows the significance of the size at selection in relation to the size at maturity (Walters and Martell, 2004). For example, SPR declines very quickly with increasing \( \frac{F}{M} \) when all size classes are selected by the fishery, with SPR=0.4 occurring between \( \frac{F}{M} \approx 0.3 \) and 0.6 for the range of \( \frac{M}{\tau} \) shown in Figure 3.5a. On the other hand, when only mature fish are selected (i.e., \( L_c = L_m \)) SPR declines at a slower rate, and it takes a much higher \( \frac{F}{M} \) to decrease SPR to 0.4 (i.e., \( \frac{F}{M} > 1 \), Figure 3.5b). If \( L_c \) is considerably larger than \( L_m \) it is possible to maintain high levels of SPR even with effectively infinite \( \frac{F}{M} \), although yield-per-recruit is likely to also decline with increasing \( L_c \).

### 3.2.7 Fished length composition in terms of \( \frac{M}{\tau} \) and \( \frac{F}{M} \)

Similarly to Equation 3.11, the probability of a fish in the fished state being greater than length \( \tilde{I} \) can be determined from Equation 3.23 (see Appendix B):

\[ \Pr\{\tilde{L} \geq \tilde{I}\} = \frac{(1 - \tilde{I})^M \frac{M}{\tau} + \frac{F}{M} (1 - \tilde{L}_c)^{\frac{M F}{\tau M}}}{(1 - \tilde{L}_c)^{\frac{M}{\tau}} \frac{M}{\tau}} \text{ for } \tilde{L}_c \leq \tilde{I} \leq 1 \tag{3.25} \]
and so:

\[
G(\tilde{l})_{\text{Fished}} = \Pr\{\tilde{L} \leq \tilde{l}\} = 1 - \left(\frac{(1 - \tilde{l})^{M + \frac{E}{M}}}{(1 - L_c)^{M + \frac{E}{M} \pi}} \frac{(1 - \tilde{L})^{M + \frac{E}{M} \pi}}{(1 - L_c)^{M + \frac{E}{M} \pi}}\right) \quad \text{for } L_c \leq \tilde{l} \leq 1 \tag{3.26}
\]

With the simplifying assumptions of knife-edge selectivity at \(L_c\), no variation of length-at-age, and given knowledge of \(\frac{F}{M}\) from meta-analysis or some other source, the ratio \(\frac{F}{M}\) can be estimated from the length composition of the catch, by minimising the following multinomial negative log-likelihood function (NLL):

\[
\text{NLL} = \sum_i O_i \ln \frac{P_i}{O^P_i} \tag{3.27}
\]

where \(O_i\) is the observed number of the catch in length class \(i\), \(O^P_i\) is the observed proportion of the catch in length class \(i\), and \(P_i\) is the predicted proportion of individuals in length class \(i\), calculated from Equation 3.26 (see Appendix B).

Equation 3.26 can also be re-written in terms of \(\frac{Z}{k}\):

\[
G(\tilde{l})_{\text{Fished}} = 1 - \left(\frac{1 - \tilde{l}}{1 - L_c}\right)^{\frac{Z}{k}} \quad \text{for } L_c \leq \tilde{l} \leq 1 \tag{3.28}
\]

which is equivalent to Wetherall et al.’s (1987) Equation 3. Assuming knife-edge selectivity at \(L_c\), and no variation in length-at-age, \(P_i\) can be calculated from Equation 3.28 and Equation 3.27 can be used to estimate the ratio \(\frac{Z}{k}\) from length composition data.

### 3.2.8 Incorporating variation in length-at-age

The assumption of no variability in length-at-age is not realistic and growth is almost always variable in fish stocks. If the growth of individual fish follows the von Bertalanffy function, variable length-at-age for the stock can arise from variability in the \(L_\infty\), \(k\) or \(t_0\) parameters for each individual (Pilling et al., 2002). The \(L_\infty\) and \(k\) parameters of the von Bertalanffy function are often found to be negatively correlated (Xiao, 1994; Pilling et al., 2002), probably caused by bioenergetic constraints (Jensen, 1997). However, it is important to distinguish between the correlation of the estimated parameters and the real biological correlation of the population parameters (Pilling et al., 2002). For simplicity, variability in length-at-age is commonly assumed to be due to variability in \(L_\infty\) alone, with \(k\) and \(t_0\) constant across individuals, although some simulations models do account for the correlation between \(L_\infty\) and \(k\) of individuals (e.g., Williams and Shertzer, 2005). Furthermore, length-at-age is often assumed to be normally distributed with a constant coefficient of variation (CV), although in reality this is not always the case (Erzini, 1994; Bowker, 1995). Using the simplifying assumption that individual growth is described by the von Bertalanffy equation, and that the sole source of variability in length-at-age is caused by
a normally distributed $L_\infty$, then the length-at-age $(L_x)$ can be standardised to the expected $L_\infty$ (i.e., the value typically thought of as the $L_\infty$ of the stock):

$$\hat{L}_x' = \frac{L_x}{E[L_\infty]} = \frac{L_\infty (1 - e^{-kxT_{\text{max}}})}{E[L_\infty]}$$  \hspace{1cm} (3.29)

The expected value and the standard deviation of the standardised length-at-age $x$ can then be given as (see Equation 3.2 and Appendix B):

$$E[\hat{L}_x'] = 1 - 0.01(x_\kappa)$$  \hspace{1cm} (3.30)

$$\sigma_{\hat{L}_x'} = CV_{L_\infty} \left( 1 - 0.01(x_\kappa) \right)$$  \hspace{1cm} (3.31)

Note that this derivation is true only if $L_\infty$ is the only source of variability in length-at-age, and that $k$ and $t_0$ are constant across all individuals. While this assumption is common in fisheries science, the implications of variability in the individual $k$ and $t_0$ parameters for individuals should be investigated with simulation testing.

These derivations can be used to construct an age-length transition matrix to determine the expected length composition of an unfished stock in terms of $\frac{M}{\kappa}$. For example, if there are $X$ elements in the standardised age vector $x$, and $I$ length classes, then $\mathbf{P}$ can be a $X \times I$ matrix which defines the probability of fish at age $x$ being in length class $i$ (see Appendix B). The expected number of individuals in each length class $i$ ($\tilde{N}_{\text{unfished}}$) for an unfished stock is then:

$$\tilde{N}_{\text{unfished}} = \tilde{N}_{\text{unfished}} \mathbf{P} = \left( 1 - E[\hat{L}_x'] \right)^{\frac{M}{\kappa}} \mathbf{P}$$  \hspace{1cm} (3.32)

The expected length frequency distribution is demonstrated in Figure 3.6 for four different values of $\frac{M}{\kappa}$, which is similar to Figure 3.3 but with the important addition of variable length-at-age. While the shape of the expected length composition for each $\frac{M}{\kappa}$ is still effectively the same, Figure 3.6 shows that some individuals may reach sizes greater than $L_\infty$. This is especially the case for species with low $\frac{M}{\kappa}$ (e.g., 0.6) where a large proportion of the unfished population is distributed around $L_\infty$. In contrast, for species with higher $\frac{M}{\kappa}$ (e.g., 3.0) individuals at lengths approaching $L_\infty$ are expected to be rare, even with variable length-at-age.

Modelling the expected length composition of only the vulnerable portion of the population is slightly more complicated, as the selectivity at length needs to be accounted for, and the variability of length-at-age means that although selectivity is assumed to be knife-edge at $L_c$, it is no longer knife-edge with respect to age. Let $\hat{L}_c' = \frac{L_c}{E[L_\infty]}$, then this can addressed
Figure 3.6: The expected standardised length composition for an unfished stock with variable length-at-age ($CV_{L_{\infty}} = 0.1$), and $\frac{M}{k}$ values of 0.6, 0.9, 1.5 & 3.0.
by modifying the matrix $P$ to have 0 probability that a fish at standardised age $x$ is $< \tilde{L}'_c$:

$$C_{x,i} = \begin{cases} 0 & \text{if } \tilde{l}_i < \tilde{L}'_c \\ P_{x,i} & \text{if } \tilde{l}_i \geq \tilde{L}'_c \end{cases}$$  \hspace{1cm} (3.33)

The matrix $C$ must be standardised so that all probabilities sum to 1:

$$\hat{C}_{x,i} = \frac{C_{x,i}}{\sum_j C_{x,j}}$$  \hspace{1cm} (3.34)

then expected number of individuals in each length class $\tilde{l}$ for the vulnerable part of a fished stock with knife-edge selectivity at $\tilde{L}_c$ is:

$$\tilde{N}_{\text{Vul}} = \tilde{N}_{\text{Fished}} \hat{C} = \begin{cases} (1 - E[L_x])^\frac{M}{F} \hat{C} & \text{if } \tilde{L}_x < \tilde{L}'_c \\ (1 - E[L_x])^\frac{M}{F} \left(1 - L'_c \right)^\frac{M}{F} \hat{C} & \text{if } \tilde{L}_c \leq \tilde{L}_x \leq 1 \end{cases}$$  \hspace{1cm} (3.35)

Assuming that the catch is a representative sample of the exploited population, the length structure of the catch is equivalent to the length structure of the vulnerable part of the population (Figure 3.7). With knowledge of the $\frac{M}{k}$ ratio, $L_{\infty}$, $CV_{L_{\infty}}$ and $L_c$ it is possible to estimate $\frac{F}{M}$ from the observed length structure of the catch, which in turn can be used to calculate SPR and inform management decisions.

### 3.2.9 Resolving the issue of non knife-edge selectivity

The simplifying assumption of knife-edge selectivity at $\tilde{L}'_c$ is often violated and more complex selectivity patterns are common. When selectivity is not knife-edge, calculating the number of individuals alive at age $x$ (or at $L_x'$) in terms of $\frac{M}{k}$ and $\frac{F}{M}$ becomes more difficult as Equation 3.23 must be modified to incorporate the more complex selectivity pattern. Currently, no analytical solution exists which gives $\tilde{N}_{\text{Fished}}$ in terms of $\frac{M}{k}$ and $\frac{F}{M}$ when selectivity is not knife-edge. However, there is a numerical solution which enables the calculation of $\tilde{N}_{\text{Fished}}$ (and so the expected fished length composition) while maintaining that the true value of the $M$ and $k$ parameters are not known.

As in the previous sections, the growth curve and length composition of a stock can be modelled with any time-scale, but the discretely modelled length composition better approximates the continuous distribution with increasingly fine temporal resolution. That is, the modelling of the length composition does not depend on the actual units of time, rather it depends on a sufficient number of age classes in the age-structured model to construct a smooth length composition. If $X$ is the minimum number of discrete age classes required to approximate a continuous length composition, then the discrete age classes $(t)$ would be a vector of integers of length $X$, with values from 0 to $t_{\text{max}}$, and $t_{\text{max}} = X - 1$. The corresponding $M$ can be calculated from Equation 3.4: $M = \frac{-\ln(0.01)}{t_{\text{max}}} = \frac{-\ln(0.01)}{X-1}$. The unit of
Figure 3.7: The expected standardised length composition for the catch for a fished stock with knife-edge selectivity at $L_C = 0.40$, and variable length-at-age (CV$_{L\infty} = 0.1$) for a) $\frac{M}{K} = 0.6$, $\frac{F}{M} = 0.5$; b) $\frac{M}{K} = 0.6$, $\frac{F}{M} = 1.0$; c) $\frac{M}{K} = 1.5$, $\frac{F}{M} = 0.5$; and d) $\frac{M}{K} = 0.6$, $\frac{F}{M} = 1.0$. 
time relating to \( t_{\text{max}} \) (and therefore \( M \)) is not known, so let this \( M \) be referred to as \( \dot{M} \) to identify it as a generic parameter with unknown time scale.

For example, suppose that a length composition was modelled with 100 discrete age classes, i.e., \( X = 100 \), then \( t_{\text{max}} = 99 \) and \( M = 0.0465 \). If the true maximum age of a species was 99 years, then \( M = 0.0465 \) year\(^{-1} \). However, if the true maximum age of a species was 99 months, then \( M = 0.0465 \) month\(^{-1} \). Of course, if the true maximum age of the species was something quite different (i.e., not 99 years, months, weeks or days), then \( M = 0.0465 \) in some arbitrary unknown unit of time. However, the fact that the unit of time is unknown is of little consequence, as the age composition is only being used to construct the length composition, and as demonstrated above, given the same \( \frac{M}{k} \), the shape of the length composition will be equivalent for these species. It is important to note that for \( \frac{M}{k} \) to be dimensionless both \( M \) and \( k \) must be in the same units. Continuing the previous example, if \( \frac{M}{k} = 1.5 \) then \( k \) would be 0.031 in the same arbitrary unit of time \( \left( \frac{M}{k} \right) \).

Total mortality at age \( t \) is then:
\[
\dot{Z}_t = \dot{F} S_t \tag{3.36}
\]
where \( S_t \) is selectivity at age \( t \), and the time scale of \( t \) is unknown (i.e., it could be years, months, days or any other arbitrary scale of time). As previously, \( x = \frac{t}{t_{\text{max}}} \), and so \( x \) is also a vector of length \( X \), with values ranging from 0 to 1, and so a vector of total mortality at standardised age \( x \) can then be defined as:
\[
\dot{Z}_x = M + \frac{F}{M} \tilde{S}_x = \dot{M} + \frac{F}{M} \tilde{S}_x \tag{3.37}
\]
where \( \tilde{S}_x \) is selectivity at standardised age \( x \). Assuming a logistic selectivity pattern, selectivity-at-length \( (S_l) \) can be described by:
\[
S_l = \frac{1}{1 + e^{-\ln(19)(t - L_{50})/L_{95} - L_{50}}} \tag{3.38}
\]
where \( L_{50} \) and \( L_{95} \) are the lengths at 50% and 95% selectivity respectively, and \( \ln(19) \) is a constant for this particular parametrisation of the logistic function. If \( \tilde{L}_{50} \) and \( \tilde{L}_{95} \) are defined as \( \frac{L_{50}}{E [L_{\infty}]} \) and \( \frac{L_{95}}{E [L_{\infty}]} \) respectively then Equation 3.38 can be used to calculate the selectivity at standardised length \( (\tilde{S}_l) \). Selectivity at standardised age \( x \) \( (\tilde{S}_x) \) can be calculated from selectivity at standardised length \( \tilde{l} \) by multiplying the vector \( \tilde{S}_l \) by the matrix \( P \):
\[
\tilde{S}_x = \tilde{S}_l P \tag{3.39}
\]
The relative number of individuals alive at standardised age \( x \) can then be calculated using the traditional fisheries model:
\[ \tilde{N}_{\text{Fished}} = \begin{cases} 1 & \text{if } x = 0 \\ \tilde{N}_{\text{Fished}} - 1 e^{-\dot{Z}_{x-1}} & \text{if } 0 < x \leq X \end{cases} \] (3.40)

As previously, the age-length transition matrix of the catch (C) can be constructed by modifying the matrix P to find the probability that an individual in the catch at standardised age x is in length class i:

\[ \text{C}_{x,i} = \text{P}_{x,i} \bar{S}_i \] (3.41)

where \( \bar{S}_i \) is the selectivity of length class i. The matrix C must be standardised so that all probabilities sum to one (Equation 3.34). The proportion of animals in the catch in each length class \( \tilde{P}L \) is then:

\[ \tilde{P}L = \frac{\tilde{C}C}{\sum_i [\tilde{C}C]} \] (3.42)

where \( \tilde{C} \) is the relative catch-at-age, calculated by the Baranov catch equation:

\[ \tilde{C}_x = \left( \frac{F_x \bar{S}_x}{\dot{Z}_x} \right) \tilde{N}_{\text{Fished}} \left( 1 - \exp^{-\dot{Z}_x} \right) \] (3.43)

Equation 3.42 can be used to calculate the expected length composition of the catch for a fished stock in terms of \( \frac{M}{M} \), \( \frac{F}{M} \), \( \bar{L}_{50} \) and \( \bar{L}_{95} \) (Figure 3.8). By substituting Equation 3.42 into Equation 3.27 the maximum likelihood estimates of \( \frac{F}{M} \), \( \bar{L}_{50} \) and \( \bar{L}_{95} \) can be obtained from the observed length structure of the catch, and, given an estimate of maturity-at-size, SPR can be calculated.

Although the selectivity-at-length pattern here is assumed to be logistic, other selectivity patterns are common (Sampson and Scott, 2012). For example, fishers may target areas with high catch rates of smaller individuals and the resulting length composition of the catch would under-represent the proportion of adults in the population. Additionally, the physical characteristics of some fishing gears types, for example gill nets or hooks, exclude larger individuals, resulting in a dome-shaped selectivity pattern. The assumption of asymptotic selectivity is crucial to apply the methodology presented in this study, and the method is likely to give biased estimates of \( \frac{F}{M} \) and SPR if the length data comes from a fishery with dome-shaped selectivity. In many cases a dome-shaped selectivity pattern may be expected. For these situations, it may be possible to generalise Equation 3.23 to accommodate a knife-edge upper selectivity limit (e.g., a protective slot limit), although this form of selectivity is not common in fisheries. If there was a priori reason to expect a dome-shaped selectivity pattern, Equation 3.38 could be modified with an extra parameter to allow for doming on the right-hand side of the selectivity curve. However, without additional information, it is difficult to estimate the shape of the descending limb of the selectivity curve with only the length composition of the catch. In practice, it is likely that the utility of the methodology presented in this study will be limited to cases where asymptotic selectivity is a reasonable assumption, although the extent of the bias introduced by
Figure 3.8: The expected standardised length composition for the catch for a fished stock with logistic selectivity ($L_{50} = 0.3, L_{95} = 0.5$), and variable length-at-age ($CV_L = 0.1$) for a) $M_k = 0.6, F_M = 0.5$; b) $M_k = 0.6, F_M = 1.0$; c) $M_k = 1.5, F_M = 0.5$; and d) $M_k = 0.6, F_M = 1.0$.

dome-shaped selectivity patterns is explored in a simulation study in Chapter 4.

3.3 Conclusion

The individual life history parameters, $M, k, L_m$ and $L_\infty$, are recognised as prescribing the life history strategy of a species. Biological studies of exploited stocks often report estimates for these parameters, and systems for assessing the ecological risk of fishing commonly use them individually in assessing the risk of being impacted by fishing (Hobday et al., 2011). When these parameters are not known for a stock, typically they are taken from other similar or closely related species and used in stock assessment to provide initial estimates of the status of the stock. Less detail is paid, however, to the ratios of the life history parameters $M_k$ and $L_m$, and how they vary across closely related species. This study has shown, however, that these dimensionless ratios give great insight into the life history strategy of a fish species.
By standardising to asymptotic size, the models developed in this study allow for growth patterns and life history strategies to be recognised and compared across a range of theoretical values for $\frac{M}{k}$, based on the comprehensive meta-analysis of 123 species of Chapter 2. While the BH–LHI values of $\frac{M}{k} = 1.5$ and $\frac{L_m}{L_{\infty}} = 0.66$ are commonly used when data are not available for all parameters, the range of $\frac{M}{k}$ reported in the literature for fish species is much more variable (Pauly, 1980; Beverton, 1992, and see Chapter 2). By examining a wide range of $\frac{M}{k}$ (0.3 – 2.3) the results of this study show the important consequences of significant divergence from the BH–LHI, which have important consequences for management. Although the $\frac{M}{k}$ ratio has long been recognised to influence the shape of the unfished length composition, this study has demonstrated that the shape of the von Bertalanffy curve is also determined by the $\frac{M}{k}$ ratio. In addition, this study has shown that there is a direct relationship between the four ratios, $\frac{M}{k}$, $\frac{L_m}{L_{\infty}}$, $\frac{F}{M}$, $\frac{L_c}{L_{\infty}}$, and SPR, which has allowed a new form of size-based assessment to be developed.

A number of important assumptions were made that underlie the methodology developed in this chapter. Like many length-based methods, this is an equilibrium based model, and assumes that the observed length composition does not deviate from the expected length structure because of variability in recruitment or mortality. The model also assumes that the fish growth is adequately described by the von Bertalanffy growth equation, with known $L_{\infty}$, $CV_{L_{\infty}}$, $\frac{M}{k}$, and $t_0 = 0$. Additionally, the model assumes that the observed length structure of the catch is representative of the population, i.e., the length composition is not affected by dome-shaped selectivity or a biased sample of the population. Finally, the models derived in this chapter are a special case of size-spectra models. The derivations assume that there is a direct relationship between age-based and size-based selectivity, and that the distribution of length-at-age is not affected by the size-specific selectivity. The utility of the methodology outlined in this chapter as a cost-effective tool for assessing data-poor fisheries is examined in Chapter 4, where sensitivity tests are conducted to examine how the model behaves under various scenarios, including parameter misspecification, population disequilibria, and small sample size.

An important challenge for fisheries science is to develop cost-effective approaches for determining the stock status of the world’s many data-poor and small-scale stocks (Worm and Branch, 2012). In data-poor situations, reliable estimates of the life history ratios $(\frac{M}{k}$ and $\frac{L_m}{L_{\infty}}$) may be easier to obtain than estimates of the individual parameters, and the methodology presented in this chapter provides a tool for the rapid and cost-effective assessment of exploited fish stocks with only minimal data requirements. Additionally, the cross-species comparison of the life history ratios holds great potential for developing a rigorous framework for borrowing biological information from well-studied species for applying to poorly studied stocks as described in Chapter 2.
A novel length-based empirical estimation method of spawning potential ratio (SPR), and tests of its performance, for small-scale, data-poor fisheries

Abstract

The spawning potential ratio (SPR) is a well-established biological reference point, and estimates of SPR could be used to inform management decisions for data-poor fisheries. The previous chapter (Chapter 3) demonstrated the link between the SPR and the life history characteristics of a species; namely, the ratio of natural mortality to the von Bertalanffy growth parameter \( \left( \frac{M}{k} \right) \) and the ratio of length at maturity to asymptotic length \( \left( \frac{L_m}{L_\infty} \right) \), and highlighted the potential of this approach for assessing the stocks of small-scale and data-poor fisheries. In the current study, simulations were used to investigate the utility of the length based model (LB–SPR) developed in Chapter 3 to estimate the SPR of exploited fisheries directly from the size composition of the catch. This was done by 1) testing some of the main assumptions of the LB–SPR model, including recruitment variability and dome-shaped selectivity, 2) examining the sensitivity of the model to error in the input parameters, and 3) completing an initial empirical test for the LB–SPR model by applying it to data from a species with complete information on the size and age composition. The method uses maximum likelihood methods to find the values of relative fishing mortality \( \left( \frac{F}{M} \right) \) and selectivity-at-length that minimise the difference between the observed and the expected length composition of the catch, and calculates the resulting SPR. When parameterised with the correct input parameters, the LB–SPR model returned accurate estimates of \( \frac{F}{M} \) and SPR. Although the model performed reasonably well with small sample sizes of length data \( (n = 100) \), variability in the estimates of SPR was reduced greatly when sample sizes were greater than 1,000. With high variability in annual recruitment the estimates of SPR became increasingly unreliable. The usefulness of the LB–SPR method was tested empirically by comparing the results predicted by the method with those for a well described species \( (Sillago schomburgkii) \) with known length and age composition data. The results from this compari-
son suggest that the length-based SPR methodology has potential to provide a tool for rapid, cost-effective, and precautionary assessment of data-poor fisheries. However, the model can be sensitive to non-equilibrium dynamics, and requires accurate estimates of the three parameters \((\frac{M}{k}, L_\infty, \text{CV}_{L_\infty})\). Care must be taken to evaluate the validity of the assumptions and the biological parameters when the model is applied to data-poor fisheries.

4.1 Introduction

Measurements of the length composition of an exploited stock are relatively cheap and simple to collect, and are one of the most common forms of data available to fisheries researchers (Quinn and Deriso, 1999). For small-scale and data-poor fisheries, where the collection of age data is often restricted by lack of technical expertise and expense, length composition data are often the only form of information available to researchers and managers. This is especially so for many tropical species, where the lack of clearly defined annual growth rings in otoliths or other hard parts make the task of aging individuals very difficult. As a result of the ready availability of length data for many stocks, a number of length-based methods have been developed and applied to estimate biological parameters and to understand the dynamics of fish populations (e.g., Beverton and Holt, 1957; Pauly and Morgan, 1987; Basson et al., 1988; Gulland and Rosenberg, 1992). Many of these size-based techniques were developed to estimate the growth and mortality rates of fish without the need for expensive and difficult to obtain age data (e.g., see Pauly and Morgan, 1987). Other length-based techniques aim to use the length structure of the population to estimate the stock status and provide useful management advice (e.g., Ault et al., 2005; O’Farrell and Botsford, 2005, 2006; Gedamke and Hoenig, 2006; Klaer et al., 2012).

Chapter 3 demonstrated that, under equilibrium conditions (i.e., constant \(F\) and no recruitment variability) and assuming von Bertalanffy growth, constant natural mortality for all age classes, no variability in length-at-age, and knife-edge selectivity, the standardised length composition of two stocks with the same ratio of natural mortality to growth rate \((\frac{M}{k})\) and the same ratio of fishing mortality to natural mortality \(\frac{F}{M}\) will be identical. The extension of this model to incorporate variability in length-at-age and logistic selectivity confirmed that, at equilibrium, the expected length composition of the catch of an exploited stock is primarily determined by the ratios of \(\frac{M}{k}\) and \(\frac{F}{M}\). The analytical models developed in Chapter 3 suggest that with knowledge of the von Bertalanffy asymptotic length \(L_\infty\) and the coefficient of variation in \(L_\infty\) (\(\text{CV}_{L_\infty}\)), the ratio of total mortality to the von Bertalanffy growth coefficient \((\frac{Z}{k})\) for a particular stock can be estimated from a representative sample of the length structure of the catch. If \(\frac{M}{k}\) is also known (from meta-analysis, life history theory, expert judgment, or biological studies of a stock), then the results of Chapter 3 suggest that it is possible to estimate \(\frac{F}{M}\) from the size composition of the catch. When \(M\) is unknown, i.e. only the ratio \(\frac{M}{k}\) is known, it is not possible to estimate \(F\) using this method. However, the ratio of \(\frac{F}{M}\) has often been used as a biological reference point, with
F_{MSY} = 0.87M considered a reasonable approximation for teleosts (Zhou et al., 2012).

The ratio of $\frac{F}{M}$ can be misleading, however, if not interpreted with care, as the selectivity of the fishery is also important. For example, it is possible that a highly selective fishery could target only a few of the oldest year classes in a stock. Under this scenario, even if $\frac{F}{M}$ is exceptionally high, the fishery is likely to be sustainable, but the yield is likely to be very low. Conversely, even a relatively low $\frac{F}{M}$ can reduce the spawning per recruit drastically if the fishery catches a high proportion of immature individuals (Walters and Martell, 2004, see also Chapter 3).

A persistent challenge for length-based methods has been to provide indicators of stock status that can be compared against pre-defined biological reference points. The spawning potential ratio (SPR) of a stock is defined as the proportion of the unfished reproductive potential left at any given level of fishing pressure (Goodyear, 1993; Walters and Martell, 2004) and is commonly used to set target and limit reference points for fisheries. By definition, the SPR equals 100% in an unexploited stock, and zero in a stock with no spawning (e.g., all mature fish have been removed, or all female fish have been caught). The $F_{40\%}$, i.e., the fishing mortality rate that results in SPR = 40%, is considered risk adverse for many species (Clark, 2002), and suitable SPR-based reference points for fisheries management can be derived from assumptions about the steepness of the stock-recruit relationship (Brooks et al., 2010). It is demonstrated in Chapter 3 that, under the assumptions of knife-edge selectivity-at-length at $L_c$, and knife-edge maturity at $L_m$, the SPR is determined by the ratios of $\frac{M}{k}$, $\frac{F}{M}$, $\frac{L_m}{L_\infty}$, and $\frac{L_c}{L_\infty}$.

The aims of this chapter were to evaluate the utility of the models developed in Chapter 3 as a methodology for assessing data-poor and small-scale stocks. This has been achieved by 1) testing some of the main assumptions of the length-based SPR (LB–SPR) model, including recruitment variability and dome-shaped selectivity, 2) examining the sensitivity of the model to error in the input parameters, and 3) empirically testing the prediction from the LB–SPR model by applying it to data from a well-studied species (Sillago schomburgkii, Coulson et al., 2005) and comparing the results with those from a conventional age-based technique. The LB–SPR model requires the following parameters: an estimate of the ratio $\frac{M}{k}$ (i.e. the individual values of the $M$ and $k$ parameters are unknown), $L_\infty$, CV_{L_\infty}, and knowledge of maturity-at-size, and uses data on the length composition of the catch to estimate the SPR. A simulation model was used to test the performance of the LB–SPR model for four species with a diverse range of life histories. These life histories where chosen on the basis of the $\frac{M}{k}$ ratios, varying from 0.53 for a species with a length composition dominated by large individuals, to 3.05, representing a species with an unfished length distribution dominated by smaller fish (see Chapter 2 and Chapter 3).

### 4.2 Methods

The length-based SPR method requires as input length composition data of the catch, as well as the three parameters: $\frac{M}{k}$, $L_\infty$, and CV_{L_\infty}. The model estimates the selectivity-at-
length and the ratio $\frac{F}{M}$, which in turn are used to calculate the SPR. To test the utility and sensitivity of the estimation model to a range of issues likely to be encountered in the real world, an age-structured operating model was developed to generate length composition data for a range of life-history types. All simulation modelling was done using the open-source statistical software $R$ (R Development Core Team, 2012).

### 4.2.1 Operating model

The population dynamics were modelled with a female-only, age-structured operating model (OM), assuming a population closed to immigration and emigration. In general, the OM used annual time-steps, however, for short-lived species (i.e., species with life-span $\leq 10$ years) monthly time-steps were used. The conversion from annual to monthly time-steps was necessary to ensure the construction of smooth length compositions for short-lived species, and was achieved by scaling the rate parameters appropriately. For example, an annual $M$ is converted to a monthly rate by dividing by 12. For the short-lived species, recruitment was assumed to be continuous and occurred on the 1st day of every month.

The abundance, $N$, at age $a$ at time $t$ is given as:

$$N_{a,t} = \begin{cases} R_t & \text{if } a = 0 \\ N_{a-1,t-1}e^{Z_{a-1}} & \text{if } 0 < a \leq a_{\text{max}} \end{cases}$$  \hspace{1cm} (4.1)

where $R_t$ is the number of recruits at time $t$, $Z_a$ is instantaneous total mortality at age $a$, and $a_{\text{max}}$ is the maximum age. Total mortality at age $a$ is given by:

$$Z_a = M + S_a F$$  \hspace{1cm} (4.2)

where $M$ is the annual instantaneous rate of natural mortality, $S_a$ is selectivity at age $a$, and $F$ is the annual instantaneous rate of fishing mortality. The catch-at-age ($C_a$) was calculated using the Baranov equation:

$$C_{a,t} = \frac{F_a}{Z_a} N_{a,t} (1 - e^{-Z_a})$$  \hspace{1cm} (4.3)

Maximum age ($a_{\text{max}}$) was determined as the first age class where the number of surviving individuals was $\leq 1\%$ of initial recruitment (Quinn and Deriso, 1999), so that:

$$a_{\text{max}} = -\frac{\ln(0.01)}{M}$$  \hspace{1cm} (4.4)

Natural mortality was assumed to be constant and independent of size or age, and fishing mortality was assumed to be constant for all $t$. Recruitment at time $t$ ($R_t$) was related to the spawning biomass by the Beverton–Holt stock-recruit relationship with multiplicative
log-normal error:

\[ R_t = \frac{SB_t}{\delta + \rho SB_t} e^{\varepsilon_t - \frac{\sigma_R^2}{2}} \]  

where \( SB_t \) is the spawning stock biomass at time \( t \), \( \delta \) and \( \rho \) are parameters of the stock-recruit function, and \( \varepsilon_t \) is the recruitment residual at time \( t \) that is normally distributed by \( N \left( 0, \sigma_R^2 \right) \), where \( \sigma_R \) is the standard deviation of the recruitment.

The \( \delta \) and \( \rho \) parameters of the stock-recruit relationship were re-parameterised in terms of steepness (\( h \)), which is defined as the fraction of virgin recruitment (\( R_0 \)) obtained when spawning biomass is 0.2 of the unfished spawning biomass (i.e. 0.2\( SB_0 \)).

Growth was modelled with the three-parameter von Bertalanffy function:

\[ L_a = L_\infty \left( 1 - e^{-k(a-t_0)} \right) \]  

where \( L_\infty \) is asymptotic length, \( k \) is the growth coefficient, and \( t_0 \) the theoretical age when length is zero. Variation of length-at-age was assumed to be normally distributed, with variance increasing with increased mean length (Sainsbury, 1980):

\[ \sigma_{L_a}^2 = \sigma_{L_\infty}^2 \left( 1 - e^{-k(a-t_0)} \right)^2 \]  

\[ \sigma_{L_\infty} = CV_{L_a} L_\infty \]

Maturity was assumed to be size-dependent, and was modelled with the two-parameter logistic function:

\[ \text{Mat}_l = \frac{1}{1 + e^{-\frac{\ln(19)\left(l - L_50\right)}{L_95 - L_50}}} \]  

where \( \text{Mat}_l \) is maturity at length \( l \), and \( L_{50} \) and \( L_{95} \) are lengths at 50% and 95% maturity respectively. Maturity-at-length was converted to maturity-at-age (\( \text{Mat}_{a} \)):

\[ \text{Mat}_{a} = \int_{t=0}^{t=\infty} \text{Mat}_{l} \frac{1}{\sigma_{L_a} \sqrt{2\pi}} e^{-\frac{(l-l_a)^2}{2\sigma_{L_a}^2}} \]  

where \( \sigma_{L_a}^2 \) is the variance of length at age \( a \). It should be noted that this equation implicitly assumes that selectivity is age-specific, and that there is a direct relationship between age-specific and length-specific selectivity patterns. In other words, the model assumes that the length-at-age distribution is not affected by the level of fishing mortality (\( F \)), which is unlikely to hold true in most cases.

Spawning stock biomass was calculated as:

\[ SB_t = \sum_{a} N_{a,t} \text{Mat}_{a} W_a \]  

where \( W_a \) is weight at age \( a \), which was calculated as:

\[ W_a = \alpha L_a^\beta \]
where \( \alpha \) and \( \beta \) are constants. Egg production at age \( a \) was assumed to be proportional to weight:

\[
E_a \propto \text{Mat}_a W_a \tag{4.13}
\]

For most cases, selectivity was assumed to be asymptotic and size dependent, and was modelled by replacing \( L_{S0} \) and \( L_{95} \) in Equation 4.9 with the lengths at 50% and 95% selectivity (\( L_{S50} \) and \( L_{S95} \)). The sensitivity of the model to dome-shaped selectivity was also examined. For these cases, selectivity-at-length \( (S_l) \) was modelled as a two-sided curve:

\[
S_l = \begin{cases} 
  e \left[ -\frac{(l - L_1)^2}{2s_1^2} \right] & \text{for } l < L_1 \\
  e \left[ -\frac{(l - L_2)^2}{2s_2^2} \right] & \text{for } l \geq L_1
\end{cases} \tag{4.14}
\]

where \( L_1, L_2, s_1 \) and \( s_2 \) are the mean and standard deviations of the two normal curves. Selectivity-at-length was converted to selectivity-at-age \( (S_a) \) in the same manner as Equation 4.10.

SPR was calculated following Goodyear (1993) and Walters and Martell (2004), by calculating the ratio of the average lifetime production of eggs per recruit \( (EP) \) at equilibrium for the fished and unfished states, assuming no density-dependent suppression of maturation or fecundity:

\[
SPR = \frac{EP_{\text{Fished}}}{EP_{\text{Unfished}}} \tag{4.15}
\]

where

\[
EP_{\text{Fished}} = \sum_a l_x_a E_a \tag{4.16}
\]

\( l_x_a \) is the survivorship to age \( a \) calculated as:

\[
l_x_a = \begin{cases} 
  1 & \text{for } a = 1 \\
  l_{x_{a-1}} e^{-Ma} (1 - F_{a-1}) & \text{for } a > 1
\end{cases}
\]

The unfished egg production is calculated by:

\[
EP_{\text{Unfished}} = \sum_a E_a e^{-Ma} \tag{4.17}
\]

An age-length transition matrix (Hilborn and Walters, 1992) was constructed from the assumptions of mean length-at-age and variation of length-at-age, where the probability of an individual at age \( a \) being in length class \( i \) is given by:

\[
P_{i,a} = \begin{cases} 
  \phi \left( \frac{l_{lo}^{i+1} - L_a}{\sigma_{l_{lo}^{i+1}}} \right) & \text{if } i = 1 \\
  \phi \left( \frac{l_{lo}^{i+1} - L_a}{\sigma_{l_{lo}^{i+1}}} \right) - \left( \frac{l_{lo}^{i} - L_a}{\sigma_{l_{lo}^{i}}} \right) & \text{if } 1 < i \leq I \\
  1 - \left( \frac{l_{lo}^{i} - L_a}{\sigma_{l_{lo}^{i}}} \right) & \text{if } i = I
\end{cases} \tag{4.18}
\]

where \( \phi \) is the standard normal cumulative distribution, \( l_{lo}^i \) is the upper bound of length
class $i$, and $I$ is the total number of length classes. The age-length probability matrix was modified for the expected age-length distribution of the catch ($p$) to account for the selectivity-at-length by multiplying the age-length transition matrix by the selectivity at length class $i$ ($S_i$):

$$ p_{i,a} = p_{i,a}S_i $$  \hspace{1cm} (4.19)

The age-length transition matrix for the catch was standardised so that the probability of an individual in the catch at age $a$ being in one of the $I$ length classes was 1:

$$ \hat{p}_{i,a} = \frac{p_{i,a}}{\sum_i p_{i,a}} $$  \hspace{1cm} (4.20)

The length composition of the catch ($N_i$) was then constructed by multiplying the vector of catch-at-age by the transpose of the matrix $\hat{p}$:

$$ N_i = C_a\hat{p}^T $$  \hspace{1cm} (4.21)

### 4.2.2 Estimation model

The estimation model was based on the analytical derivations developed in Chapter 3, but for completeness, it is described fully here. To ensure that there was no possibility of cross-contamination of parameter values between the operating model and the estimation model, the estimation model was coded separately in ADMB (Fournier et al., 2012). Chapter 3 demonstrated that, once standardised (to $L_\infty$, or some other standardisation, e.g. $L_{\text{max}}$), the expected length composition of the catch is determined by the interaction of selectivity and $Z_k$. If $M_k$ is known, from meta-analysis or some other method, then there is the potential to estimate $F$ and selectivity-at-length from length frequency data of the catch. In turn, these estimated parameters can be used to calculate the SPR, which can be used as an indicator of the status of the stock for management of the fishery.

To make the problem numerically tractable, the estimation model was constructed from a modified age-structured model, with “age” defined in arbitrary units. Let $X$ be the number of discrete “age” classes in the estimation model, where $X$ is a fixed parameter of the estimation model. The vector $x$ is then defined as a sequence of “ages” in an arbitrary temporal scale from 0 to $X-1$ (i.e., maximum “age”= $X-1$), and $\tilde{x}$ is a vector of relative “ages” defined between 0 and 1:

$$ \tilde{x} = \frac{x}{X} $$  \hspace{1cm} (4.22)

It is important to remember that the units of $x$ are undefined, and that any ages in the estimation model are only meaningful in relative terms. Mean standardised length ($\tilde{l}$) at age $x$ can then be given in terms of $\frac{M}{k}$ (see Chapter 3):

$$ \tilde{l}_x = 1 - 0.01^{\frac{x}{1/M/k}} $$  \hspace{1cm} (4.23)

Assuming that length-at-age is normally distributed with constant CV, the standard devia-
tion of \( \bar{I}_i \) is (see Chapter 3):

\[
\sigma_{\bar{I}_i} = CV \left( 1 - 0.01^\frac{1}{\bar{I}_i} \right) \tag{4.24}
\]

If there are \( I \) length classes in the observed length composition of the catch, and the length composition is standardised to \( L_\infty \), then the probability of an individual at age \( x \) being in length class \( i \) (\( \bar{P} \)) can be calculated by using Equation 4.18. Assuming a logistic selectivity pattern, selectivity at standardised length \( \bar{l} \) (\( \bar{S} \)) can be calculated by substituting \( \bar{l} \) into Equation 4.9 and standardising the \( L_{50} \) and \( L_{95} \) parameters to asymptotic size. Using Equation 4.19 the matrix \( \bar{P} \) can be modified to account for the selectivity-at-length, to calculate the probability that an individual in the catch at age \( x \) is in size class \( i \) (\( \bar{C} \)). The matrix \( \bar{C} \) must be standardised so that there is a probability of 1 that an individual in the catch at age \( x \) is in one of the \( I \) length classes (\( \bar{C} \)):

\[
\bar{C}_{i,x} = \sum_i \bar{C}_{i,x} \tag{4.25}
\]

Chapter 3 demonstrated that it is possible to calculate the number of individuals at age \( x \) in terms of \( \frac{M}{k} \) and \( \frac{F}{M} \) by using the assumed relationship between longevity and natural mortality. If \( X \) is the number of discrete age classes, then the corresponding \( M \) can be calculated from Equation 4.4:

\[
M = -\ln(0.01) = -\ln(0.01) \frac{t_{\max}}{X-1}. \tag{4.26}
\]

The unit of time relating to \( t_{\max} \) (and therefore \( M \)) is not known, so let this \( M \) be referred to as \( \bar{M} \) to identify it as a generic parameter with unknown time scale. The value of the \( X \) parameter (and hence the value of \( \bar{M} \)) is fixed, and determined by the analyst. Although the value of \( \bar{M} \) will depend on the value of \( X \) chosen by the analyst, the ratio of \( \frac{M}{k} \) remains fixed, and \( \bar{k} \) scales accordingly so that \( \frac{\bar{M}}{\bar{k}} = \frac{M}{k} \). Sensitivity tests were conducted to the value of \( X \) (see below), but in general the model is insensitive to this parameter and it can remain fixed at some arbitrary value (e.g., \( X = 100 \); see Chapter 3 for further discussion). A vector of total mortality at age \( x \) can then be given as:

\[
\bar{Z}_x = \bar{M} + \bar{M} \frac{F}{\bar{M}} \bar{S}_x \tag{4.27}
\]

The relative number of individuals at age \( x \) can then be calculated using the traditional fisheries model:

\[
\bar{N}_x = \begin{cases} 
1 & \text{if } x = 0 \\
\bar{N}_{x-1} e^{-\bar{Z}_{x-1}} & \text{if } 0 < x \leq X
\end{cases} \tag{4.28}
\]

The expected proportion of individuals in the catch in length class \( i \) is then calculated by multiplying the age structure of the vulnerable portion of the population (\( \bar{N}_x \bar{S}_x \)) by the
transpose of the catch age-length transition matrix \((\hat{\mathbf{C}})\), and standardising:

\[
\hat{\mathbf{p}}_{\text{Catch}}^i = \frac{(\breve{N}_x\breve{S}_x)\breve{\mathbf{C}}^T}{\sum_i (\breve{N}_x\breve{S}_x)\breve{\mathbf{C}}^T}
\]  

This equation has the assumption that the relative number of animals at age in the part of the population that is vulnerable to fishing \((\breve{N}\breve{S})\) is equivalent to the relative age distribution in the catch (i.e., an asymptotic selectivity pattern). With the assumptions of constant CV of length-at-age, logistic selectivity, and constant natural mortality, the above algorithm gives the expected proportion of the catch in length class \(i\) in terms of \(M\), \(F\) and selectivity at relative length \((l_{50}, l_{95})\). When the observed length composition of the catch is standardised to \(L_\infty\) then the two selectivity parameters are equal to \(\frac{l_{50}}{L_\infty}\) and \(\frac{l_{95}}{L_\infty}\) respectively. Given knowledge of \(M\), the parameters \(F\), \(l_{50}\), and \(l_{95}\) can be estimated from the standardised length composition of the catch by minimising the following multinomial negative log-likelihood function (NLL):

\[
NLL = \arg\min_{F, l_{50}, l_{95}} \sum_i O_i \ln \frac{\hat{\mathbf{p}}_{\text{Catch}}^i}{O_i^P}
\]  

where \(O_i\) and \(O_i^P\) are the observed number and proportion of the catch respectively in length class \(i\).

Chapter 3 demonstrated that, with the simplifying assumptions of no variation of length-at-age, and knife-edge selectivity, SPR is invariant with respect to the ratios \(M\) and \(F\). They extended the model further to relax some of the assumptions and showed the relationship between SPR and \(M\) and \(F\) holds with logistic selectivity and variable length-at-age. Using the generic age-structure of the estimation model, and given estimates of maturity-at-age and the size-fecundity relationship, SPR can be calculated from the estimated parameters. Assuming that maturity is a logistic function of length, then maturity at relative length \(\breve{l}\) can be calculated by substituting the relative lengths at maturity, \(\breve{l}_{50}\) and \(\breve{l}_{95}\) for 50% and 95% maturity respectively, into Equation 4.9. Similarly to selectivity-at-length, maturity-at-length can be converted to maturity at age \(x\) by multiplying the vector \(\text{Mat}_i\) by the age-length transition matrix \(\hat{\mathbf{P}}\):

\[
\text{Mat}_x = \text{Mat}_i\hat{\mathbf{P}}
\]  

where \(\text{Mat}_i\) is the probability that an individual in length class \(i\) is mature. Assuming that fecundity is linearly related to weight, and that weight is a cubic function of length, the relative egg production \((\breve{E})\) at relative age \(x\) is:

\[
\breve{E}_x = \text{Mat}_x\breve{l}_x^3
\]  

Total relative egg production for the fished state \((\breve{EP}_{\text{Fished}})\) and unfished \((\breve{EP}_{\text{Unfished}})\) states can then be calculated by substituting \(\breve{E}_x\) and \(Z_x\) into Equation 4.16 and \(\breve{M}\) into Equation...
4.17. SPR can then be calculated using Equation 3.22.

4.2.3 Simulation and evaluation

The utility of the LB–SPR method was evaluated by using the operating model to generate length data, and comparing the estimates of \( \frac{M}{k} \), selectivity-at-length, and SPR from the estimation model with the true values of the OM. Biological parameters for the simulated data were based on four species with a range of life-histories: I) sand sole (Psettichthys melanostictus), II) Puget Sound rockfish (Sebastes emphaeus), III) yellowtail flathead (Platycephalus endrachtensis) and IV) Pacific saury (Cololabis saira) (Hughes, 1974; Beckmann et al., 1998; Watanabe et al., 1988; Pearson and McNally, 2005; Pember et al., 2007). These species were chosen because of the range of life-histories that they represented. The \( t_0 \) of these species were all set to 0 to test the sensitivity of the model to variation in this parameter, \( CV_{L_{\infty}} \) was set to 0.1, steepness set to 0.7 for all species, and the selectivity-at-length parameters were arbitrarily set lower than maturity-at-length for each species (Figure 4.1). Hence, hereafter these species are referred to as Species I, II, III, & IV (Table 4.1).

**Table 4.1:** The biological and selectivity parameters for the four test species used in the robustness tests of the length-based SPR model. Biological parameters are based on I) sand sole (Psettichthys melanostictus) (Pearson and McNally, 2005); II) Puget Sound rockfish (Sebastes emphaeus) (Beckmann et al., 1998); III) yellowtail flathead (Platycephalus endrachtensis) (Pember et al., 2007); and IV) Pacific saury (Cololabis saira) (Hughes, 1974; Watanabe et al., 1988).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Species</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>( L_{\infty} )</td>
<td>I</td>
<td>Asymptotic size</td>
</tr>
<tr>
<td>( cv_{L_{\infty}} )</td>
<td>II</td>
<td>Coefficient of variation of ( L_{\infty} )</td>
</tr>
<tr>
<td>( M )</td>
<td>III</td>
<td>Natural mortality</td>
</tr>
<tr>
<td>( k )</td>
<td>IV</td>
<td>Growth coefficient</td>
</tr>
<tr>
<td>( t_0 )</td>
<td></td>
<td>Theoretical age at zero length</td>
</tr>
<tr>
<td>( \frac{M}{k} )</td>
<td>I</td>
<td>( \frac{M}{k} ) ratio</td>
</tr>
<tr>
<td>( L_{50} )</td>
<td>II</td>
<td>Length at 50% maturity</td>
</tr>
<tr>
<td>( L_{95} )</td>
<td>III</td>
<td>Length at 95% maturity</td>
</tr>
<tr>
<td>( L_{550} )</td>
<td>IV</td>
<td>Length at 50% selectivity</td>
</tr>
<tr>
<td>( L_{955} )</td>
<td></td>
<td>Length at 95% selectivity</td>
</tr>
</tbody>
</table>

The utility of the LB–SPR model was tested using a number of robustness tests to understand the sensitivity of the model to various assumptions, values of the input parameters and life-histories (Table 4.2). The assessment model was parameterised with the “true” value of the \( \frac{M}{k} \), \( L_{\infty} \), \( CV_{L_{\infty}} \) parameters, except in the cases where sensitivity to those parameters was being tested (i.e., Tests 1–3 & 11). Similarly, the entire catch was sampled except in Test 5. Fishing mortality was set equal to natural mortality for all cases except Test 7. For Test 1–7, \( \sigma_R \) was set to 0 (i.e. no variability in recruitment), and the operating model was projected forward until the stock was at fished equilibrium. The \( X \) parameter of
the estimation model was set at 100 for all cases except Test 4.

Table 4.2: Description of the 12 tests to understand the robustness and sensitivity of the length-based SPR (LB–SPR) model to a range of parameter misspecification and assumption violations for the four test species of Table 4.1.

<table>
<thead>
<tr>
<th>Test</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>assumed $\frac{M}{K}$ parameter ranging $\pm 25%$ of true value</td>
</tr>
<tr>
<td>2</td>
<td>assumed $L_\infty$ parameter ranging $\pm 25%$ from true value</td>
</tr>
<tr>
<td>3</td>
<td>assumed $CV_{L_\infty}$ parameter ranging $\pm 25%$ from true value</td>
</tr>
<tr>
<td>4</td>
<td>$X$ (the length of vector $x$ in the estimation model) ranging from 10–208</td>
</tr>
<tr>
<td>5</td>
<td>Sample size reduced to 100, 500, 1,000, 5,000 &amp; 10,000 individuals</td>
</tr>
<tr>
<td>6</td>
<td>Length-at-birth ($L_0$) ranging 0–0.25$L_\infty$</td>
</tr>
<tr>
<td>7</td>
<td>True $\frac{F}{M}$ ranging 0.01–5</td>
</tr>
<tr>
<td>8</td>
<td>Recruitment variability with $\sigma_R = 0.1, 0.3, 0.6$ &amp; 0.9</td>
</tr>
<tr>
<td>9</td>
<td>Same as Test 8, with auto-correlated recruitment variability</td>
</tr>
<tr>
<td>10</td>
<td>Same as Test 8, with episodic recruitment failure</td>
</tr>
<tr>
<td>11</td>
<td>$\frac{M}{K}, L_\infty$ and $CV_{L_\infty}$ drawn from triangle distributions, and $\sigma_R = 0.6$</td>
</tr>
<tr>
<td>12</td>
<td>Increasing levels of dome-shaped selectivity, and $\sigma_R = 0.6$</td>
</tr>
</tbody>
</table>

Tests 1–3 examined the sensitivity of the estimation model to misspecification of the $\frac{M}{K}, L_\infty$, and $CV_{L_\infty}$ parameters respectively (Table 4.2). For each test, the estimation model was run 100 times with the assumed value of the relevant parameter arbitrarily allowed to range from $-25\%$ to $+25\%$ of the true value. Results for these tests were summarised as the relative error in $\frac{F}{M}$ and the resulting SPR for the range of the assumed parameters. Relative error (RE) was calculated as:

$$RE = \frac{\hat{\lambda} - \lambda}{\lambda}$$

where $\lambda$ and $\hat{\lambda}$ are the true and estimated parameters respectively.

Test 4 determined the sensitivity of the estimation model to changes in $X$, the temporal resolution of the estimation model. For this test, the estimation model was run 100 times with $X$ in Equation 4.22 ranging from 10 to 208. The results of this test were summarised as the relative error in $\frac{F}{M}$ and the resulting SPR as a function of $X$.

Although samples of the length composition of the catch are relatively cheap and simple to obtain, it is unlikely that the entire catch would be measured in most cases. Test 5 examined the impact of sample size on the effectiveness of the LB–SPR method. Five levels of sampling coverage were examined, with sample sizes of 100, 500, 1,000, 5,000, and 10,000 individuals respectively. For each case and test species, length compositions were generated from 200 Monte Carlo simulations by randomly sampling with replacement from the age composition of the catch, with the probability proportional to that in the true age composition of the catch. The estimation model was run on each generated length composition, and results summarised as boxplots of the relative error in the estimated parameters for each sample size.

The estimation model assumes that length at birth ($L_0$) is zero (Equation 4.23) which,
for the purposes of this model, is probably a reasonable assumption for many species of fish. However, in some species, for example live-bearing teleosts and many sharks, \( L_0 \) is considerably larger than zero. When modelling fish growth with the von Bertalanffy function, this is accounted for with the inclusion of the \( t_0 \) parameter, which is the theoretical age at which the length of the animal would be 0. In most cases the \( t_0 \) is \( \leq 0 \), which indicates that \( L_0 \geq 0 \). In cases where \( t_0 > 0 \), \( L_0 \) is \( < 0 \) which is biologically impossible, and the von Bertalanffy growth function may not be the most appropriate model to use in these situations. The sensitivity of the estimation model to \( L_0 > 0 \) was examined in Test 6. For this test, the length compositions were generated with \( L_0 \) ranging from 0 to \( 0.25L_{\infty} \) for each species. To generate the length compositions, the appropriate \( t_0 \) parameter was calculated in the operating model by manipulating Equation 4.6:

\[
t_0 = \frac{\ln \left( 1 - \frac{L_0}{L_{\infty}} \right)}{k}
\]  

(4.34)

Test 7 investigated the sensitivity of the assessment model to variation in the value of \( \frac{F}{M} \). For this test, length compositions were generated from 100 Monte Carlo simulations with the true \( \frac{F}{M} \) ranging from 0.01 to 5, and the estimated \( \frac{F}{M} \) was compared against the true value.

Like many length-based methods, the LB–SPR technique is an equilibrium-based method, which compares the observed length composition of the catch with the expected length composition in equilibrium conditions. In reality, an exploited stock is rarely at equilibrium. Even if exploitation rates are held constant for some time, a stock is still likely to be at disequilibrium due to variability in recruitment. The last three tests examined the sensitivity of the estimation model to population disequilibrium by generating length compositions from stocks with variable recruitment. For Test 8, the number of Monte Carlo simulations was increased to two hundred, with the operating model projected forward under four levels of log-normally distributed recruitment variability, with \( \sigma_R \) set at 0.1, 0.3, 0.6 and 0.9 respectively. For each of the Monte Carlo simulations, a length composition of the catch was generated from the last year. Test 9 repeated a similar test to Test 8, but with the addition of auto-correlated recruitment variability, with a lag of 1 year and an auto-correlation coefficient of 0.6. Test 10 further extended the examination of recruitment variability by investigating the impact of episodic recruitment failure. For this test there was a 15% chance in any given time-step (usually yearly, but monthly for short-lived species) of recruitment failure. Two hundred Monte Carlo simulations were conducted for each of the four species types (Table 4.1) for the same range of recruitment variability as Tests 8 & 9 (Table 4.2).

While Tests 1–3 evaluated the impact of misspecification of the parameters of the LB–SPR model, all three input parameters may be uncertain and the equilibrium assumptions may not hold. Test 11 involved 5,000 Monte Carlo simulations for each test species, with recruitment variability (\( \sigma_R = 0.6 \)), and, for each simulation, selected each of the three LB–SPR input parameters from a triangle distribution, with the mode at the true value, and the
same range as that used in Tests 1–3. The results from Test 11 are presented as boxplots of the estimated SPR and the relative error in the estimated \( \frac{F}{M} \). The results from Test 2 indicated that when the \( L_\infty \) parameter was specified to be too low, the model hit the lower bound on \( \frac{F}{M} (\frac{F}{M} = 0) \), and returned estimates of SPR of 1 (see Figure 4.2b and below for discussion). In reality, such an extreme under-estimate of the \( L_\infty \) parameter would be unlikely, and the poor model fit would raise suspicions about the validity of the LB–SPR estimate of SPR \( \approx 1 \). To address this issue, for Test 11 the LB–SPR estimates where SPR \( \geq 0.99 \) were discarded, which occurred in 20%, 12%, 4%, and 4% of the simulations for Species I, II, III, and IV respectively.

A common problem with many fishing gears, such as gill nets and trawls, is dome-shaped selectivity, where large fish are not caught by the fishery. The LB–SPR model assumes asymptotic selectivity, and it is expected that the method will over-estimate \( \frac{F}{M} \) and under-estimate SPR when confronted with data from a fishery with dome-shaped selectivity. To test the performance of the LB–SPR model where selectivity is dome-shaped, 200 Monte Carlo simulations were run, with recruitment variability \( (\sigma_R = 0.6) \), for a range of increasingly dome-shaped selectivity patterns for each species. The dome-shaped selectivity curves were modelled as a two-sided function, with one asymptotic curve (the base case) and four curves with increasing doming (Figure 4.1). The results from Test 12 are presented as a series of boxplots showing the relative error in the SPR estimates for the five different selectivity curves and the four test species.

4.2.4 Preliminary empirical test

An empirical test of the LB–SPR method was carried out using detailed biological data for the temperate yellowfin whiting (\( Sillago schomburgkii \), Sillaginidae) in Shark Bay, Western Australia (Coulson et al., 2005). The data on the female length composition was used as a case study for the LB–SPR method. Currently, there is no stock assessment for the Shark Bay \( S. schomburgkii \) and Coulson et al. (2005) did not estimate natural or fishing mortality for the species. However unpublished work suggests that \( S. schomburgkii \) is lightly exploited in Shark Bay (Coulson 2013, Murdoch University, pers. comm), and this study used the maximum age of female fish in the Coulson et al. (2005) study (10 years; \( n = 997 \)) with the Hoenig method (Hoenig, 1983) to estimate natural mortality \( (M = 0.42) \). This study used the catch-curve method with the age composition data to estimate total mortality \( (Z = 0.55) \), resulting in an estimate of \( F = 0.13 \) and \( \frac{F}{M} = 0.31 \). The female length composition data was also used to estimate \( \frac{F}{M} \) and SPR with the LB–SPR model, parameterised with the female biological parameters \( (L_\infty = 345.97 \text{ mm}, k = 0.477 \text{ year}^{-1}, L_{50} = 223 \text{ mm}, L_{95} = 259 \text{ mm} \) Coulson et al., 2005, and assumed that CV\( L_\infty = 0.1 \). The results from this estimation of SPR were compared with those based on conventional age-based techniques, i.e., \( Z \) estimated using a catch curve and \( F \) calculated as \( F = Z - M \). This study evaluated the sensitivity of the LB–SPR model to alternative values for the \( L_\infty \) and \( \frac{M}{k} \) parameters by re-running the model with a combination of different \( L_\infty \) and
Figure 4.1: The five selectivity curves used to assess the sensitivity of the length-based SPR model to length data from a fishery with dome-shaped selectivity for Species I, II, III and IV (a, b, c and d respectively, Table 4.1). Curve 1 (solid line) is the asymptotic selectivity curve used in all base case scenarios, and curves 2-5 are two-sided selectivity curves with increased doming. For reference, the maturity curve for each species is represented as a solid gray line.
parameters ($L_\infty = 330, 345, 360$ and $M_k = 0.60, 0.88, 1.15$. $CV_{L_\infty}$ was held constant at 0.1). This empirical test provides an indication of the performance of the LB–SPR model, and comprehensive testing of the model is now being carried out by applying the LB–SPR model to empirical data from a wide range of species (Prince et al., Murdoch University, unpublished data).

4.3 Results

The sensitivity tests revealed that, for all 4 species, the accuracy of the estimated $\frac{F_M}{M}$ and the assumed values of the parameters for the LB–SPR method was closely related (Figures 4.2a, b & c). When the 3 parameters of the LB–SPR model were set equal to the true values, the estimation model returned estimates of $\frac{F_M}{M}$, the selectivity parameters, and SPR that were equal to the true values (Figures 4.2a, b & c). The model had similar behaviour for all 4 species when $M_k$ was misspecified (Test 1), with $\frac{F_M}{M}$ over-estimated by about 70% when $M_k$ was assumed to be 25% lower than the true value, and under-estimated by about 40% when $M_k$ was assumed to be 25% higher than the true value (Figure 4.2a). The estimates of the selectivity parameters $L_{50}$ and $L_{95}$ were insensitive to the assumed $M_k$. The exact relationship between $\frac{F_M}{M}$ and SPR depends on the selectivity pattern; however, in general SPR decreases as $\frac{F_M}{M}$ increases. As expected, the relationship between estimated SPR and the degree of misspecification in the assumed $M_k$ parameter is the reverse to the pattern observed between the estimated $\frac{F_M}{M}$ and assumed $M_k$, with SPR being increasingly over-estimated as the $M_k$ parameter is assumed to be higher than the true value (Figure 4.2a).

The estimation model was most sensitive to the assumed $L_\infty$, with considerable over-estimation in $\frac{F_M}{M}$ when the assumed $L_\infty$ was specified to be higher than the true value, par-

![Figure 4.2](http://example.com/figure4_2.png)

**Figure 4.2:** The relative error (RE) in the estimated $\frac{F_M}{M}$ and resulting estimate of the spawning potential ratio (SPR) for the four simulated species for a) Test 1: misspecification of $\frac{M_k}{M}$, b) Test 2: misspecification of $L_\infty$, c) Test 3: misspecification of $CV_{L_\infty}$, and d) resolution of the age-structured estimation model ($X$). The solid black points in the SPR panels of a), b) & c) indicate the true SPR for each species.
particularly when >0.1 of the true $L_\infty$ (Test 2; Figure 4.2b). Sensitivity to the assumed $L_\infty$ increased with decreasing $\frac{M}{k}$, with Species I the most sensitive to misspecification of $L_\infty$ ($\frac{F}{M}$ over-estimated by about 400% when $L_\infty$ assumed to be 25% higher than true value) and Species IV the least ($\frac{F}{M}$ over-estimated by about 100% when $L_\infty$ assumed to be 25% higher than true value). The model under-estimated $\frac{F}{M}$ when $L_\infty$ was assumed to be lower than the true value, with $\frac{F}{M}$ estimated to be 0 (i.e., $F$=0) when the assumed $L_\infty$ was specified to be 10-20% lower than the true value. As with Test 1, the selectivity-at-length parameters were well estimated and were not sensitive to the misspecification of the assumed $L_\infty$ parameter (Figure 4.2b). However, SPR showed the same sensitivity as $\frac{F}{M}$, with the estimated SPR rapidly increasing as the assumed $L_\infty$ was decreased below the true value, and rapidly decreasing when the assumed $L_\infty$ was increased above the true value (Figure 4.2b).

The estimation model was relatively insensitive to variation in the assumed CV$_{L_\infty}$ for all four life-history types, although species with low $\frac{M}{k}$ appeared the most sensitive to this parameter (Figure 4.2c). The model was also completely insensitive to the temporal scale of the estimation model when $X$ was above about 25 (Figure 4.2d). Below this value, the model behaved somewhat chaotically and often did not fit the data well.

As expected, the variability in the estimates of $\frac{F}{M}$, selectivity-at-length and SPR increased when the number of measurements decreased, particularly at a sample size of 100 individuals. However, even with the error in these parameters, the estimates of SPR were relatively consistent across all sample sizes (Figure 4.3). The median relative error in $\frac{F}{M}$ was close to 0 for all sample sizes, and SPR was well estimated, particularly for sample sizes of 1,000 individuals or greater (Figure 4.3).

Species with higher $\frac{M}{k}$ appear to be the most sensitive to the assumption that $L_0=0$ (i.e. $t_0=0$), however the estimation model was relatively insensitive to $L_0>0$, with $\frac{F}{M}$ being over-estimated by 5-10% when $L_0=0.25L_\infty$ (Test 6; results not shown). The estimation model was not sensitive to the true $\frac{F}{M}$ of the operating model and returned accurate estimates for the entire range of $\frac{F}{M}$ (Test 7; results not shown).

The relative error in the estimates of $L_{50}$ and $L_{95}$ was consistent over the range of recruitment variability, $\sigma_R=0.1$ to 0.9, for all four species (Test 8; Figure 4.4). Not unexpectedly, the relative error in the selectivity parameters increased with increasing recruitment variability, however in most cases the selectivity parameters were estimated within 10% of the true values. A similar pattern was observed in the estimated $\frac{F}{M}$ for all four species, with variance increasing with increased recruitment variability (Figure 4.4). However, with the exception of the scenarios with high recruitment variability ($\sigma_R = 0.9$) where the estimates were positively biased, the median relative error in the estimated $\frac{F}{M}$ for all four life history types was centred around 0, indicating that on average the method was successful in correctly estimating the parameters (Figure 4.4). The variability in the estimates of $\frac{F}{M}$ and the selectivity parameters directly translates through to the estimates of SPR; however SPR appeared to be consistently well estimated for all four life-history types and four levels of recruitment variability (Figure 4.4).

The inclusion of auto-correlated recruitment variability resulted in increased variance in
Figure 4.3: Boxplots showing the 5th, 25th, 50th, and 95th percentiles of the relative error (RE) in the estimated $F_M$, $L_{50}$, $L_{95}$ and resulting estimate of the spawning potential ratio (SPR) for a range of sample sizes for a) Species I, b) Species II, c) Species III, and d) Species IV. The biological attributes for the test species are given in Table 4.1.
Figure 4.4: Boxplots showing the 5th, 25th, 50th, and 95th percentiles of the relative error (RE) in the estimated $F_m$, $L_{50}$, $L_{95}$ and resulting estimate of the spawning potential ratio (SPR) with recruitment variability (Test 8) for a) Species I, b) Species II, c) Species III, and d) Species IV. The biological attributes for the test species are given in Table 4.1.
Figure 4.5: Boxplots showing the 5th, 25th, 50th, and 95th percentiles of the relative error (RE) in the estimated $F_M$, $L_{50}$, $L_{95}$ and resulting estimate of the spawning potential ratio (SPR) with auto-correlated recruitment variability (Test 9) for a) Species I, b) Species II, c) Species III, and d) Species IV. The biological attributes for the test species are given in Table 4.1.

the four estimated parameters, particularly when $\sigma_R$ was 0.6 or 0.9 (Test 9; Figure 4.5). Although the estimates of the selectivity parameters were consistent, the relative error in $\frac{F_M}{M}$ was often quite large. While the median relative error in $\frac{F_M}{M}$ was centred around 0, $\frac{F_M}{M}$ was sometimes considerably over-estimated, which resulted in SPR being considerably underestimated (Figure 4.5). In addition, $\frac{F_M}{M}$ was also occasionally under-estimated by close to 100%, resulting in SPR being greatly over-estimated (see 95 and 5 percentiles of $\frac{F_M}{M}$ and SPR respectively in Figure 4.5). There appeared to be little extra impact from the inclusion of episodic recruitment variability, with the estimation model appearing to behave in a similar manner to Test 8 (Test 10; results not shown). As with the other tests involving recruitment variability, the relative error in the estimated parameters increased with increasing recruitment variability, with $\frac{F_M}{M}$ being occasionally over-estimated and under-estimated by up to 100% when $\sigma_R = 0.9$.

The variability in the model estimates increased as simultaneous error in the three LB-
Figure 4.6: Boxplots showing the 5\textsuperscript{th}, 25\textsuperscript{th}, 50\textsuperscript{th}, and 95\textsuperscript{th} percentiles of the relative error in the estimated $\frac{F}{M}$ and the resulting estimates of the spawning potential ratio (SPR) for the 4 test species from 5,000 Monte Carlo simulations with simultaneous error in the three parameters of the length-based SPR method and recruitment variability ($\sigma_R = 0.6$). The solid black points indicate the true SPR for the four species. The biological attributes for the test species are given in Table 4.1.

SPR parameters was introduced, with the model tending to over-estimate $\frac{F}{M}$ and underestimate SPR, particularly for Species I and II (Test 11; Figure 4.6). Species I ($M_k = 0.53$) was most sensitive to misspecification in the three parameters (Figure 4.6), with the median relative error in the estimated $\frac{F}{M}$ positively biased about 36\%, and in some cases $\frac{F}{M}$ was over-estimated by up to four times the true value and in others under-estimated by nearly 100\%. The median estimates of SPR were negatively biased by some 20\%, and the estimates ranged from close to 1 to essentially 0 (Figure 4.6). The sensitivity of the model decreased with the increasing $M_k$ of the other three species, with the median relative error in the estimated $\frac{F}{M}$ positively biased by 18\%, 6\% and 5\% for Species II ($M_k = 0.82$), III ($M_k = 1.54$) and IV ($M_k = 3.05$) respectively. Species IV was the least sensitive to error in the assumed parameters, with the resulting estimate of SPR ranging from close to 0.6, and the median estimated SPR close to the true value of 0.19.

The LB–SPR model under-estimated SPR for all four test species when provided with length data from a fishery with dome-shaped selectivity (Figure 4.7). Species I and II (Figure 4.7a, b) were the most sensitive to dome-shaped selectivity, with SPR significantly under-estimated by over 50\% for curves 4 and 5. Species III and IV (Figure 4.7c, d) were less sensitive to the dome-shaped selectivity, especially for the curves with only slight doming (curves 2 and 3).

Although the length frequency distribution of the female $S. schomburgkii$ was bimodal, with one group from 165 to 215 mm total length, and the other from 255 to 295 mm, the LB–SPR model appeared to fit the data fairly well (Figure 4.8). The LB–SPR model estimates of $\frac{F}{M} = 0.55$ and SPR = 0.44 were more conservative than the estimates from the age-based catch curve ($\frac{F}{M} = 0.42$ and SPR = 0.62). The LB–SPR model was
Figure 4.7: Boxplots showing the 5th, 25th, 50th, and 95th percentiles of the relative error in the estimated spawning potential ratio (SPR) for the five different selectivity curves (one asymptotic and four with increasing doming) for Species I, II, III and IV (a, b, c, and d respectively). The biological attributes for the test species are given in Table 4.1.
Figure 4.8: The female length frequency distribution of *Sillago schomburgkii* (Coulson 2013, Murdoch University, unpublished data) with the fit from the length-based SPR (LB–SPR) model overlaid as a black solid line. When parameterised with the biological parameters from Coulson et al., 2005, the LB–SPR model estimated $F_M = 0.55$ and SPR=0.44. For comparison, the $F_M$ estimated from the age data was 0.42, which corresponds to a SPR of 0.62.

The simulated length data in this study was based on four species with diverse life histories sensitive to the various combinations of $M_k$ and $L_\infty$, with the resulting SPR varying from 0.18 ($L_\infty = 360, M_k = 0.6$) to 1.00 ($L_\infty = 330, M_k = 1.15$) (Table 4.3).

Table 4.3: The estimated spawning potential ratio (SPR) from the length-based SPR model (LB–SPR) model for the *Sillago schomburgkii* data (Coulson et al., 2005) for the combination of three different values for the $L_\infty$ and $M_k$ parameters.

<table>
<thead>
<tr>
<th>$L_\infty$(mm)</th>
<th>$\frac{M}{k}$0.60</th>
<th>$\frac{M}{k}$0.88</th>
<th>$\frac{M}{k}$1.15</th>
</tr>
</thead>
<tbody>
<tr>
<td>330</td>
<td>0.31</td>
<td>0.62</td>
<td>1.00</td>
</tr>
<tr>
<td>345</td>
<td>0.23</td>
<td>0.44</td>
<td>0.78</td>
</tr>
<tr>
<td>360</td>
<td>0.18</td>
<td>0.34</td>
<td>0.58</td>
</tr>
</tbody>
</table>

4.4 Discussion

The length-based technique developed in this study offers an alternative method to estimate $F_M$, selectivity-at-length and the spawning potential ratio (SPR) for an exploited stock based only on length frequency data. Length frequency data are one of the easiest and most affordable metrics to collect, and for many small-scale, data-poor fisheries, may be the only data available. This technique provides a means of estimating the biological reference points, $F_M$ and SPR, which previously required expensive and technically challenging catch-at-age analyses.

The simulated length data in this study was based on four species with diverse life hist-
tories, spanning the range of $\frac{M}{\tau}$ (0.53 to 3.05) in the meta-analysis of Chapter 2. The $\frac{M}{\tau}$ values correspond to species that mature and reach their maximum length relatively early in life ($\frac{M}{\tau} = 0.53$), and those that continue growing throughout life ($\frac{M}{\tau} = 3.05$). The results from the simulations showed that the length based SPR (LB–SPR) method appeared to work well, especially for species with $\frac{M}{\tau} > 0.53$. However, it is likely that the model will be increasingly biased for species with $\frac{M}{\tau} < 0.53$, as the method relies on detecting the signal of fishing mortality in the right-hand side of the length composition. Species with low $\frac{M}{\tau}$ are expected to have an unfished length composition very strongly skewed to the left, with the length composition consisting of adults of widely varying age, but at a similar (near asymptotic) size (see Figure 3.1 in Chapter 3). Consequently, fishing is not likely to have a visible impact on the length composition until fishing mortality is very high and SPR is very low.

As modelled here, the LB–SPR method assumes that length-at-age is normally distributed with a constant coefficient of variation (CV), an assumption that does not always appear to hold (Bowker, 1995; Erzini, 1994). Detailed costly ageing studies are required to test this assumption, research that is not feasible for small-scale, data-poor fisheries. However, meta-analyses of existing length-at-age studies are likely to provide a cost-effective way to determine whether the assumption of normally distributed length-at-age is commonly violated, or if there are predictable violations of this assumption amongst some species. The impact of violating the assumption of normally distributed length-at-age has not been investigated in this study but knowledge of the distribution of length-at-age could be incorporated into the LB–SPR method for specific species.

### 4.4.1 Influence of variation in parameters on estimating SPR

The simulation tests involving uncertainty in all three parameters showed clearly that the accuracy of the estimated SPR from the LB–SPR method depends on the bias of the parameters $\frac{M}{\tau}$, CV$_{L_{\infty}}$ and $L_{\infty}$ (Figure 4.6). When tested empirically for a species with known age and length composition, the LB–SPR model returned a more conservative estimate of SPR than the age-based catch curve. However, it is important to note that the catch curve method is also an equilibrium method, and these estimates do not necessarily reflect the ‘true’ status of the stock. Furthermore, depending on the assumed values for the $\frac{M}{\tau}$ and $L_{\infty}$ parameters, the LB–SPR suggests that the status of the *S. schomburgkii* stock ranges from unfished (SPR=1) to a fully or heavily exploited (SPR<0.2, Table 4.3), which reinforces the importance of accurate and reliable estimates of the biological parameters for the LB–SPR model.

When parameterised with the ‘true’ biological parameters, the LB–SPR method returned an estimate of SPR that was comparable, although more precautionary, to the estimate of a more traditional age-based method. However, the LB–SPR method may be sensitive to different life history types, and the comparison of the results between the two methods may be more variable for species with different life history strategies. An important area of fur-
ther research is comparing the output of the LB–SPR model to traditional stock assessment outputs for species with a wide range of life history types.

The research required to estimate these three parameters directly from the stock is time-consuming, somewhat complex, and expensive; precisely the factors that limit age-based population modelling from being applied to data-poor and small-scale fisheries. Without relatively expensive ageing studies, it is difficult to obtain reliable estimates of the individual parameters $M$ and $k$. A number of length-based methods exist which aim to estimate $k$ from size-frequency or tagging studies (e.g., Pauly and Morgan, 1987; Smith et al., 1998; Siegfried and Sansó, 2006). Estimating $M$ is often more difficult, even with data rich techniques (Lee et al., 2011) especially for stocks with a long history of exploitation. However, the ratio of $\frac{M}{k}$ is known to be often less variable between species than either of the individual parameters in the ratio (Beverton, 1992, see also the meta-analysis in Chapter 2).

Numerous rules-of-thumb have been developed to estimate $L_{\infty}$ in data-poor stocks. For example, Taylor (1958) suggested that the life-span of a fish species could be estimated as the age at which fish reach 95% of their asymptotic length; i.e. the mean length of the cohort is $0.95L_{\infty}$ at $a_{\text{max}}$. Assuming that a cohort is at its mean maximum length ($L_{\text{max}}$) at $a_{\text{max}}$, $L_{\infty}$ can be estimated by: $L_{\infty} = \frac{L_{\text{max}}}{0.95}$ (Pauly, 1984). If a stock is exploited only relatively lightly, $L_{\text{max}}$ could be approximated by the maximum observed length. However, as demonstrated by Figure 3.1 in Chapter 3, the assumption that fish are $0.95L_{\infty}$ at $a_{\text{max}}$ does not hold for species where $\frac{M}{k}$ diverges away from the Beverton–Holt Life History Invariant value of 1.5. For example, a species with a $\frac{M}{k}$ ratio of 0.7, i.e., species where individuals reach maximum size relatively early in life, would be expected to reach $L_{\infty}$ at about $0.7 \times a_{\text{max}}$ (i.e. $L_{\text{max}} = L_{\infty}$). In contrast, a species with a $\frac{M}{k}$ ratio of 2.3, i.e., a species that has indeterminate growth, would be expected to only reach $0.8L_{\infty}$ at the end of its life (i.e., $L_{\text{max}} = 0.8L_{\infty}$) (see Figure 3.1 in Chapter 3). If an estimate of the ratio $\frac{M}{k}$ is known, then the equations derived in Chapter 3 could be used to estimate $L_{\infty}$ from $L_{\text{max}}$ and $\frac{M}{k}$, which could then be used to as an estimate of $L_{\infty}$ for the LB–SPR model developed in the current study.

Beverton (1992) demonstrated that a relationship between $\frac{M}{k}$ and the ratio of size at maturity to asymptotic size ($\frac{L_{m}}{L_{\infty}}$) can be derived analytically for teleosts. Chapter 2 and Chapter 3 confirm this relationship from an empirical analytical approach with a meta-analysis of these ratios for 123 species in the literature. The results of Chapter 2 suggest that the co-varying ratios can be predicted for species on the basis of taxonomic relationships and a species’ life history strategy. Meta-analysis and life-history theory appear to offer a way of estimating these parameters for small-scale and data-poor stocks. Assuming that other closely related species, or nearby stocks, have a similar life-history and are well studied, the ratio $\frac{L_{m}}{L_{\infty}}$ from these stocks could be used as a starting estimate for use in the LB–SPR model for estimating SPR for the data-poor stock of interest (see Chapter 2).
4.4.2 Representative length data

Hilborn and Walters (1992) warn against using length-based methods, and note that length compositions are often not representative of the whole stock. Unrepresentative samples would cause bias in any stock assessment method and the resulting evaluation of the condition of the stock. Consequently, ensuring that high quality, representative length data are collected for the stock should be an important research priority, and care must be taken in designing a rigorous sampling program to collect length data. Since the LB–SPR method assumes that any large fish that are missing from the data have been removed by fishing, if the large fish are under-represented in the length sample for any reason, the LB–SPR method will over-estimate $F_M$ and under-estimate the SPR (see Figure 4.7).

The precision of the estimated SPR from the length composition data can be increased by simply increasing the sample size of the length measurements (Figure 4.3). Gerritsen and McGrath (2006) recommend a rule-of-thumb where the minimum sample size is 10 times the number of length classes in the sample. These results and those from other simulation studies suggest that sample sizes of 1,000 length measurements are required to sufficiently capture the features of a length composition (Erzini, 1990). The results indicate that the variation in the estimated SPR was reduced greatly when $\geq 1,000$ measurements were taken (Figure 4.3). Importantly, this sample size refers to the effective sample size, and assumes that each length measurement was a simple random sample from the catch-at-length. In reality this is often difficult to achieve, as fish often aggregate by size, and care must be taken to ensure a representative size sample, and a large effective sample size. In addition to measuring an adequate number of fish to increase the precision of the estimated SPR, the sampling design should consider the temporal and spatial distribution of the fished stocks to ensure that the sample is a true representation of the length structure of the stock (Gerritsen and McGrath, 2006). For example, if 1,000 samples are taken from a single vessel that targeted a spawning aggregation, the effective sample size would be much lower than 1,000 and the length data is unlikely to be representative of the stock.

Not surprisingly, the LB–SPR model is particularly sensitive to length composition data from a fishery with dome-shaped selectivity. In particular, species with low $M_k$ ($<0.8$) are especially sensitive to dome-shaped selectivity. Such species are expected to have a large proportion of the individuals at or near $L_\infty$ (see Chapter 3), and the LB–SPR model interprets the absence of the large individuals from the size structure as evidence for a high level of exploitation. Species with higher $M_k$ are less sensitive to dome-shaped selectivity, as even in the unfished state, few individuals live long enough to reach asymptotic size, and a smaller fraction of the population is affected by the size-based dome-shaped selectivity. It is often difficult to detect the presence of dome-shaped selectivity, especially when the length composition of the catch are the only available data. If there are multiple fleets targeting the same stock, the LB–SPR model should be applied to the data from the fleet that targets the adult portion of the stock, and data that is suspected to come from a fishery with dome-shaped selectivity should be used cautiously. Furthermore, the effects of any recent management changes should also be considered. For example, if there has been a
recent change in mesh size, or another form of management that influences the selectivity of the fishery, the length structure of the catch will be affected which may introduce bias into the LB–SPR estimates.

### 4.4.3 Dynamic effects on estimating SPR

The model developed in this study assumes that the stock is in equilibrium, which means that the current size composition of the stock is assessed against the expected size composition if the stock had experienced a constant level of fishing pressure and constant recruitment. The small-scale fisheries that are the focus of this methodology often experience high levels of fishing pressure. For example, experience with artisanal fisheries of the western Pacific has shown that uncontrolled and unmanaged fisheries are often heavily exploited. Fishing pressure in such fisheries often changes relatively slowly in response to economic forces, rather than in response to management changes which can cause changes on a faster timescale. The second assumption of constant recruitment, however, is unlikely to hold for many stocks (Myers, 2001). The simulation of variation in recruitment examined in this study ranged from low, where the standard deviation of recruitment = 0.1 (i.e., \( \sigma_R = 0.1 \)); and the difference between the strongest and weakest year classes is \( \approx 1.5:1 \), to reasonably high, where \( \sigma_R = 0.9 \) and the difference in magnitude between the strongest and weakest year classes is \( \approx 30:1 \). Not unexpectedly, the results of the LB–SPR model are most variable when the annual recruitment variability is high. The results from these simulations showed that high recruitment variability is likely to cause considerable variation in the estimates from the LB–SPR method, especially when \( \sigma_R \) is \( \geq 0.6 \) (difference in years class strength \( \approx 10:1 \)), and the model performed the worst when the recruitment variability was auto-correlated. At low levels of recruitment variability \( (\sigma_R = 0.1) \) and constant \( F \), the stock is essentially at equilibrium, and \( \frac{F}{M} \), the selectivity parameters, and the SPRs are estimated with minimal error (Figures 4.4 & 4.5). However, as the recruitment variation was increased \( (\sigma_R = 0.6 \text{ and } 0.9) \), the estimated \( \frac{F}{M} \) in any given year could be under-estimated by close to 100\% \( (\frac{F}{M} = 0, \text{SPR} = 1) \), or over-estimated by over 100\% (Figures 4.4 & 4.5). The relative error in the estimated parameters in the simulations with recruitment variability, however, was centred on 0, and SPR was estimated reasonably well, i.e. within 30\% of the real value, in most of the Monte Carlo simulations for all four species. Occasionally, particularly for high recruitment variability \( (\sigma_R = 0.9) \), the estimates of \( \frac{F}{M} \) and the selectivity parameters were very biased, resulting in large over- or under-estimates of SPR.

As the LB–SPR model is an equilibrium based method, and assumes constant recruitment, it cannot fit multi-modal length compositions well. Modes in length compositions often occur from a disparity in year class strength, and following the progression of these modes through time is the foundation for many length-based techniques used to estimate growth and mortality (Pauly and Morgan, 1987). If the length frequency of a population is highly multi-modal, the LB–SPR model will not fit the data well, and any estimates of \( \frac{F}{M} \), selectivity and SPR are likely to be unrealistic. This is demonstrated in the poorer perfor-
mance of the LB–SPR model in the simulations with highly variable, and auto-correlated, recruitment trends. While a good fit of the LB–SPR model does not necessarily imply that the estimates are accurate (the model can potentially fit the data very well even if $\frac{M}{L}$ or $L_\infty$ are misspecified), a poor fit of the model to multi-modal length data indicates that the results are likely to be untrustworthy. If the year-classes are clearly identified as modes in the length data, the LB–SPR method may not be the most suitable technique for estimating the status of the stock and other, more traditional, length-based methods may be more applicable. Alternatively, collecting data at a higher temporal resolution (e.g., monthly for short lived species) and then aggregating the data over a year, may provide a means of constructing a length composition more representative of the equilibrium size composition. Furthermore, perfect knowledge of the biological parameters, $\frac{M}{T}$, $L_\infty$, and $CV_{L_\infty}$, is unlikely, especially for data-poor stocks. Therefore, it is important to carefully evaluate the results of a single ‘snapshot’ approach using the LB–SPR method, and the validity of the model assumptions and parameter estimates should be examined prior to implementing the method.

This study did not examine the influence of temporal variability in $F$. A time-varying $F$ implies that SPR also varies temporally, and the equilibrium-based LB–SPR model will undoubtedly not track the true SPR during this transitional period. A full examination of the dynamic effects (i.e., time-varying $F$ and recruitment variability) on estimating SPR with the LB–SPR model is outside the scope of this study. However, management strategy evaluation (MSE) modelling conducted by Wayte and Klaer (2010) and Prince et al. (2011) on harvest control rules based on equilibrium-based catch-at-age and SPR-based size targets, shows that while individual assessments of size composition may be imprecise due to the transitory dynamics of a population’s size structure, smoothed trends estimated over several years provided an accurate basis for harvest control rules. Additionally, Klaer et al. (2012) demonstrate a length-based harvest control rule that iteratively manages catch to drive to stock to a target level. Prince et al. (2011) noted that size composition is often far from equilibrium, and affected by recent recruitment trends, and they included other forms of data (i.e., catch rates) to calibrate the size data. Without these other sources of data the LB-SPR-based harvest control rule is likely to be less stable. However, these observations support their finding, in that some of the transitory size dynamics gave LB–SPR estimates that were quite variable, but the median error across estimates was close to zero. In the following chapter, Chapter 5, a management strategy evaluation framework is used to incorporate a harvest control rule into the LB–SPR methodology, and a number of simulations are carried out to understand the behaviour of the LB–SPR model in a dynamic context.

When confronted with a data-poor fishery with only data on the length frequency distribution of the stock, the LB–SPR model may be an effective tool to providing an initial estimate of the stock status, and inform preliminary management advice. However, it is important that the assumptions and sensitivities of the LB–SPR model are considered carefully when interpreting the estimates of SPR from this method. For example, the impact
of the violation of the equilibirum assumption on the performance of the LB–SPR method has important implications. Many data-poor stocks may be over-exploited, and the stock size is likely to be heavily influenced by recruitment trends. Similarly, the assumption of no temporal trend in fishing mortality and an asymptotic selectivity pattern may not hold in many cases. By definition, the assessment of data-poor fish stocks is always going to be difficult, and, in many cases, a wrong or heavily biased assessment may be worse than no assessment at all. It is important to keep this in mind when applying the LB–SPR model, or other similar methods, to data-poor fish stocks. In many cases, a ‘weight-of-evidence’ approach may be most useful, where a number of different indicators of stock status are used to inform management advice. In the case of competing or contradictory indicators from different methods, the best action may be to delay management and focus on the collection of more data. Finally, the application of the LB–SPR model will highlight these important research needs, e.g., a better understanding of the growth or maturity schedule, and efforts should be made to collect additional data required for more comprehensive assessment methodologies (e.g., Prince et al., 2011).
5 An evaluation of a harvest strategy for data-poor fisheries using the length-based SPR assessment method

Abstract

Conventional approaches to fisheries management rely on data-intensive methods that are difficult to apply to data-poor stocks. Moreover, data-poor fisheries are often located in developing regions, where, despite the fact that they support millions of people, the lack of funding and expertise limits the data collection and analysis required for many modern assessment methods. Data on the length structure of exploited stocks are one of the easiest sources of information to obtain for data-poor fisheries, and have the potential to provide cost-effective solutions to the management of data-poor fisheries. However, length-based methods often have significant limitations, and currently, methods for assessing very data-poor fisheries are a gap for managers. This chapter describes a management strategy evaluation framework that is used to investigate the utility of the LB–SPR methodology, and uses an effort-based harvest control rule to iteratively drive fishing pressure towards a target level. The study examined various degrees of error and model uncertainty in a number of scenarios, and simulated the performance of the model for three species with a diverse range of life-histories and $\frac{M}{K}$ ratios ranging from 0.36 (unfished population dominated by large fish) to the Beverton–Holt invariant $\frac{M}{K}$ of 1.5 (unfished population dominated by smaller fish). The results from these simulations demonstrate that the combination of the LB-SPR assessment model with an effort-based harvest control rule has the potential to successfully rebuild an overfished stock back to sustainable levels. However, the research also highlights the trade-off between yield and the probability of the spawning stock declining to low levels, and demonstrates that managers must carefully assess these trade-offs when selecting a SPR target for a data-poor stock.

5.1 Introduction

During its development, fisheries science has tended to focus on large scale stocks and industrial scale fisheries, and fisheries management often relies on technically challenging
mathematical and statistical models to estimate the current stock status and the exploitation rates of a fishery (Hilborn and Walters, 1992). These models often include hundreds of estimated parameters, require substantial amounts of data, are based on numerous assumptions, require considerable technical expertise to develop and run, and are often poorly understood by policy makers and other stakeholders (Hilborn, 2003; Cotter et al., 2004). In the last 15 years, the need to develop simple data-driven harvest policies that are understood by all stakeholders has received increasing recognition (Hilborn, 2003, 2012; Cotter et al., 2004; Kelly et al., 2006).

In addition to the issues arising from the complex nature of modern assessment models, the collection and analysis of the extensive data required for these models can be prohibitively expensive (Berkes et al., 2001). Many fisheries are small-scale and data-poor, and lack the data and the funds required for conventional assessment techniques (Mahon, 1997; Berkes et al., 2001; Stanford et al., 2013). In recent years, research in assessment techniques for data-poor fisheries has increased, and a suite of tools is evolving for scientists and managers to assess and manage stocks with limited data (Kelly et al., 2006; MacCall, 2009; Wayte and Klaer, 2010; Klaer et al., 2012). However, many of these methods still require considerable amounts of data, including a time-series of historical catch, catch-per-unit-effort (CPUE) trends, or information on the age structure of the stock, all of which are difficult to obtain for many data-poor fisheries.

Chapter 3 and Chapter 4 described the development of a model to estimate the spawning potential ratio (SPR) from the length structure of the catch; referred to as the length-based SPR (LB–SPR) model. Numerous SPR reference points have been developed through simulation studies and meta-analyses (Clark, 1993, 2002; Mace and Sissenwine, 1993; Brooks et al., 2010) and SPR reference points have been recognised in international fisheries law for some time (Restrepo and Powers, 1999; Australian Government, 2007). The LB–SPR method has the advantage of requiring only minimal data: a representative length sample of the stock and basic life history information. Information on the length structure of an exploited stock is often one of the cheapest and easiest data sets to collect (Quinn and Deriso, 1999). Furthermore, the basic biological parameters required for the LB–SPR method (see Chapter 3) can either be obtained with relatively simple biological studies, or “borrowed” from other similar species by meta-analysis (see Chapter 2). Because the LB–SPR model has few data requirements and is relatively simple to understand and apply, the method has potential as a valuable tool for the assessment and management of data-poor fisheries.

Fisheries managers often have a range of management objectives, and as a consequence, management decisions almost always involve a trade-off between competing objectives (Hilborn and Walters, 1992; Hilborn, 2007a). For example, management objectives could include maximizing catch and ensuring the size of the stock remains above some predefined biological reference point. Because of the difficulty of conducting large-scale experiments on fisheries to explore the effect of different management choices on fish, computer simulations are often used to develop and test management strategies that meet the various management objectives. Originally developed by the International Whaling Com-
mission, this procedure has become known as management strategy evaluation (MSE), and is now routinely applied to fisheries around the world (Smith, 1994; Sainsbury et al., 2000; Butterworth, 2007; Punt and Ralston, 2007). In contrast to a real-world experiment, within the MSE framework researchers have perfect knowledge of the ‘true’ state of the stock, and can compare the various management choices directly against the benchmark of perfect knowledge. Such an understanding is important for scientists and managers to determine the risks of depleting a stock associated with a particular management or harvest strategy.

In most cases, MSEs are used by managers to identify the most appropriate harvest strategy for a particular species or fishery, and the specific biology of the species and management objectives are usually clearly defined. For example, Punt and Smith (1999) used a MSE framework to develop an understanding of the various trade-offs presented by a range of alternative management procedures, and uncertainty in the biological characteristics, for gemfish (Rexea solandri) on the east coast of Australia. In other cases, MSE is used to test the general applicability and utility of a new assessment or management methodology, with less focus on finding the optimal management procedure for a specific fishery (Wilson et al., 2010; Little et al., 2011; Klaer et al., 2012).

This study follows the latter approach, and uses a MSE framework to develop, test, and compare two effort-based harvest control rules which use the LB–SPR assessment methodology for species with different life histories. The utility of the LB–SPR methodology as a viable management tool for data-poor fisheries, was tested on three species with different life history strategies characterised by a range of $M_k$ ratios, ranging from a ‘typical’ species, well described by the Beverton–Holt life history invariant ratio ($M_k = 1.5$), to a species with a life history more typically associated with marine mammals ($M_k = 0.36$) (Table 5.1; see also Chapter 2). The MSE simulations focused on the important elements identified by previous robustness testings of the LB–SPR (Chapter 4), firstly investigating the performance of the LB–SPR management strategy when faced with non-equilibrium dynamics, and secondly examining the impact of uncertainty in the $M_k$ and $L_\infty$ parameters of the LB–SPR methodology. Furthermore, the study investigates the impact of two different SPR targets, and examines the trade-off between yield and the probability of the stock declining below biologically sustainable levels.

### 5.2 Methods

#### 5.2.1 Management Strategy Evaluation

A typical MSE is comprised of four components: (i) an operating model (OM) that describes the population dynamics, (ii) a data generation model which simulates the collection of data from the fishery, (iii) an assessment model that assesses the stock status, and (iv) a management model that implements a harvest control rule which feeds back to influence the population dynamics (Figure 5.1). The LB–SPR management strategy uses
the estimate of the current SPR from the LB–SPR method, together with an effort-based harvest control rule to iteratively, and indirectly, adjust fishing mortality until the stock stabilises around the target SPR.

5.2.1.1 Operating Model

The population dynamics were modelled with a single-gender, age-structured model, with the assumption that the population is closed with respect to immigration and emigration. To facilitate greater resolution in the generated length data, the time component of the OM was modelled on a quarterly basis (i.e., every three months), with recruitment occurring at the beginning of the first two quarters each year. Recruitment was assumed to be described by the Beverton–Holt stock-recruitment function with log-normally distributed recruitment deviations ($\sigma_r$). The operating model was run for an initial period of 100 years, where the stock was fished down, with constant fishing mortality but variable recruitment, from an unfished state to an initial starting level of $0.25B_{MSY}$. The model was then projected forward for 60 years, with the LB–SPR assessment methodology and harvest control rule applied on an annual basis. The equations for the OM are described in detail in Appendix C, and the associated parameters values for the species simulated in the MSE are summarised in Table 5.1.

5.2.1.2 Data Generation

The data collection model assumed that 5% of the catch was sampled at the end of each quarter. The model had no spatial component, and in each quarter the sampled length
composition was a representative random draw from the entire catch, with the length composition of the catch divided in fifty equally spaced size classes. At the end of each year, the data from the four samples was combined, and used as an input for the LB–SPR model (Figure 5.1). The quarter-annual time-steps allow for greater resolution in the generation of the size data. This is especially the case for shorter lived species, where, on an annual time-scale, there may only be a small number of age classes represented in the catch, which may result in a low resolution size composition. Increasing the temporal resolution to quarter-annual time-steps effectively multiplies the number of age-classes by four, and allows for greater resolution of the generated length structure.

5.2.1.3 Assessment Model

The LB–SPR model, described and tested for robustness in Chapter 3 and Chapter 4, was applied at the end of each year to the sampled length data. The LB–SPR model returned annual estimates of the ratio of fishing to natural mortality ($\frac{F}{M}$), as well as an estimate of the selectivity-at-length, which were used to calculate the estimated annual SPR of the exploited stock (see Chapter 4), which was then used as an input for the harvest control rule (Figure 5.1).

Like many length-based methods, the LB–SPR model is an equilibrium based method, and relies on a number of important assumptions, including: (i) asymptotic selectivity, (ii) growth is adequately described by the von Bertalanffy equation, (iii) both sexes have the same growth curve and sex ratio of catch at parity, or biological parameters and length composition of female fish only, (iv) length-at-age is normally distributed, and (v) natural mortality and growth rates are constant for fish that are vulnerable to the fishery. Furthermore, simulation testing of the LB–SPR model has shown that it is sensitive to non-equilibrium population dynamics and misspecification of the life history parameters (Chapter 4).

5.2.1.4 Harvest Control Rule

An important component of a management strategy evaluation is a harvest control rule that links the management action to the estimate of the stock status (Figure 1). This management strategy evaluation compared the performance of two different effort-based harvest control rules: a linear control rule (HCR 1) and a logarithmic control rule (HCR 2) (Figure 5.2). For each control rule, the level of fishing effort was modified at the beginning of each year from the effort of the previous year by a rule based on the distance of the current estimate of SPR ($SPR_{\text{curr}}$) from the SPR target reference point ($SPR_{\text{targ}}$). Fishing effort was held constant throughout the year (i.e., quarters 2, 3, and 4). The combination of observation and process error means that the estimates of SPR from the LB–SPR method can vary considerably, even when the true SPR remains unchanged (Figure Chapter 4). To account for uncertainty in the estimated SPR, the annual estimates of SPR were smoothed by an exponentially weighted five-year moving average. The estimates of SPR for the first five years of the projection period were not smoothed, and the estimates of SPR from the
LB-SPR model were applied directly to the harvest control rule. To avoid large changes in fishing effort over short periods of time, the maximum change in any year in either direction was set to 30%.

Fishing mortality \((F)\) was assumed to be linearly related to effort \((E)\), with log-normally distributed error on the catchability coefficient \((q)\):

\[
F_t = E_t q e^{\epsilon_q - \sigma_q^2 / 2}
\]  

(5.1)

where \(\epsilon_q \sim N(0, \sigma_q^2)\) and \(\sigma_q = 0.3\). The model was not tuned to real data, and the q parameter was set to an arbitrary value of 0.1. Likewise, the effort was defined on an arbitrary scale, with the initial effort determined from the fishing mortality in the first year (Equation 1). At the beginning of each year the fishing effort at the beginning of each year by the recursive equation:

\[
E_t = E_{t-1} V_t
\]  

(5.2)

where \(V_t\) is the Effort Modifier calculated at the beginning of each year, and determined by the harvest control rule.

The first harvest control rule (HCR 1), was defined by the linear relationship based on the smoothed estimate of SPR \((\text{SPR}_{\text{curr}})\) from the previous year, by:

\[
V_t = \varphi_1 + \frac{1 - \varphi_1}{\text{SPR}_{\text{targ}}} \text{SPR}_{\text{curr}}
\]

where \(\varphi_1\) is a gain parameter that controls responsiveness of the control rule, and \(0 < \varphi < 1\). The value for the gain parameter was set at 0.7, and was chosen by running the model over a range of different values and finding the value that resulted in the SPR reaching the target level in the shortest time, while simultaneously minimising the fluctuations around \(\text{SPR}_{\text{targ}}\).

A linear harvest control rule may not be ideal as the change in effort is a constant proportion of the distance between the current and target SPR, which may promote over-capitalization when the stock is above the SPR target. For this reason, a logarithmic harvest control rule (HCR 2) was also tested, which has a more precautionary approach to managing effort: effort is decreased quickly but only allowed to increase slowly. For HCR 2, the Effort Modifier was defined by the logarithmic function:

\[
V_t = \varphi_2 \log \frac{\text{SPR}_{\text{curr}}}{\text{SPR}_{\text{targ}}}
\]

(5.3)

where \(\varphi_2\) is a gain parameter which was set at 0.15 for all simulations and determined in the same way as the gain parameter for HCR 1.

Once stabilised at the target level by the LB–SPR harvest strategy, this approach effectively results in a constant \(F\) harvest policy and catches would be expected to be an invariant fraction of the population, with annual fluctuations that reflect variability in the available biomass.
Figure 5.2: The two effort-based harvest control rules used in this management strategy evaluation: HCR 1 (solid black line, Equation 3) where the Effort Modifier is a linear relationship to the difference between the estimated and target SPR, and HCR 2 (dashed black line, Equation 4) which has a logarithmic relationship between the ratio of the estimated SPR and target SPR and the resulting value of the Effort Modifier. In this example the target SPR is shown as 0.40. Both control rules had the constraint of a maximum absolute value of the Effort Modifier of 0.3.
5.2.1.5 Test Species

The $\frac{M}{K}$ ratio is important in determining the shape of the unfished size composition, and the biological parameters for the MSE were based on three species that covered a range of $\frac{M}{K}$ ratios (Table 5.1). The three species used in the MSE are: (i) Pacific mackerel (*Scomber japonicus*), a small pelagic that is wide-spread throughout the Indo-Pacific with $\frac{M}{K}$ = 1.5, a population dominated by small individuals and growth that continues through life (Carvalho et al., 2002), (ii) the silver warehou (*Seriolella punctata*), a demersal species caught off south-eastern Australia and New Zealand, with $\frac{M}{K}$ = 0.97, a population with a mix of individuals across all size classes and growth that reaches an asymptote (Day et al., 2012), and (iii) crimson snapper (*Lutjanus erythropterus*) a long-lived reef species that is wide-spread throughout the Indo–West Pacific, with $\frac{M}{K}$ = 0.36, a population with an accumulation of fish at maximum size and growth that asymptotes relatively early in life (McPherson et al., 1992; Newman et al., 2000) (Table 5.1). For simplicity, these species are referred to throughout this study as Species I, II and III respectively. These species were chosen to represent species showing a range of $\frac{M}{K}$ values from the Beverton Holt Life History Invariant (BH–LHI) ratio of 1.5 (Jensen, 1996) to those with a much lower $\frac{M}{K}$ of 0.36 (Table 5.1). The $\frac{M}{K}$ ratio is often assumed to be around 1.5 for many species of teleost, which is likely a result of the early work which focused mainly on Clupeidae and Engraulidae stocks (Beverton, 1963). However, the meta-analysis presented in Chapter 2 found that the $\frac{M}{K}$ values for marine species spanned a much broader range (0.1 to 3.5), with low values found for marine mammals and chondrichthians, as well as a range of teleosts.

For the base case scenarios, both the maturity and selectivity schedules were modelled with a logistic function, with the selectivity-at-length parameters arbitrarily set lower than maturity-at-length for each species (Figure 5.3). However, the impact of dome-shaped selectivity was also investigated, with the selectivity curve modelled with a two-sided curve (Figure 5.3).
Table 5.1: The biological and selectivity parameters for the three test species (Species I: Pacific mackerel *Scomber japonicus*\(^1\); Species II: Silver warehou *Seriolella punctata*\(^2\); Species III: Crimson snapper *Lutjanus erythropterus*\(^3\)) used in the management strategy evaluation of the length-based spawning potential ratio assessment methodology.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Species</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>(L_\infty) (mm)</td>
<td>I</td>
<td>575.2</td>
</tr>
<tr>
<td></td>
<td>II</td>
<td>504.1</td>
</tr>
<tr>
<td></td>
<td>III</td>
<td>584.8</td>
</tr>
<tr>
<td>(CV_{L_\infty})</td>
<td>I</td>
<td>0.1</td>
</tr>
<tr>
<td></td>
<td>II</td>
<td>0.1</td>
</tr>
<tr>
<td></td>
<td>III</td>
<td>0.1</td>
</tr>
<tr>
<td>(M)</td>
<td>I</td>
<td>0.3</td>
</tr>
<tr>
<td></td>
<td>II</td>
<td>0.3</td>
</tr>
<tr>
<td></td>
<td>III</td>
<td>0.14</td>
</tr>
<tr>
<td>(k)</td>
<td>I</td>
<td>0.2</td>
</tr>
<tr>
<td></td>
<td>II</td>
<td>0.31</td>
</tr>
<tr>
<td></td>
<td>III</td>
<td>0.39</td>
</tr>
<tr>
<td>(M_k) ratio</td>
<td>I</td>
<td>1.50</td>
</tr>
<tr>
<td></td>
<td>II</td>
<td>0.968</td>
</tr>
<tr>
<td></td>
<td>III</td>
<td>0.359</td>
</tr>
<tr>
<td>(A_{max})</td>
<td>I</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td>II</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td>III</td>
<td>33</td>
</tr>
<tr>
<td>(L_{50}) (mm)</td>
<td>I</td>
<td>277.8</td>
</tr>
<tr>
<td></td>
<td>II</td>
<td>370</td>
</tr>
<tr>
<td></td>
<td>III</td>
<td>468</td>
</tr>
<tr>
<td>(L_{95}) (mm)</td>
<td>I</td>
<td>308</td>
</tr>
<tr>
<td></td>
<td>II</td>
<td>400</td>
</tr>
<tr>
<td></td>
<td>III</td>
<td>480</td>
</tr>
<tr>
<td>(L_{550}) (mm)</td>
<td>I</td>
<td>194</td>
</tr>
<tr>
<td></td>
<td>II</td>
<td>259</td>
</tr>
<tr>
<td></td>
<td>III</td>
<td>327</td>
</tr>
<tr>
<td>(L_{959}) (mm)</td>
<td>I</td>
<td>246</td>
</tr>
<tr>
<td></td>
<td>II</td>
<td>320</td>
</tr>
<tr>
<td></td>
<td>III</td>
<td>384</td>
</tr>
<tr>
<td>(l_1)</td>
<td>I</td>
<td>250.6</td>
</tr>
<tr>
<td></td>
<td>II</td>
<td>311.7</td>
</tr>
<tr>
<td></td>
<td>III</td>
<td>389.6</td>
</tr>
<tr>
<td>(s_1)</td>
<td>I</td>
<td>45.9</td>
</tr>
<tr>
<td></td>
<td>II</td>
<td>42.9</td>
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<tr>
<td></td>
<td>III</td>
<td>50.7</td>
</tr>
<tr>
<td>(s_2)</td>
<td>I</td>
<td>575.2</td>
</tr>
<tr>
<td></td>
<td>II</td>
<td>403.3</td>
</tr>
<tr>
<td></td>
<td>III</td>
<td>467.8</td>
</tr>
<tr>
<td>(h)</td>
<td>I</td>
<td>0.7</td>
</tr>
<tr>
<td></td>
<td>II</td>
<td>0.7</td>
</tr>
<tr>
<td></td>
<td>III</td>
<td>0.7</td>
</tr>
<tr>
<td>(SPR_{targ})</td>
<td>I</td>
<td>0.39</td>
</tr>
<tr>
<td>(B_{MSY})</td>
<td>II</td>
<td>0.36</td>
</tr>
<tr>
<td>(SPR_{targ})</td>
<td>III</td>
<td>0.36</td>
</tr>
<tr>
<td>(B_{0.55})</td>
<td>I</td>
<td>0.60</td>
</tr>
<tr>
<td>(SPR_{targ})</td>
<td>II</td>
<td>0.60</td>
</tr>
<tr>
<td>(B_{0.55})</td>
<td>III</td>
<td>0.60</td>
</tr>
<tr>
<td>Assumed (\frac{M}{k})</td>
<td>I</td>
<td>1.370</td>
</tr>
<tr>
<td></td>
<td>II</td>
<td>0.757</td>
</tr>
<tr>
<td></td>
<td>III</td>
<td>0.488</td>
</tr>
</tbody>
</table>

Data from: \(^1\)Carvalho et al. 2002; \(^2\)Day et al. 2012; \(^3\)McPherson et al. 1992, Newman et al. 2000
5.2.1.6 Scenarios Considered in the MSE

A total of ten scenarios were considered for each of the three species. Each scenario consisted of a different set of specifications for the operating model. The simulations were repeated using both HCR 1 and HCR 2 (Table 5.2; Figure 5.2).

The base case, Scenario 1, investigated the performance of the LB–SPR harvest control rule with a logistic selectivity pattern, medium recruitment variability ($\sigma_r = 0.6$), with the estimation parameters ($M_k$, $L_\infty$, and $CV_{L_\infty}$) fixed at the true values (Table 5.2). Scenario 2 was identical to the first scenario, but with higher recruitment variability ($\sigma_r = 0.9$). The third scenario looked at the effect of dome-shaped selectivity on the LB–SPR management strategy, with medium recruitment variability and fixed assessment parameters (Figure 5.3, Table 5.2). Scenario 4 included time-varying natural mortality, i.e., $M$ was constant for all age classes in each quarter, but, following the approach of Maunder (2011), varied in each time step as a random variable drawn from a lognormal distribution with a standard deviation of 0.2.

In many data-poor fisheries where the LB–SPR method could be applied, the life history parameters required for the model will be unknown, and Scenario 5 examined the effect of uncertainty in the assessment parameters, $M_k$ and $L_\infty$. Due to the impact of fishing on the length structure of a stock, it is difficult to estimate the $M_k$ ratio from the length composition of an exploited stock (see Chapter 3). However, the $M_k$ ratio has been shown to be less variable across species and family groups than the individual $M$ and $k$ parameters and it may be possible to use meta-analysis or comparative studies to estimate this ratio for a data-poor stock (Beverton 1992, Chapter 2).

For Species I and III (Scomber japonicus and Lutjanus erythropterus) the $M_k$ ratio was assumed to be the mean value of $M_k$ from the Scombridae and Lutjanidae families respectively from data used in the meta-analysis of Chapter 2. This meta-analysis did not contain any other species from the Centrarchidae family (Species II). For this species, the assumed $M_k$ was taken from a biological study of the same species in New Zealand (Horn and Sutton, 1996). The sensitivity tests of the method demonstrated that the model was least impacted by misspecification in the $CV_{L_\infty}$ parameter (Chapter 4), and it was fixed at the true value of 0.1 (Table 5.1).

The LB–SPR model is particularly sensitive to misspecification in the $L_\infty$ parameter (Chapter 4), and care must be taken to estimate a reasonable value for this parameter. Unlike the $M_k$ ratio, the length structure of a stock does contain some information on the $L_\infty$ parameter. For example, it is generally recognised that there is a relationship between the maximum length in the stock ($L_{max}$) and the $L_\infty$ parameter (Pauly, 1984). However, in Chapter 3 it was demonstrated that this relationship is also impacted by the $M_k$ ratio, the distribution of length-at-age, and the exploitation history of the stock. If the $M_k$ ratio is known, or assumed, from meta-analysis or biological studies, it may be possible to estimate the $L_\infty$ parameter from length structure of the stock, which increases the general applicability of the LB–SPR methodology. As the relationship between the maximum observed size and $L_\infty$ is influenced by the assumed $M_k$ value as well as the state of the
exploited stock, a simulation model was used to estimate the relationship between the 95th percentile of observed length in the catch and the assumed $M_k$ ratio, size at full selectivity, and the estimated level of exploitation (see Appendix D). In Scenario 5, the $L_\infty$ parameter was estimated in each year based on the assumed $M_k$, the estimated status of the stock, and the observed length structure of the catch from the previous year, and this estimated value was used as an input for the LB–SPR model.

For this study the assumed management objective was for the spawning stock biomass (SSB) to be at, or fluctuating around, $SSB_{MSY}$. Accordingly, the target reference point ($SPR_{targ}$) was set to $SPR_{MSY}$ for each species. The relationship between $SPR$ and the equilibrium SSB depletion level ($\%SSB_0$) is determined by the steepness parameter (often denoted as $h$) in the Beverton–Holt stock-recruitment model, and can be described by:

$$\%SSB_0 = \frac{4hSPR + h - 1}{5h - 1}$$

If steepness is equal to 1 (i.e., recruitment is completely independent of the size of the spawning stock biomass) then, under equilibrium conditions, the $SSB_0$ and $SPR$ are equivalent (Walters and Martell, 2004; Cordue, 2012).

While once advocated as a target, $F_{MSY}$ is now often considered an upper limit, and when fishing mortality ($F$) is greater than $F_{MSY}$ it is stated that overfishing is occurring (Caddy and McGarvey, 1996; Punt et al., 2014). In addition, previous simulation tests of the LB–SPR model have shown that, in some cases, the estimates of SPR can vary considerably from the true values (see Chapter 4). Consequently, a further five scenarios were examined (Scenarios 6–10), where the simulation tests of the 5 scenarios previously described were repeated with a more conservative target level of spawning stock biomass ($SSB_{0.55}$). This level of $B_{0.55}$ was chosen as it is likely to be above the size that would maximise the yield for many species, while at the same time within the range that is likely to maximise profit (Punt et al., 2014). The corresponding SPR target reference point ($SPR_{targ}$) was calculated for the biomass reference points ($B_{MSY}$ and $B_{0.55}$) for the three species (Table 5.2) The SPR targets for the biomass target of $B_{MSY}$ was 0.36 for Species I and 0.30 for Species II and III, and for the target of $B_{0.55}$ were 0.60 for all three species (Table 5.2).

Two hundred iterations were run for each scenario and each species, and a number of performance measures, described below, were used to evaluate the performance of the harvest strategy.

### 5.2.1.7 Performance Measures

The harvest control rule was developed to return, and maintain, the estimated SPR as close as possible to $SPR_{targ}$. If the harvest control rule performs well, and the estimated SPR is close to the true real static SPR, the spawning stock biomass (SSB) is expected, at equilibrium, to be close to, or fluctuating around $SSB_{targ}$. A number of performance measures were used to compare the performance of the LB–SPR harvest strategy using the two different harvest control rules, and across the different scenarios and species. The median
Table 5.2: The ten scenarios used in the management strategy evaluation of the length-based spawning potential ratio assessment methodology for three test species with different life history strategies. Scenarios 1–5 had a SPR target of SPR\textsubscript{MSY}, and the tests were repeated with a more precautionary SPR target of SPR\textsubscript{0.60} in Scenarios 6–10.

<table>
<thead>
<tr>
<th>Scenario</th>
<th>$\sigma_r$</th>
<th>Selectivity</th>
<th>$M$</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>1, 6</td>
<td>0.6</td>
<td>Logistic</td>
<td>fixed</td>
<td>Base case</td>
</tr>
<tr>
<td>2, 7</td>
<td>0.9</td>
<td>Logistic</td>
<td>fixed</td>
<td>Increased recruitment variability</td>
</tr>
<tr>
<td>3, 8</td>
<td>0.6</td>
<td>Domed</td>
<td>fixed</td>
<td>Dome–shaped selectivity</td>
</tr>
<tr>
<td>4, 9</td>
<td>0.6</td>
<td>Logistic</td>
<td>variable</td>
<td>Variable natural mortality</td>
</tr>
<tr>
<td>5, 10</td>
<td>0.6</td>
<td>Logistic</td>
<td>fixed</td>
<td>$\frac{M}{k}$ ratio estimated from meta-analysis and $L_\infty$ estimated from catch</td>
</tr>
</tbody>
</table>

and 5th and 95th percentiles of the following metrics were used to evaluate the relative performance of the two harvest control rules:

1. The spawning stock biomass in the final year of the projection period (year 60);

2. The SPR in the final year of the projection period (year 60);

3. The catch (relative to MSY) in the final year of the projection period (year 60);

4. The time taken for the SSB to first rebuild to the target level;

5. The catch in the first 10 years of the projection period;

6. The effort variability: the average absolute percentage inter-annual change in effort (%AAV) over the projection period:

$$%AAV = 100 \frac{\sum_{i=2}^{60} |E_i - E_{i-1}|}{\sum_{i=1}^{60} E_i}$$ (5.5)

To evaluate the performance of the LB-SPR effort-based management strategy, the relative error of the estimated model outputs ($\frac{F}{M}$, SPR, and the two selectivity parameters) was calculated for the final year of the projection period. Additionally, to develop an understanding of the behaviour and limitations of the LB-SPR management strategy, the trajectories of the 5th, 50th and 95th percentiles of the relative spawning biomass, the relative catch, the estimated SPR, and the true SPR of the operating model (here termed static SPR, but see Discussion for further details) over the 60 year projection period were examined for each of the 10 scenarios.
5.3 Results

5.3.1 Comparison of the linear and logarithmic harvest control rules

The performance of the two harvest control rules (a linear control rule (HCR 1) and a logarithmic control rule (HCR 2; see Figure 5.2)) are summarised in Tables 5.3, 5.4 and 5.5 for Species I, II and III respectively. For most of the scenarios, the median SSB, SPR and catch in the final year (year 60) was similar between the two harvest control rules (Tables 5.3, 5.4 and 5.5 for Species I, II and III respectively). For example, in the two base case scenarios (Scenario 1; medium recruitment variability, a logistic selectivity pattern, and perfect knowledge of the biological parameters, SPR$_{targ}$ = SPR$_{MSY}$, and Scenario 6; same as Scenario 1 but with SPR$_{targ}$ = SPR$_{0.60}$) the median SSB and median SPR in the final year were slightly above the target level, indicating that both HCR 1 and HCR 2 were successful in rebuilding the overfished stocks back to the target levels (Tables 3, 4 and 5). The median catch in the final year was similar between the two harvest control rules for most of the scenarios, except Scenarios 5 and 10 (see further detail below; Tables 5.3, 5.4 and 5.5). This result suggests that both the linear (HCR 1) and logarithmic (HCR 2) harvest control rules are likely to be successful in rebuilding an overfished stock using the LB-SPR methodology.

There were several notable differences in the performance of the two harvest control rules. The variability in the final SSB, SPR and catch was lower for HCR 2; indicating that this harvest control rule resulted in a more stable performance and less fluctuations in the performance metrics. Compared to HCR 1, HCR 2 caused less dramatic reductions in fishing effort in the first 10 years of the projection period, which resulted in a higher median annual catch for the first 10 years (Tables 5.3, 5.4 and 5.5). However, corresponding to these higher catches in the early years of the projection period, the median time until the SSB first reached the target level was longer for HCR 2 for all 10 scenarios for the three test species (in general by two or three years). The difference in the performance between the two harvest control rules is further emphasized in the average absolute percentage inter-annual change in fishing effort (%AAV) over the projection period. The %AAV was 1-5% lower for HCR 2 across all 10 scenarios for the three test species (Tables 5.3, 5.4 and 5.5), suggesting that the logarithmic harvest control rule (HCR 2) is more suitable to rebuild an overfished stock while simultaneously minimizing variability in the annual fishing effort and catch. However, there is a clear trade-off between the rebuilding time and the amount of variability in fishing effort and catch. As the logarithmic harvest control rule (HCR 2) appeared to perform better than the linear harvest control rule (HCR 1), the following results focus only on the performance of the LB-SPR harvest strategy using HCR 2.
Table 5.3: The summary statistics comparing the performance of the LB-SPR assessment method with two different effort-based harvest control rules for Species I (Pacific mackerel *Scomber japonicus*), showing the median and 5th and 95th percentiles of the spawning stock biomass (SSB), the static SPR, and the relative catch in the final year of the projection period (Year 60), as well as the time to first reach the target SSB, the relative catch in the first 10 years of the projection period, and the absolute average variation (%AA V) in fishing effort for a) Scenarios 1 – 5 and b) Scenarios 6 – 10.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Scenarios 1 – 5</th>
<th>Scenarios 6 – 10</th>
</tr>
</thead>
<tbody>
<tr>
<td>Median (5th and 95th percentiles) for Scenario</td>
<td></td>
<td></td>
</tr>
<tr>
<td>a) Target SPR = 0.39</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Time to Target SSB (years)</td>
<td>12 (8, 18)</td>
<td>15 (11, 19)</td>
</tr>
<tr>
<td>Relative Catch (first 10 years)</td>
<td>0.50 (0.33, 0.76)</td>
<td>0.42 (0.26, 0.72)</td>
</tr>
<tr>
<td>%AA V (Effort)</td>
<td>4.18 (3.34, 5.02)</td>
<td>7.24 (6.50, 8.03)</td>
</tr>
<tr>
<td>b) Target SPR = 0.60</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Time to Target SSB (years)</td>
<td>16 (11, 26)</td>
<td>17 (11, 26)</td>
</tr>
<tr>
<td>Relative Catch (first 10 years)</td>
<td>0.42 (0.26, 0.71)</td>
<td>0.42 (0.24, 0.74)</td>
</tr>
<tr>
<td>%AA V (Effort)</td>
<td>10.30 (8.50, 12.30)</td>
<td>11.06 (8.93, 13.83)</td>
</tr>
</tbody>
</table>

Legend:
- **SSB** - Spawning Stock Biomass
- **HCR** - Harvest Control Rule
- **AV** - Assessment Version
- **AV (Effon)** - Assessment Method
- **First 10 years** - Relative Catch (%)
Table 5.4: The summary statistics comparing the performance of the LB-SPR assessment method with two different effort-based harvest control rules for Species II (Silver warehou *Seriolella punctata*), showing the median and 5th and 95th percentiles of the spawning stock biomass (SSB), the static SPR, and the relative catch in the final year of the projection period (Year 60), as well as the time to first reach the target SSB, the relative catch in the first 10 years of the projection period, and the absolute average variation (%AAV) in fishing effort for a) Scenarios 1 – 5 and b) Scenarios 6 – 10.

<table>
<thead>
<tr>
<th>Variable</th>
<th>HCR</th>
<th>Species I – Median (5th and 95th percentiles) for Scenario</th>
<th>Scenarios 1–5</th>
<th>Scenarios 6–10</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>a) Target SPR = 0.39</td>
<td>b) Target SPR = 0.60</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>(SSB&lt;sub&gt;Targ&lt;/sub&gt; = 0.32)</td>
<td>(SSB&lt;sub&gt;Targ&lt;/sub&gt; = 0.55)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>SSB (Year 60)</td>
<td></td>
<td></td>
<td>0.30 (0.18, 0.47)</td>
<td>0.32 (0.22, 0.45)</td>
</tr>
<tr>
<td>Static SPR (Year 60)</td>
<td></td>
<td></td>
<td>0.37 (0.16, 0.59)</td>
<td>0.37 (0.25, 0.53)</td>
</tr>
<tr>
<td>Relative Catch</td>
<td></td>
<td></td>
<td>0.43 (0.26, 0.62)</td>
<td>0.43 (0.31, 0.58)</td>
</tr>
<tr>
<td>Time to Target SSB (years)</td>
<td></td>
<td></td>
<td>14 (11, 19)</td>
<td>14 (11, 19)</td>
</tr>
<tr>
<td>Relative Catch (first 10 years)</td>
<td></td>
<td></td>
<td>0.41 (0.23, 0.75)</td>
<td>0.41 (0.23, 0.75)</td>
</tr>
<tr>
<td>%AAV (Effort)</td>
<td></td>
<td></td>
<td>7.75 (5.96, 10.36)</td>
<td>9.96 (7.44, 13.05)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>7.66 (5.95, 10.37)</td>
<td>9.96 (7.44, 13.05)</td>
</tr>
</tbody>
</table>
Table 5.5: The summary statistics comparing the performance of the LB-SPR assessment method with two different effort-based harvest control rules for Species III (Crimson snapper *Lutjanus erythropterus*), showing the median and 5th and 95th percentiles of the spawning stock biomass (SSB), the static SPR, and the relative catch in the final year of the projection period (Year 60), as well as the time to first reach the target SSB, the relative catch in the first 10 years of the projection period, and the absolute average variation (%AA V) in fishing effort for a) Scenarios 1 – 5 and b) Scenarios 6 – 10.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Scenarios 1 – 5 (Target SPR = 0.39)</th>
<th>Scenarios 6 – 10 (Target SPR = 0.60)</th>
</tr>
</thead>
<tbody>
<tr>
<td>SSB Targ</td>
<td>0.32 (0.20, 0.48)</td>
<td>0.55 (0.37, 0.73)</td>
</tr>
<tr>
<td>Static SPR Year 60</td>
<td>0.42 (0.25, 0.59)</td>
<td>0.56 (0.41, 0.71)</td>
</tr>
<tr>
<td>Relative Catch Year 60</td>
<td>0.89 (0.51, 1.39)</td>
<td>0.82 (0.44, 1.40)</td>
</tr>
<tr>
<td>Time to Target SSB Years</td>
<td>15 (11, 21)</td>
<td>20 (15, 26)</td>
</tr>
<tr>
<td>Relative Catch First 10 Years</td>
<td>0.42 (0.27, 0.69)</td>
<td>0.33 (0.19, 0.68)</td>
</tr>
<tr>
<td>%AA V (Effort)</td>
<td>8.37 (6.61, 11.46)</td>
<td>11.69 (9.66, 13.61)</td>
</tr>
</tbody>
</table>

Note: Time to reach SSB is measured in years, and the relative catch is calculated as a percentage of the median catch.
5.3.2 Relative error in the parameters estimated by the LB-SPR method

The relative error in the estimated model outputs for the final year of the projection period (year 60) for the three test species are shown in Figure 5.4. The median relative error in the two selectivity parameters \((S_{L_{50}}\) and \(S_{L_{95}}\)) was close to zero for all 10 scenarios for the three test species (Figure 5.4a and b, 4e and f, and 4i and j, for Species I, II and III respectively).

Species I (\(S. japonicus\)) had the highest variability in relative error in the estimated selectivity parameters, particularly for Scenarios 2 and 7 (increased recruitment variability) (Figure 5.4a and b). For Species I, the median relative error in the estimate of \(F_M\) in the final year was close to zero for Scenarios 1, 2, 4, 6, 7 and 9 (Figure 5.4c). Corresponding to these estimates, the median relative error in SPR was also close to zero for these scenarios (Figure 5.4d). As expected, the relative error in \(F_M\) was higher for the two scenarios with dome-shaped selectivity (Scenarios 3 and 8; Figure 5.4c), and the SPR was consistently under-estimated in these scenarios (Figure 5.4d). For Species I, the model performed similarly in Scenarios 5 and 10 (empirical estimation of \(M_k\) and \(L_\infty\)) as in Scenarios 3 and 8, respectively, with \(F_M\) over-estimated and SPR under-estimated considerably (Figure 5.4d).

In general, the results of the LB–SPR model in the final year were similar for Species II (\(S. punctata\)) as for Species I (Figure 5.4e, f, g and h). However, the relative error in the selectivity parameters was lower for Species II than for Species I (Figure 5.4e and f). The relative error in \(F_M\) was most pronounced for Scenarios 5 and 10 (empirical estimation of \(M_k\) and \(L_\infty\)) with the median \(F_M\) over-estimated by approximately 500% and 800% respectively for these two scenarios (Figure 5.4g). Likewise, the relative error in the estimates of SPR for these scenarios demonstrates that the model under-estimated SPR considerably for these scenarios (Figure 5.4d).

The two selectivity parameters were well estimated for Species III (\(L. erythropterus\)), with the median relative error generally less than 3% and most estimates within 20% of the true values (Figure 5.4i and j). As with Species I and II, the LB-SPR model tended to over-estimate \(F_M\) and under-estimate the SPR for the two scenarios with dome-shaped selectivity (Scenarios 3 and 8; Figure 5.4k and l). For Scenarios 5 and 10, the model performed markedly different for Species III compared to the other two species, with \(F_M\) in general under-estimated, and SPR over-estimated (Figure 5.4k and l). The difference in performance between the three species for these scenarios is discussed in more detail below.

5.3.3 Performance of the LB-SPR management strategy

For the base case (Scenario 1; medium recruitment variability, a logistic selectivity pattern, and perfect knowledge of the biological parameters; Table 5.2), the LB-SPR harvest control rule successfully rebuilt the depleted stocks, with the median SSB in each stock initially rebuilding above the target in 15-18 years, before gradually being reduced back towards the target (solid lines Figure 5.5a, f and k). The SSB of Species I (solid lines...
Figure 5.4: Boxplots (central line: median; box: 25% and 75% quantiles; whiskers: greatest observation less than 1.5 times the interquartile range from the median) showing the distribution of relative error in the outputs of the LB–SPR model in the final year of the projection period: the length at 50% and 95% selectivity ($S_{L50}$ and $S_{L95}$), the relative fishing mortality ($\frac{F}{M}$) ratio, and the spawning potential ratio (SPR) for Species I (a–d), Species II (e–h), and Species III (i–l). For purposes of clearer plotting, the extreme outliers have not been shown.
Figure 5.5a), Species II (solid lines Figure 5.5f), and Species III (solid lines Figure 5.5k) stabilised at the target level around year 45, with the final median SSB close to the target level (Tables 5.3, 5.4 and 5.5). The median catch followed a similar trajectory for the three species, with the HCR 2 initially decreasing catches for the first 5–10 years, and then a gradual increase in catch as the biomass of the stocks rebuilt to higher levels (Figure 5.6a, f and k for Species I, II and III respectively). At the end of the projection period (year 60) the median catch for the three species had stabilised close to the target level (MSY; Tables 5.3, 5.4 and 5.5; solid lines Figure 5.6a, f and k). The final median estimated SPR was similar to the median static SPR for all three species for the first scenario, with the median SPR rebuilding from low levels, and initially over-shooting the target level before gradually decreasing back towards the SPR target (solid lines Figure 5.7a, f and k and Figure 5.8a, f and k for the estimated and true static SPR for Species I, II and III respectively; Tables 5.3, 5.4 and 5.5). However, as mentioned previously, the trend of the estimated SPR did not follow the initial static SPR during the rebuilding phase (solid lines Figure 5.7a, f and k and Figure 5.8a, f and k).

When the alternative, more conservative, target reference point of SPR=0.60 was used (Scenario 6), the logarithmic harvest control rule rebuilt the SSB of three species above the target level within 15 to 20 years (dashed lines Figure 5.5a, f and k). The median SSB over all three species initially overshot the target level (SSB0.55) and gradually decreased back towards the target level (dashed lines Figure 5.5a, f and k). However, by the end of the projection period, the median SSB was still above the target level for all three species (Tables 5.3, 5.4 and 5.5). The catches for Scenario 6 followed a similar trajectory for the three species, with an initial marked decrease in catch in the first several years, followed by a gradual increase in catch throughout the projection period (dashed lines, Figure 5.6a, f and k). The final median catch for the three species stabilised around 70-80% of MSY (Tables 5.3, 5.4 and 5.5). Similar to Scenario 1, the estimated SPR tended to follow the trend of the SSB, and initially lagged behind the trend of the static SPR (dashed lines Figure 5.7a, f and k and Figure 5.8a, f and k for the estimated and true static SPR for Species I, II and III respectively). The estimated SPR in the final year was close to the true static SPR for all three years, with the stock stabilised slightly above the SPR target of 0.60 (Tables 5.3, 5.4 and 5.5).

The model performance for Scenarios 2 and 7 (increased recruitment variability) was similar to the behaviour in Scenarios 1 and 6 respectively, although with increased variation in the SSB, catch, and estimated and true static SPR (solid lines Figures 5.5, 5.6, 5.7 and 5.8b, g and l respectively). For Scenario 2, the final median catch for the three species was close to, but slightly below, the target level of MSY (solid lines Figure 5.6b, g and l; Tables 5.3, 5.4 and 5.5). However, the final median SSB was very close to the target level for all three species for this scenario (solid lines Figure 5.5b, g and l; Tables 5.3, 5.4 and 5.5). Likewise, for Scenario 7, with the more precautionary SPR target, the final median SSB was similar to that of Scenario 6, stabilising slightly above the target for all three species (dashed lines Figure 5.5b, g and l; Tables 5.3, 5.4 and 5.5).
As expected from the results of previous sensitivity tests (Chapter 4), the presence of a dome-shaped selectivity pattern (Scenarios 3 and 8) resulted in precautionary behaviour of the LB–SPR management strategy, with the SSB of all three species rebuilding well above the target levels (solid and dashed lines Figure 5.5c, h and m for Scenario 3 and 8 and Species I, II and III respectively). After the initial rebuild, which overshot the target level considerably, the median SSB of the three species in Scenario 3 began to decline back towards the target level (solid lines Figure 5.5c, h and m). However, by the end of the projection period the final median SSB was considerably above the target (solid lines Figure 5.5c, h and m; Tables 5.3, 5.4 and 5.5). After the initial decline, the catch of the three species continued to increase, and the final median catch was close to the target level of MSY (solid lines Figure 5.6c, h and m; Tables 5.3, 5.4 and 5.5). Throughout the projection period the median estimated SPR of the three species was considerably lower than the actual static SPR, indicating that the LB–SPR method tended to under-estimate the SPR (solid lines Figures 5.7 and 5.8c, h and m; Tables 5.3, 5.4 and 5.5).

The combination of the alternative target reference point (SSB0.55) and dome-shaped selectivity (Scenario 8) resulted in very precautionary behaviour of the model, with the median SSB of the three stocks rebuilding well above the target level (dashed lines Figure 5.5c, h and m; Tables 5.3, 5.4 and 5.5). Likewise, the catch for all three species was low, with the final median catch much below MSY (Figure 5.6c, h and m; Tables 5.3, 5.4 and 5.5). The median estimated SPR of the three species was close to the target level by the end of the projection period, indicating that the harvest control rule had iteratively adjusted fishing effort until the estimated SPR of the stock stabilised around the target level (Figure 5.7c, h and m). However, as the LB–SPR model consistently under-estimated the actual static SPR throughout the time-series, the actual static SPR was considerably higher than the target level (dashed lines Figure 5.8c, h and m; Tables 5.3, 5.4 and 5.5).

The inclusion of time-varying natural mortality (Scenarios 4 and 9) had little impact on the performance of the LB-SPR harvest control rule, with the model behaving similarly to the base case (Scenarios 1 and 6 respectively) for all three species (Figures 5.5, 5.6, 5.7 and 5.8d, i and n for SSB, catch, estimated and true static SPR for Species I, II and III respectively; Tables 5.3, 5.4 and 5.5).

The performance of the model varied considerably among the three species for the final two scenarios (Scenarios 5 and 10). In Scenario 5, the median SSB of Species I rebuilt rapidly to approximately 0.8SSB0 in just over 20 years, before decreasing and stabilising around 0.55SSB0 in the final years of the projection period (solid lines Figure 5.5e; Table 5.3). Correspondingly, the median catch of Species I decreased initially, before increasing close to the target level of MSY by the final year (solid line Figure 5.6e; Table 5.3). The estimated SPR was relatively variable, and initially increased well above the target level before declining back towards the target SPR in the final years of the projection period (solid line Figure 5.7e). However, the trajectory of the true static SPR indicates that the LB–SPR model under-estimated the SPR for the entire projection period, with the final static SPR stabilising around SPR=0.60, well above the target level of SPR=0.36 (Figure
Figure 5.5: The trajectories of the relative spawning stock biomass (Rel. SSB) for Scenarios 1–5 (left to right; median solid line and 5th and 95th percentiles light grey) and Scenarios 6–10 (left to right; median dash line and 5th and 95th percentiles dark grey) for Species I *Scomber japonicus* ($\frac{M}{F} = 1.5$, a–e), Species II *Seriolella punctata* ($\frac{M}{F} = 0.97$, f–j), and Species III *Lutjanus erythropterus* ($\frac{M}{F} = 0.36$, k–o) projected for 60 years. For Scenarios 1–5 the target SPR was SPR$_{MSY}$, while for Scenarios 6-10 target SPR was 0.60. The corresponding targets for the SSB (5.4) are shown for Scenarios 1–5 and Scenarios 6–10 as dashed and dotted horizontal lines respectively.
Figure 5.6: The trajectories of the relative catch (Rel. Catch) for Scenarios 1–5 (left to right; median solid line and 5th and 95th percentiles light grey) and Scenarios 6–10 (left to right; median dash line and 5th and 95th percentiles dark grey) for Species I *Scomber japonicus* (*$M_k$* = 1.5, a-e), Species II *Seriolella punctata* (*$M_k$* = 0.97, f-j), and Species III *Lutjanus erythropterus* (*$M_k$* = 0.36, k-o) projected for 60 years. For Scenarios 1–5 the target SPR was SPR$_{MSY}$, while for Scenarios 6–10 target SPR was 0.60. The maximum sustainable yield (MSY) is shown as a dashed line (Rel. Catch = 1).

The variability in the annual estimates of SPR can be attributed to the variation in the empirically estimated $L_\infty$ parameter, which was over-estimated by over 15–20% in the years where the stock was rebuilding (Figure 5.9a). The assumed value of $M_k$ for this species was also lower than the true value, which further added to the over-estimate of $F_M$ and the under-estimate of the SPR (Figures 5.7 and 5.8e; Table 5.3). The impact of the miss-specification in the $M_k$ and $L_\infty$ parameters was even more pronounced when the more conservative SPR target was used (Scenario 10) for Species I, with the median SSB rebuilding well above the target level, and stabilising close to 0.90SSB$_0$ (dashed line Figure 5.5e; Table 5.3). The relative error in the empirically estimated $L_\infty$ parameter was similar in Scenario 10 to that in Scenario 5 for Species I, with an initial over-estimation of the asymptotic length during the rebuilding phase, before stabilising close to the true value (Figure 5.9b). Corresponding to the high level of spawning biomass, the catch for Scenario 10 remained low, and did not increase after the initial decrease in the first several years (dashed line Figure 5.5e; Table 5.3). The trajectory of the estimated SPR followed a similar pattern to Scenario 5, with an initial decline in the first 10–12 years (corresponding to the over-estimation of the $L_\infty$ parameter) before rebuilding and stabilising around the target level (dashed line Figure 5.7e). However, the model consistently under-estimated the SPR, and the true static SPR rebuilt quickly and stabilised much higher than the target level (dashed line Figure 5.8e; Table 5.3).
Figure 5.7: The trajectories of the estimated SPR (Est. SPR) for Scenarios 1–5 (left to right; median solid line and 5th and 95th percentiles light grey) and Scenarios 6–10 (left to right; median dash line and 5th and 95th percentiles dark grey) for Species I *Scomber japonicus* \( \left( \frac{M}{T} = 1.5, \text{a-e} \right) \), Species II *Seriolella punctata* \( \left( \frac{M}{T} = 0.97, \text{f-j} \right) \), and Species III *Lutjanus erythropterus* \( \left( \frac{M}{T} = 0.36, \text{k-o} \right) \) projected for 60 years. For Scenarios 1-5 the target SPR was SPR\(_{MSY}\), while for Scenarios 6–10 target SPR was 0.60, which are shown for Scenarios 1–5 and Scenarios 6–10 as dashed and dotted horizontal lines respectively.
Figure 5.8: The trajectories of the static SPR (equilibrium SPR of the operating model) for Scenarios 1–5 (left to right; median solid line and 5th and 95th percentiles light grey) and Scenarios 6–10 (left to right; median dash line and 5th and 95th percentiles dark grey) for Species I *Scomber japonicus* ($\frac{M}{K} = 1.5$, a-e), Species II *Seriolella punctata* ($\frac{M}{K} = 0.97$, f-j), and Species III *Lutjanus erythropterus* ($\frac{M}{K} = 0.36$, k-o) projected for 60 years. For Scenarios 1–5 the target SPR was SPR$_{MSY}$, while for Scenarios 6–10 target SPR was 0.60, which are shown for Scenarios 1–5 and Scenarios 6–10 as dashed and dotted horizontal lines respectively.

The median SSB for Species II in Scenario 5 rapidly rebuilt well above the target level and stabilised around 0.77SSB$_0$ (solid line Figure 5.5j; Table 5.4). Likewise, the catches remained low throughout the entire projection period, with the final median catch around 55% of MSY (Figure 5.6j; Table 5.4). Similar to Species I, the $L_\infty$ parameter was initially over-estimated by 10–15% during the rebuilding phase, with the relative error in the estimates of the $L_\infty$ parameter stabilising around 2.5% greater than the true value (Figure 5.9c).

The estimated SPR remained low during the first 20 years of the projection period, before increasing and stabilising above the target level in the final 40 years (solid line Figure 5.7j). Similar to Species I, the true static SPR was under-estimated throughout the time-series, with the final SPR well above the target level (solid line Figure 5.8j; Table 5.4). The model behaved similarly when the alternative SPR target was used (Scenario 10), with the final SSB well above the target level, and low catches throughout the projection period (dashed lines Figures 5.5j and 5.6j; Table 5.4). The relative error in the estimated $L_\infty$ parameter followed a similar pattern to Scenario 5 for the same species, with an initial over-estimation of the parameter before stabilising slight above the true value (Figure 5.9d). The estimated SPR gradually increased but did not reach the target level in the 60 year projection period (dashed line Figure 5.7j), while the true static SPR increased to well above the target (dashed line Figure 5.8j; Table 5.4).
For Scenarios 5 and 10, Species III performed markedly different than Species I and II, with the LB–SPR model typically under-estimating $\frac{F}{M}$ and over-estimating the SPR (solid and dashed lines Figures 5.7o and Figure 5.8o for Scenario 5 and Scenario 10 respectively). In Scenario 5, the SSB gradually rebuilt in the first 20 years, before decreasing and stabilising below the target level (solid line Figure 5.5o; Table 5.5). Unlike Species I and II, the $L_\infty$ parameter was well estimated throughout the time-series, with the relative error typically less than 5% for both Scenario 5 and Scenario 10 (Figure 5.9e and f). The median catch for Scenario 5 was close to, but slightly below, MSY (solid line Figure 5.6o; Table 5.5). The estimated SPR increased to above the target level in the first 20–25 years, before declining down towards the target level in the last several years (solid line Figure 5.7o). The true static SPR increased initially before stabilising very close to the target level (solid line Figure 5.8o; Table 5.5). Similar behaviour was observed with the more conservative SPR target (Scenario 10), with the SSB increasing to slightly above the target level in just over 20 years, before declining below the target level in the last several years of the projection period (dashed line Figure 5.5o; Table 5.5). Likewise, the median catch for Scenario 10 decreased initially, before increasing and stabilising slightly below MSY (dashed line Figure 5.6o; Table 5.5). The SPR was over-estimated throughout most of the time-series, with the final estimated SPR slightly above the target level (dashed line Figure 5.7o) while the true static SPR in the final year was slightly below the target level (dashed line Figure 5.8o; Table 5.5).

5.4 Discussion

The results from the management strategy evaluation of the length-based spawning potential ratio (LB–SPR) assessment model and an effort-based harvest control rule revealed that, under certain conditions, this methodology is able to rebuild an overfished stock back to sustainable levels, while still allowing relatively stable effort in the fishery. The LB–SPR approach combined with a simple effort-based control rule requires little data compared with other stock assessment models, and uses a simple procedure to iteratively drive fishing effort to an appropriate level that results in the SPR and spawning stock biomass stabilising at the target levels. Such an approach may be valuable in data-poor situations, where there is little biological information on the stock, or the history of catches and exploitation rates of the fishery. With few data and technical requirements, the combination of the LB–SPR assessment model and an effort-based harvest control rule described in this chapter offers a simple and transparent methodology for an initial quantitative assessment of an exploited stock, and provides fisheries managers and other stakeholders with a framework for beginning to manage a data-poor fishery.

The value of a specific harvest control rule depends on the particular objectives of management in different situations. In some cases, there may be conflicts in the various management objectives, and management strategy evaluation can be used to identify the trade-offs among objectives for any chosen strategy (Sainsbury et al., 2000; Wiedenmann et al.,
Figure 5.9: Boxplots (central line: median; box: 25% and 75% quantiles; whiskers: greatest observation less than 1.5 times the interquartile range from the median) showing the distribution of relative error in the estimated $L_\infty$ in each year for Species I, II and III in Scenario 5 ($\text{SPR}_{\text{targ}} = \text{SPR}_{\text{MSY}}$: a, c, and e respectively) and in Scenario 10 ($\text{SPR}_{\text{targ}} = 0.60$: b, d, and f respectively). As a visual aid, horizontal dashed lines depicting zero relative error have been added to each plot.
2013). For example, both of the harvest control rules used in this MSE were successful, on average, in rebuilding the overexploited stocks back to or above the target levels. However, the logarithmic control rule (HCR 2), with its fast-down/slow-up approach for controlling changes in fishing effort (Figure 5.2), resulted in less variation in the SSB and lower interannual variation in fishing effort. Yet, the median time for the SSB to rebuild back to the target level was longer with HCR 2 compared to the more aggressive decrease in fishing effort prescribed by HCR 1 when the estimated SPR was below the target (Figure 5.2). In this study only one value was used for the gain parameter for HCR 1 and HCR 2 respectively across all species and scenarios. Modifying the gain parameters would have resulted in different behaviour of the model by changing the slope of the control rule in HCR 1 and the curvature of the control rule in HCR 2, which would lead to a further trade-off in catch variability and rebuilding time. While HCR 2 appeared to work best in this MSE, the optimal parameterization of the harvest control rule for a particular fishery would likely depend on the biological characteristics and life-history traits of the targeted species, as well as the specific objectives of the management and characteristics of the fishery, and should be explored with a case-specific simulation study (Sainsbury et al., 2000; Deroba and Bence, 2008; Wiedenmann et al., 2013).

The MSE demonstrated the potential use of the LB–SPR approach for three species with a diverse range of life histories. The $\frac{M}{\tau}$ ratio determines the shape of the length composition of an unfished stock (Chapter 2), and is an important parameter for the LB–SPR methodology. The three species used in this MSE had $\frac{M}{\tau}$ ratios that ranged from 1.5 (Species I Scomber japonicus), a species where unfished stocks are dominated by small sized individuals and large animals are relatively rare, to 0.36 (Species III Lutjanus erythropterus), where the unfished length composition is expected to be comprised of almost entirely adult sized animals (see Chapters 2 and 3). These species represent a range of life histories that are common in marine species, although the $\frac{M}{\tau}$ ratios for a number of species are considerably greater than 1.5 (e.g., up to 3.5; Chapter 2).

The species examined in this study were relatively long-lived (maximum age of 15–33 years; Table 5.1). The performance of the LB–SPR harvest strategy has not, however, been examined in detail for shorter lived species. If the $\frac{M}{\tau}$ ratio of two species with very different life spans and maximum sizes are the same, the relative shape of the unfished length structure (i.e., length standardized to maximum length) is expected to be identical (see Chapters 2 and 3). This result means that, in theory, the LB–SPR methodology should perform similarly across a range of different lifespans, provided that the sampling of the length composition is scaled to the lifespan of the animal. For example, for a short-lived species that lives for a maximum of one or two years, such as a penaeid prawn (=shrimp) or small pelagic teleost, an annual sample of the length structure would be strongly influenced by the variation in recruitment, and is unlikely to be useful for the LB–SPR method. More frequent sampling of the length data (e.g., monthly) and then aggregating the data across an entire year would, assuming fishing mortality is relatively constant throughout the year, provide a more valuable dataset for the LB–SPR method. One of the main underlying
assumptions of the LB–SPR model is that the length frequency data is representative of the exploited stock, and the sampling regime and length data from short-lived species should be carefully evaluated before applying the LB–SPR management strategy.

The simulations in Chapter 4 demonstrated that length data from a fishery with dome-shaped selectivity results in precautionary estimates of SPR from the LB-SPR model (see also Tables 5.3, 5.4 and 5.5). One of the main assumptions of the LB–SPR method is that the length data is representative of the exploited stock, and the model interprets the absence of large fish in the sample as evidence of high fishing mortality, consequently over-estimating $\frac{F}{M}$ and under-estimating SPR. It may be possible to modify the LB–SPR model to include dome-shaped selectivity (see Discussion in Chapter 4). However, understanding the shape of dome-shaped selectivity patterns is notoriously difficult, and is not likely to be possible to do this for the data-poor fisheries that this method was developed for. If dome-shaped selectivity was suspected or the fishery-dependent data was poor quality, it may be possible to use the length data collected from a fishery-independent survey as input into the LB–SPR model.

Although the LB–SPR method under-estimated SPR, and the final SSB was higher than the target, the final median relative catch for three species in Scenario 3 was still relatively high; $\sim 0.9$MSY, especially for HCR 2 (Tables 5.3, 5.4 and 5.5). Hilborn (2010) defines catches that are at least 80% of MSY as “Pretty Good Yield”, and shows that a small reduction in potential yield from MSY significantly decreases the probability of recruitment overfishing. This flat-topped property of the yield curve means that despite the precautionary performance of the LB–SPR assessment model, the total catches were not reduced greatly below MSY.

When the higher SPR target was used (i.e., $\text{SPR}_{60}$; Scenarios 6 to 10), the stocks rebuilt to a higher SSB and had a lower probability of declining to critically low levels (Figure 5.5). However, under such conditions, the total catch is also likely to be considerably less than the maximum potential yield, as the LB–SPR management strategy typically rebuilds the stock above $\text{SSB}_{\text{MSY}}$ and controls fishing effort so that catches are below MSY; particularly for the scenario with dome-shaped selectivity (Scenario 8; all three species) and the case where the parameters for the LB–SPR method were estimated (Scenario 10; Species I and II; Figure 5.6). This demonstrates the importance of choosing an appropriate SPR target reference point for the LB–SPR management strategy, and highlights that managers must consider the relative importance of the management objectives when considering the trade-off between increased catch and reducing the probability of the stock declining to unsustainable levels.

The results of the simulations from Scenarios 5 and 10 are perhaps the most interesting as they reflect the more realistic situation in data-poor fisheries, where the parameters for the LB–SPR assessment model are not known with any certainty. These results show that the assumption of the $\frac{M}{k}$ ratio plays an important role in both the estimation of $L_\infty$ and the performance of the LB–SPR methodology. Deciding on appropriate values of the parameters is critical to the successful application of the LB–SPR method (see Chapter
4). The different behaviour of the model for the three species in these scenarios can be attributed to the different error in the assumed parameters for the LB–SPR model. The assumed $M_k$ ratios for Species I and II were less than the true values (8.6% and 22%), which leads to precautionary estimates from the LB–SPR method (see Chapter 4). In contrast, the assumed $M_k$ ratio for the third species was higher than the true value (by 36%), resulting in over-estimates of the SPR. Of course, without knowledge of the true values of these ratios, it is difficult to know how biased these values are.

In many data-poor fisheries the biological parameters required for the LB–SPR method may not be available for a local stock, and the only alternative may be to borrow information from other stocks or studies. For example, the FishBase database (Froese and Pauly, 2000) provides easily accessible estimates of biological parameters for a large number of fish species. Furthermore, FishBase offers a Life–History Tool that estimates unknown parameters using empirical relationships (Froese and Binohlan, 2000; Binohlan and Froese, 2009). However, while FishBase is a valuable and important tool, fisheries scientists should be wary of the indiscriminate borrowing of parameters from other stocks or regions, particularly when using the estimates provided by the Life–History Tool (Thorson et al., 2013). Obtaining locally derived empirical data has important consequences for many stock assessment methods. For example, by using local estimates of biological parameters for the dusky shark (*Carcharhinus obscurus*) in west Australia, McAuley et al. (2007) showed that the species was more vulnerable to overexploitation compared to the initial assessments that used values from the more productive waters of South Africa (Simpfendorfer, 1999). This is further emphasized by the results of the meta-analysis presented in Chapter 2, which shows the variability in the life-history ratios of fish, with $M_k$ ranging from 0.1 up to 3.5, considerably different to the default value of 1.5 often assumed for data-poor stocks. This highlights the importance of, where possible, high quality biological studies for data-rich species and stocks, and meta-analysis and comparisons with other stocks of the same species to determine appropriate starting estimates of the biological parameters for the LB-SPR method (e.g., Froese and Pauly, 2000, and Chapter 2).

The algorithm used to estimate $L_\infty$ from the length structure of the catch tended to over-estimate $L_\infty$, especially for Species I and II. This over-estimation is likely to be caused, at least in part, by the error in the assumed $M_k$ ratio, especially for Species I and II where the assumed values were considerably lower than the true (see Chapters 3 and 4). The estimation of $L_\infty$ is an important challenge for this method, especially for species with low $M_k$, as the LB–SPR model under-estimates SPR when the assumed $L_\infty$ is higher than the true value, and over-estimates SPR when the assumed $L_\infty$ is lower than the true value (Chapter 4). However, the $L_\infty$ parameter is also likely to be more easily estimated from length data for species with low $M_k$ as this species tend to have a high proportion of animals at or near asymptotic size (Chapter 3). The relationship between $L_{\text{max}}$ and $L_\infty$ is primarily a function of the $M_k$ ratio, and as the value of the $M_k$ increases above 1.5, typical of species with indeterminate growth and size failing to asymptote, the biological significance of the $L_\infty$ parameter becomes increasingly vague (see Chapter 3). Therefore, the $L_\infty$ parameter
is expected to be more difficult to estimate using empirical methods for species with a high $\frac{M}{K}$ ratio. A reasonable estimate of the $L_\infty$ parameter is essential for the satisfactory performance of the LB–SPR methodology. This parameter is unlikely to be known with any certainty in data-poor fisheries. The ratio between the length at maturity ($L_m$) and $L_\infty$ ($\frac{L_m}{L_\infty}$) is relatively consistent across species groups, and several empirical methods have been developed to estimate $L_\infty$ from $L_{\text{max}}$ and $L_m$ (Froese and Binohlan, 2000). However, empirical data and theoretical predictions also suggest that the relationship between $L_m$ and $L_\infty$ is also related to the $\frac{M}{K}$ ratio, and knowledge of this parameter would also influence the prediction of the $L_\infty$ parameter (Beverton, 1992, and Chapters 2 and 3). The $\frac{L_m}{L_\infty}$ ratio shows considerable variation across species groups, which can lead to a wide range of estimates of $L_\infty$, and varied estimates of the SPR of an exploited stock (Chapter 4). Unlike the $\frac{M}{K}$ parameter, length data does contain some information on the $L_\infty$ parameter. This study approached this issue by developing an algorithm to estimate $L_\infty$ based on the assumed $\frac{M}{K}$ and estimated stock status (Appendix D). An important area for further research is to develop these methods further, and to test the model with empirical data, to present a robust methodology to estimate $L_\infty$ from a sample of the length structure of a stock.

The LB–SPR method differs from many conventional approaches in that it is based on estimating fishing mortality ($F$–based) and not biomass ($B$–based) to develop a management strategy. In contrast to conventional $B$–based methods which compare the estimate of absolute current biomass to the estimated unfished biomass ($\frac{SSB}{SSB_0}$), $F$–based methods are focused on estimating the current rate of exploitation and the relative trajectory of the exploited stock. For example, a recovering stock could have a high SPR while the absolute biomass is still a small fraction of the unfished level. Maintaining a stock at a suitable level of SPR will, on average, result in the spawning biomass rebuilding and stabilising at the level associated with that SPR (Equation 5.5; Walters and Martell, 2004; Cordue, 2012). However, the relationship between SPR and equilibrium %SSB is governed by the steepness of the stock-recruit function (Equation 5.5), a parameter that is difficult to estimate and unlikely to be known with any certainty for data-poor stocks. Several studies have explored general levels of SPR to be used as reference points, and it is generally accepted that a SPR of 35–40% is considered sustainable for most species (Clark, 1993; Mace and Sissenwine, 1993), although a risk-adverse target for some species may be higher (e.g., Dorn, 2002).

While a suitable choice of target SPR (e.g., $\text{SPR}_{\text{MSY}}$) will result in a corresponding equilibrium stock size ($SSB_{\text{MSY}}$), a purely SPR based approach, such as the LB–SPR method, has no index of abundance and no ability to estimate the current status of the stock in terms of relative spawning stock biomass. For this reason, a management strategy that aims to control fishing effort (and thus fishing mortality, assuming a relationship between fishing effort and fishing mortality) is likely to be more appropriate than one based on controlling catch. By including additional information, such as an index of relative abundance, it may be possible to link the LB–SPR harvest strategy to include recommendations of change in catch. However, this approach has not been explored in this chapter.
The use of controlling fishing effort to manage fisheries is not new, and has been widely practiced around the world for many years (Beddington and Rettig, 1984). However, the traditional assumption that fishing mortality is directly proportional to fishing effort is known not to hold in many cases. For example, the catchability coefficient, often denoted \( q \), is usually not constant, and can increase over time with improvements in technology, such as electronic equipment, satellite information and more efficient engines, or be inversely related to the density of the stock (Hilborn and Walters, 1992; Walters and Martell, 2004). The MSE carried out in this study included random deviations in the catchability coefficient, but did not include a systematic increase in catchability over time. However, the LB–SPR management strategy does not attempt to directly estimate the appropriate level of fishing mortality or effort, but rather uses an iterative process to make relative changes to the current fishing effort. While the impact of increasing catchability on the LB–SPR predictions should be investigated, the signal of the increase in fishing mortality over time should be present in the length frequency data, and the iterative nature of the harvest control rule would be expected to recommend an appropriate modification to the current level of fishing effort.

Information on the length structure of the catch is often one of the most accessible sources of data for fish stocks (Quinn and Deriso, 1999), and numerous methods have been developed to use this information to manage data-poor fish stocks. For example, Froese (2004) presented a simple method where the proportion of large fish in an exploited population can be used as an indicator of stock status. Cope and Punt (2009) extended the application of this method, and demonstrated that the interpretation of length data is more complex, and requires some knowledge of life history and selectivity patterns. Other length-based techniques use length composition data to estimate the stock status and provide useful management advice (e.g., Ault et al., 2005; O'Farrell and Botsford, 2005, 2006; Gedamke and Hoenig, 2006; Klaer et al., 2012). The LB–SPR approach differs from many of these approaches by removing the time component from the estimation model. By parameterizing the model with the \( \frac{M}{k} \) ratio, rather than the individual parameters \( M \) and \( k \), it is possible to evaluate the length data and provide an estimate of stock status that can be compared against existing, widely accepted, reference points and incorporated into management decisions, without a complete understanding of the species’ growth pattern and natural mortality rate. It could be argued that using the \( \frac{M}{k} \) ratio only transfers the problem from estimating the individual parameters to estimating the ratio. However, the ratio of \( \frac{M}{k} \) is known to be often less variable between species than either of the individual parameters in the ratio Beverton (1992, see also Chapter 2) and meta-analysis and comparative studies may be useful to estimate the \( \frac{M}{k} \) ratio for data-poor stocks without the need for expensive ageing studies. As more information is collected, and better estimates of the biological parameters become available, other assessment methods could be employed to complement the LB–SPR approach.

The MSE carried out in this study projected the simulations over a 60 year period, and assumed no increase in knowledge of the fishery or stock during this time. In reality, a con-
siderable amount of data could be collected over the 60 years that would refine and improve the assessment and management process. For example, biological studies could be carried out to provide better estimates of the life history ratios needed for the LB-SPR model. In addition, data on total catch and effort could be collected, and incorporated into more sophisticated assessment methodologies. For example, Prince et al. (2011) showed that size-based catch-per-unit-effort (CPUE) trends could be used to modify catch limits to iteratively drive a stock to a target level of SPR. Dick and MacCall (2011) demonstrated that a time-series of estimated catch, together with estimates of $M$ and age-at-maturity, could be used to set sustainable catch recommendations for data-poor stocks. It is important to note that the LB–SPR management strategy evaluation illustrated in this study is not proposed as a once-off solution to the assessment and management of data-poor stocks. Rather, this MSE demonstrates that the LB–SPR methodology has potential as a cost-effective tool for the initial assessment and management of a data-poor fishery, identifies where further research and data collection would reduce the uncertainty of the assessment and provides an additional approach to the assessment. As knowledge of the stock increases, managers can progress to including more sophisticated methodologies in the assessment process (Cope, 2013).

It is important to distinguish between the different meanings of the term SPR. In general, the SPR is defined as the ratio of the total egg production at equilibrium for a given level of fishing mortality divided by the egg production in the unfished state (Mace and Sissenwine, 1993). This metric is usually referred to as static or equilibrium SPR (Slipke et al., 2002), and represents the expected equilibrium SPR if a stock was held indefinitely at the given fishing mortality. Another, less common, use of the term SPR refers to the current ratio of egg production compared to the unfished state, denoted as transitional SPR (Slipke et al., 2002). The transitional SPR is dynamic and difficult to estimate, and requires knowledge of the recent recruitment history of a stock, as well as estimates of fishing mortality for each age class (Slipke et al., 2002). At equilibrium, the static and transitional SPR are identical, but during dynamic stages of the fishery, they can be quite different. For example, if a stock was at equilibrium and overfished, the static and transitional SPR would both be the same (e.g., SPR=0.15). If managers decided to close the fishery, or significantly reduce catches to almost zero, $F$ approaches 0 and the static SPR approaches 1; i.e., if no catch was taken from the stock for an indefinite period, the stock would rebuild back to unfished conditions assuming equilibrium conditions. However, it is clear that the actual egg production of the stock could not be equal to the unfished level immediately after the close of the fishery, and the time taken for the transitional SPR to rebuild back to the unfished state would be determined by the lifespan and age-at-maturity of the species and the future recruitment dynamics. Because the LB–SPR model estimates SPR by comparing the observed length structure against the expected unfished length composition, it appears to estimate the transitional SPR better than the static SPR during dynamic phases of the fishery. In the results of this study, the estimated SPR from the LB–SPR model is compared against the static SPR of the operating model. As explained above, during the dynamic
phase of the fishery, the two metrics are not expected to be the same. However, if the LB–SPR management strategy performs well, the harvest control rule should iteratively modify the fishing pressure and the stock should approach a new equilibrium, where the static and estimated SPR converge to the target level. Compared to the equilibrium SPR, the estimate of the transitional SPR may be a more useful metric as it provides an estimate of the current stock status rather than the expected equilibrium state of the stock. This effect equally applies to other length-based methods that estimate SPR or its proxies (e.g., Ault et al., 2005; O’Farrell and Botsford, 2005, 2006) and must be kept in mind whenever comparing the estimates of one of these methods to the output of models such as Stock Synthesis which present the equilibrium SPR (Methot and Wetzel, 2013).

The LB–SPR management strategy developed and tested in this chapter has the advantage of requiring little biological information and uses relatively easily obtainable data. However, the simplicity of the technique means that the model does not perform as well as more sophisticated assessment models and harvest strategies when more data are available. In data-poor situations managers often have very little information on which to base their decisions. The LB–SPR framework provides managers and stakeholders with a simple and transparent framework for assessing and sustainably managing a data-poor fishery, while simultaneously identifying and prioritising key areas for further research. Under the scenarios examined in this study, the LB–SPR management strategy successfully decreased fishing effort and initially brought the spawning stock biomass of the depleted stocks back to sustainable levels in 10–20 years. In the absence of any information on current stock status, or records of historical catch trends, it is difficult to determine appropriate management action. The results of this study suggest that a suitably precautionary SPR target ($\text{SPR}_{\text{targ}} > \text{SPR}_{\text{MSY}}$) could be initially set, and the LB–SPR management strategy could be used to determine the initial management actions required to rebuild an overfished data-poor stock.
6 General Conclusion

6.1 Introduction

The sustainable exploitation and management of the world’s fish stocks is an important but formidable challenge. It has become clear that in order to maintain the long-term stability of yield from capture fisheries, the dynamics of fish populations and the impact of harvesting these populations must be studied and understood. Despite falling fertility rates in many countries, the world’s population continues to increase and is projected to reach 9.6 billion people by 2050, with essentially all the growth occurring in less developed regions (UN, 2012). In addition to the increased demand for food from an increasing population, climate change is also expected to present a significant challenge to terrestrial food production, further increasing the importance of fish for food security (Rice and Garcia, 2011). Since its inception in the early 20th century, the field of quantitative fisheries science has made considerable inroads in the understanding and management of fisheries (Hilborn, 2012). However, many conventional methods require large amounts of data, including good biological information on the exploited stock and a historical time series for the fishery (Kelly et al., 2006). For a variety of reasons, including lack of funding and low commercial value of the stock, many fisheries around the world, including the United States and Australia, do not have the necessary data required for conventional methodologies, and are considered data-poor (Honey et al., 2010). The severity of the problem is further exemplified by the fact that many of the world’s data-poor stocks are in areas of high marine biodiversity, high population density, low management capacity, and considerable poverty (Andrew et al., 2007; Worm and Branch, 2012; Pitcher and Cheung, 2013). Furthermore, the inhabitants of these nations are often disproportionately reliant on fish as vital sources of protein, and fisheries play an important role providing livelihoods for millions of people (Kent, 1997; Béné, 2003; Walmsley et al., 2006). The immensity of the issues faced by data-poor fisheries is generally recognised by fisheries science, and recently an increasing literature on the development of alternative methods for data-poor fisheries has been building (Kelly et al., 2006; Honey et al., 2010; Dick and MacCall, 2011; Prince et al., 2011).

The aim of the research in this thesis was to investigate the potential to use basic life history information to assess data-poor stocks. This was achieved by an extensive meta-analysis of a wide range of marine species that identified previously unrecognised patterns between relative size and spawning potential (Chapter 2), a thorough analytical examination of how these patterns relate to the life-history ratios (Chapter 3), the development and testing of a length-based SPR (LB–SPR) assessment model (Chapter 4), and the development and simulation testing of a harvest control rule which uses the LB–SPR assessment
methodology to iteratively control fishing effort to bring on overfished stock back to a target level (Chapter 5). In this chapter, I briefly review and summarise the main findings of the research presented in this thesis, and discuss the implications of this work for the assessment and management of data-poor fish stocks. Finally, I identify several important areas for further research.

6.2 Significance of findings and implications for management

The ‘borrowing’ of information from data-rich stocks to inform data-poor stocks is widely practiced in fisheries science. For example, it is not unusual for parameters that are difficult to estimate (e.g., natural mortality or the steepness of the stock-recruit relationship) to be borrowed from other stocks or studies for use in a stock assessment, a method as the ‘Robin Hood’ approach (Punt et al., 2011). The temptation to borrow information from other stocks or studies is often great, as for many stocks the information required for quantitative stock assessments is simply not available. For example, the FishBase database (Froese and Pauly, 2000) provides easily accessible estimates of biological parameters for a large number of fish species. Furthermore, FishBase offers a Life-History Tool that estimates unknown parameters using empirical relationships (e.g., Froese and Binohlan, 2000; Binohlan and Froese, 2009). A recent study identified several biases in the FishBase database, particularly in the estimates provided by the Life-History Tool (?). The authors also recognised that FishBase is a valuable and important tool for fisheries science, and cautioned researchers to ensure that they enter high quality estimates to the database. However, the results of the meta-analysis presented in Chapter 2 add an extra layer of caution to the notion of borrowing or assuming parameter values.

The general consistency of the life history ratios \( \left( \frac{M}{k} \right) \) and \( \frac{L_m}{L_\infty} \) between taxonomic groups (e.g., families) has been recognised for many years (e.g., Beverton and Holt, 1959), and has led to the concept of the Beverton–Holt life history invariants (BH–LHI) (Charnov, 1993). For example, when little is known of \( M \), a common approach has been to assume that the Beverton–Holt life history invariant of \( \frac{M}{k} = 1.5 \), and to estimate \( M \) from the more easily estimated parameter \( k \): \( M = 1.5k \) (e.g., see many papers citing Jensen, 1996). However, the results of Chapter 2 show that an assumed \( \frac{M}{k} \) ratio also implies a particular relationship between size (length or weight) and the spawning potential of a stock. Furthermore, the results of this study show that the \( \frac{L_m}{L_\infty} \) ratio also varies together with \( \frac{M}{k} \), as predicted from life history theory (Beverton, 1992, also see Chapter 3). By assuming the default value of \( \frac{M}{k} = 1.5 \) when the true value is higher, e.g., \( \frac{M}{k} = 3.0 \), a species dominated by small sized individuals, researchers will be under-estimating the productivity of the stock considerably. More importantly, when the true value of \( \frac{M}{k} \) is lower than 1.5, species with the population dominated by large, adult-sized fish, researchers will be over-estimating the productivity of the stock. Furthermore, many of the empirical methods that are used to
estimate $M$ are based on the notion of life-history invariants (Kenchington, 2013) and do not account for the wide variability in $\frac{M}{\ell_{\infty}}$ observed across marine species. When using the Robin Hood approach to borrow biological parameters from another stock or species (e.g., using FishBase or some other data source), fisheries scientists should be careful to consider the implications of the $\frac{M}{\ell_{\infty}}$ and $\frac{t_{\text{sp}}}{\ell_{\infty}}$ ratios that are not close to the real values for the stock.

Chapter 3 demonstrates that the $\frac{M}{\ell_{\infty}}$ ratio is important in determining the shape of von Bertalanffy growth curve. Many fisheries scientists tend to think in terms of “young, small fish” and “old, large fish”, a description which appears to apply to species with $\frac{M}{\ell_{\infty}} \approx 1.5$ or higher, where growth continues throughout the life of the animal, and, in general, older fish are larger than younger fish (see Figure 3.1). However, a considerable number of marine fish have much lower $\frac{M}{\ell_{\infty}}$, where growth is rapid while the fish is relatively young and asymptotes relatively early in life (see curves in top left of Figure 3.1). For example, female sea sweep ($\text{Scorpsis aequipinnis}$) are expected to live to 70 years but typically reach maturity at about 20 years of age, or about 30% of their life span and 90% of asymptotic size, living the remaining 50 years with little or no growth (Coulson et al., 2012). Species with high $\frac{M}{\ell_{\infty}}$ tend to mature at relatively small sizes (i.e., low $\frac{t_{\text{sp}}}{\ell_{\infty}}$), as few individuals live long enough to achieve great size. Species with low $\frac{M}{\ell_{\infty}}$ tend to mature at a relatively greater size (i.e., high $\frac{t_{\text{sp}}}{\ell_{\infty}}$) as the species grow relatively fast to maturity and asymptotic size, and the unfished stocks are dominated by large individuals. On this relative scale, tuna can be considered as ‘larger, slower’ anchovies, which rarely reach asymptotic size and mature are relatively small size, while some fish (e.g., $\text{S. aequipinnis}$) are ‘smaller, faster’ versions of marine mammals that breed multiple times close to asymptotic sizes. This finding has important implications for fisheries management, especially when length-based indicators are used to assess stock status.

The proportion of large fish in an exploited population is often considered an indicator of stock status (Froese, 2004). Cope and Punt (2009) demonstrated that the interpretation of length data is more complex, and requires some knowledge of life history and selectivity patterns. However, the results of Chapter 3 explicitly link the expected size composition of a stock under various levels of exploitation to two ratios $\frac{F}{M}$ and $\frac{M}{\ell_{\infty}}$, and demonstrate that the ‘ideal’ proportion of large fish in a stock is influenced by the $\frac{M}{\ell_{\infty}}$ ratio. For example, the length structure of stocks with very low $\frac{M}{\ell_{\infty}}$ (e.g., 0.3) contains very little information on the status of the stock, as there is little discernible change in the length composition until the stock is heavily overfished. Conversely, stocks with high $\frac{M}{\ell_{\infty}}$ (e.g., 3.0) may still be sustainably fished even when there are very few large fish left in the population.

The results from Chapter 3 also demonstrate that, given the simplifying assumptions of knife-edge maturity and selectivity, there is a direct and predictable relationship between $\frac{F}{M}$ and SPR. This information has important applications for management. For example, the SPR is an important metric for fisheries management, and can be linked to various reference points including $\text{SPR}_{\text{MSY}}$ and $\text{SPR}_{\text{crash}}$ (the level of SPR that will result in the eventual demise of the stock) (Brooks et al., 2010). The results of Chapter 3 show that a SPR target can be achieved by managing two different aspects of a fishery: the relative level
of fishing pressure \((\frac{F}{M})\), which can be estimated and controlled using a variety of methods, and the selectivity of the fishery, which can be manipulated by setting minimum size limits or regulating mesh size (see Figure 3.5 in Chapter 3). For example, fisheries managers could use the methodology presented in Chapter 3 to set appropriate size limits for stocks targeted by recreational or commercial fishers that effectively ‘locks up’ a certain level of SPR; i.e., even almost infinite \(F\) would not decrease the SPR below a minimum threshold.

Chapter 3 also provides an initial answer to the question posed at the beginning of this thesis: is it possible to develop a methodology that relies on the apparent consistent ratios of these life history parameters to assess data-poor fisheries? The chapter demonstrates that, theoretically, the SPR of an exploited stock can be estimated from length composition data and basic life history information (the life history ratios), and that the length structure of the catch of an exploited stock is primarily determined by the selectivity pattern and the \(\frac{Z}{X}\) ratio (where \(Z\) is total mortality: \(Z = F + M\)). If \(\frac{M}{X}\) is known from a meta-analysis (see Chapter 2) or some other method (e.g., expert knowledge or local biological studies), the ratio \(\frac{F}{M}\) can be calculated, which in turn can be used to calculate the SPR.

Like many length based methods, the LB–SPR method (developed in Chapter 3 and tested for robustness in Chapter 4) is an equilibrium method, and relies on a number of important assumptions, including:

1. asymptotic selectivity,
2. growth is adequately described by the von Bertalanffy equation,
3. both sexes have same growth curve and sex ratio of catch at parity, or biological parameters and length composition of female fish only,
4. length-at-age is normally distributed, and
5. natural mortality and growth rates are constant for fish that are vulnerable to the fishery.

The simulation testing of Chapter 4 demonstrated that the model is sensitive to misspecification of the biological parameters, particularly the \(L_\infty\) parameter, as well as the presence of dome-shaped selectivity. Furthermore, the model is sensitive to non-equilibrium dynamics, and in some cases SPR can be severely over- or under-estimated. However, the development of the effort-based harvest control rule in Chapter 5 has shown that, in spite of its limitations, the LB–SPR methodology can be a useful tool in assessing and managing data-poor stocks.

The simulation testing carried out in Chapter 5, for three species with a range of life history ratios, demonstrated that the LB–SPR harvest strategy has the potential to successfully recover an overfished stock and rebuild it back to sustainable levels. Like many length-based methods, the LB–SPR model is equilibrium based and the estimates of the SPR are affected by non-equilibrium dynamics. While the individual estimates of the SPR are often highly variable, over time the model was able to reliably estimate the SPR state (e.g., below
or above the SPR target) and adjust the fishing effort iteratively to move the stock towards the target level. However, the simulation testing also highlighted a number of limitations of the LB–SPR model. For example, the methodology is sensitive to the assumed values of the life-history parameters, especially the $L_\infty$ parameter. In data-poor fisheries, reliable estimates of these parameters are unlikely to be available for the stock or region, and, in many cases, the values will have to be assumed or borrowed from other sources. Underestimating the $L_\infty$ parameter by more than 10% can lead to significant over-estimation of the SPR, and result in the LB–SPR harvest strategy failing to correctly identify and make the correct adjustments for an overfished stock. Conversely, if $L_\infty$ is over-estimated by more than 10%, the LB–SPR methodology can significantly under-estimate the SPR, resulting in the fishing effort being reduced to unnecessarily low levels, and low yield from the fishery. While the model is less sensitive to error in the $M_k$ ratio, misspecification of this parameter causes bias in the estimates of the SPR. In data-poor fisheries, finding an appropriate value for the $M_k$ ratio may be more difficult than estimating $L_\infty$, as the length structure of an exploited stock contains little information to suggest the value of the true ratio. This emphasises the value of rigorous, high quality, research documenting the biology of marine species (e.g., studies on age, growth, and reproduction), especially early in the development of a fishery, when fishing mortality ($F$) is still low), and the importance of meta-analysis and comparative studies. For example, Chapter 5 showed how meta-analysis could be used to estimate the $M_k$ parameter for the LB–SPR model, and successfully recover an overfished stock with the LB–SPR harvest strategy.

The LB–SPR model presented in this thesis provides a cost-effective tool for using information on the life-history ratios to assess and manage data-poor fisheries when only data on the length structure of the catch are available. Like many data-poor methods, the LB–SPR model has some important limitations, and is not a ‘quick fix’ to the problem of assessing and managing fisheries with little data. However, although sophisticated assessment methods have been developed over the last two decades, even data-rich fisheries are not often not fully understood, resulting in poor management advice (Schnute and Richards, 2001; Hilborn, 2003). In recent years there has been an increased call for simple harvest rules that rely directly on empirical indicators from the exploited stock (Hilborn, 2003; Kelly et al., 2006). The LB–SPR method is a such a technique, relying on simple and cheaply collected data. However, care must be taken when determining the appropriate values of the life history parameters used in the model. Furthermore, the model is an equilibrium-based method and often does not adequately describe the dynamics of a stock. Therefore the results of the method should be carefully interpreted in the light of other knowledge of the fishery, and management action should be based on a smoothed output of the LB–SPR model, rather than individual estimates of SPR at single points in time.

The LB–SPR methodology is a viable method for assessing data-poor stocks, and uses information of the life history parameters to make a quantitative assessment of stock status. These estimates can be directly incorporated into a transparent and easily understandable harvest control rule. However, the main advantage of the LB–SPR method is that it pro-
vides a framework to rapidly and cost-effectively assess and manage a data-poor fishery. By carefully selecting the life history parameters, e.g., the lowest $\frac{M}{K}$ ratio observed elsewhere for the species or family, researchers and managers can be assured that they are taking a precautionary approach to management (see Chapter 4 and Chapter 5). The initial estimates of the status of the stock can be used to prioritise further research efforts, while simultaneously allowing managers to make decisions based on a quantitative assessment of the stock. For example, the establishment of a program to collect fisheries catch and effort data would be very beneficial, and could augment the management of the fishery by incorporating other assessment and management techniques (e.g., Little et al., 2011; Prince et al., 2011).

6.3 Avenues for further research

The research carried out in this study has identified and highlighted several areas for future research. By standardising to maximum size and age, the meta-analysis of Chapter 2 revealed interesting patterns in the relationship between relative age, relative size, and the spawning potential of a wide range of marine species. Furthermore, the study showed that, while the life history strategies of marine species are more diverse than suggested by the Beverton–Holt life history invariants, the $\frac{M}{K}$ and the $\frac{L_m}{L_\infty}$ ratios are correlated. However, in reality this pattern is more complex than the simple theoretical relationship of $\frac{L_m}{L_\infty} = \frac{3}{3 + \frac{M}{K}}$ that is presented in Chapter 2 (see also Chapter 3 and Beverton, 1992). Further research should investigate the relationship between these life history ratios and parameters in greater detail, and continue to develop a framework to robustly predict the $\frac{M}{K}$ and $\frac{L_m}{L_\infty}$ for marine species. For example, although this meta-analysis did include a number of species from the same family, further work could focus on specific species groups within families (such as the mackerels and tuna (Scombridae), the snappers (Lutjanidae), or prawns and shrimp (Penaeidae)). Investigating the patterns of variation in life history strategy among species within the same family may reveal interesting patterns in the life history parameters, and may lead to the ability to predict the distribution of $\frac{M}{K}$ and $\frac{L_m}{L_\infty}$ based on other life history and environmental characteristics (e.g., body size or shape, latitude or depth).

The meta-analysis presented in Chapter 2 includes over 120 marine species, but contains only a small proportion of the fish species that are exploited by humans. Furthermore, the meta-analysis did not consider intra-species variation among geographic regions, or fully explore inter-species variation within families, in the life history ratios. However, the results of Chapter 2 provide an important theoretical framework for borrowing knowledge from well-studied species to apply to related, unstudied species and populations. This framework can be further refined and developed, and will provide a useful tool for researchers who need to borrow biological information to assess and manage data-poor stocks. Furthermore, by using relative size and age to put all marine species on the same scale, patterns in the relationship between the life history parameters can be revealed that previously were not recognised. For example, the results of Chapter 2 demonstrate that
the life history of marine species is spread over a wide spectrum, ranging from species that live relatively fast, mature at relatively small sizes, and die before they have stopped growing (i.e., Type I species with high $\frac{M}{k}$ and relatively low $\frac{L_{\infty}}{L_m}$; e.g., some tunas, clupeids and gobies), to species that reach maturity and adult size relatively early in life and continue to live with little further growth (Type III with low $\frac{M}{k}$ and high $\frac{L_{\infty}}{L_m}$; e.g., some lethrinids and sharks, and marine mammals).

Although the ratios of $\frac{M}{k}$ and $\frac{L_{\infty}}{L_m}$ have been observed to be relatively consistent across species and family groups (Beverton, 1992), they are not constant, and considerable variation can occur, even between different stocks of the same species (e.g., see data in Pauly, 1980). Furthermore, life history characteristics are known to be plastic, and have been observed to rapidly change in response to exploitation (Ziegler et al., 2007). Currently, the impact of exploitation and density dependence on the life history parameters is not fully understood, which emphasises the importance of further research on the intra-species variation in the life history characteristics. The life history ratios are an important component of the LB–SPR model presented in this thesis, and developing a framework to robustly predict these parameters for data-poor stocks is crucial to the successful implementation of the LB–SPR methodology.

Of all the biological parameters required for the meta-analysis, reliable estimates of natural mortality were the most difficult to obtain. Because it is so hard to obtain estimates of $M$ for exploited fish stocks, natural mortality is often estimated by empirical methods (e.g., Pauly, 1980; Hoenig, 1983; Jensen, 1996). However, many of these empirical methods use some empirical relationship between $M$ and other life history parameters (e.g., $k$; Pauly, 1980). To avoid circular reasoning in using the life history ratios to estimate SPR, these empirically based parameters can not be used in a meta-analysis to compare patterns in life history ratios. Furthermore, obtaining robust estimates of other parameters also requires careful consideration. For example, an inadequate sampling regime can lead to biased samples of length and age composition, and parameter estimates will be imprecise and potentially biased if the full range of age and size classes are not sampled (Goodyear, 1995; Kritzer et al., 2001). This emphasises the importance of high quality biological studies to determine the life history parameters of marine species, and the significance of carefully designed sampling programs to collect these data. Hilborn (2003) notes that a significant problem with many modern model-based methodologies is the lack of attention paid to rigorous data collection protocols. The LB–SPR model is reliant on length data that is simple and relatively cheap to collect. However, ensuring that the length data are representative of the exploited stock should be an important research priority, and the reliability of the estimates of the LB–SPR method are directly related to the quality of the length data and assumed parameters. Therefore, an important area for future research is the development and maintenance of cost-effective and unbiased sampling programs to collect the high quality biological and fisheries data required for use in stock assessment models and meta-analyses.

Like all assessment methods, the LB–SPR model developed and presented in this thesis
relies on a number of important assumptions. Some of these assumptions were identified and examined in detail using simulation in this thesis (Chapters 3, 4 and 5). These results identified the sensitivities of the LB–SPR model, and caution must be exercised in using the model without being aware of its limitations. However, a number of other assumptions of the LB–SPR model were not able to be examined in the same detail. For example, the model assumes constant natural mortality, at least for the animals selected by the fishery. This assumption is unlikely to hold for some species, such as tuna, that are known to have size-dependent natural mortality rates (Hampton, 2000). Furthermore, tuna are often caught by a number of fisheries targeting different size classes, with the smallest of these likely to have higher natural mortality than the larger classes (Griffiths, 2010). Additionally, while the LB–SPR model assumes that growth is adequately described by the von Bertalanffy growth equation, this assumption does not hold for some fish (e.g., Bodianus frenchii, (Cossington et al., 2010), and Haliotis rubra, (Helidoniotis et al., 2011)). Understanding of the significance of the violation of these assumptions is an important area for further research, and must be considered before the method is applied to species with other growth forms.

Another further area for research is the utility of the LB–SPR model for short-lived species with highly variable recruitment. If a species lives for only 1 to 2 years, e.g., many penaeids, and annual recruitment is highly variable, then the length structure each year is likely to vary considerably, as it will be primarily a function of year class strength. Theoretically, by matching the temporal scale of sampling with the dynamics of the species, e.g., weekly or monthly sampling of length structure for short-lived species, the LB–SPR model should be able to perform adequately. However, currently the performance of the model for these species has has not been examined intensively by simulation or empirical studies.

The results from my thesis show that the LB–SPR model has potential as a cost-effective tool for the assessment and management of data-poor fisheries. However, the methodology has a number of limitations, and is not likely to be applicable in all situations. The successful management of data-poor fisheries requires a holistic approach (Berkes et al., 2001), where managers are equipped with a ‘toolbox’, containing a diverse range of techniques and methodologies, to sustainably manage a large range of fisheries (Prince, 2010). The LB–SPR method is one such tool, and will be useful in very data-poor situations, with little knowledge of the biology of the stock, and no data on catch and effort in the fishery. In particular, the LB–SPR method provides a starting point for managers of data-poor fisheries, and allows initial, informed, management decisions to be made for data-poor stocks. In addition to providing information for informed management decisions when data are scarce, the logic underlying the LB–SPR approach is easily understood and intuitive, and the method has potential to strengthen the link between managers, industry, conservation groups, and other stakeholders. This helps build trust and understanding between different interest groups, and significant attribute for successful fisheries management (Hilborn, 2002; Gutiérrez et al., 2011). Furthermore, the application of the LB–SPR methodology
to data-poor fisheries will assist in identifying important data gaps, and help prioritise key areas for further research, including biological studies to validate the unknown biological parameters, and sampling and data recording programs to begin building a time series of information on the fishery that can be incorporated later into more sophisticated assessment methodologies.

An important area for further research is the integration the LB–SPR methodology with other assessment and management methodologies. For example, Prince et al. (2011) present a model where size-based CPUE trends are used to iteratively manage catches to drive a stock to an appropriate SPR target. Such a technique uses the same reference point as the LB–SPR model (i.e., SPR) and could be considered the next rung of a tiered assessment framework. For example, once an appropriate SPR target has been defined, initially the LB–SPR model could be used to estimate the status of the stock and inform management decisions for a number of years. At the same time, data collection programs could be put into place to begin collecting the size-based catch and effort data required by the method of Prince et al. (2011). Once an adequate time-series of data has been collected (e.g., 10 years), this could be used to assess and manage the fishery. However, the LB–SPR model could be continued to be used to assess the status of the stock, and provide an additional layer of information for managers.

The overall aim of this thesis was to investigate the potential use of the life history ratios to develop an assessment methodology for data-poor fisheries. The development of the LB–SPR harvest strategy provides an easily understood and transparent data-driven management framework for data-poor and small-scale fisheries. The research carried out in this thesis has revealed a number of previously unknown and significant findings. The methodology will undoubtedly be refined and improved as it is applied to real world situations. Even so, in its current form, the LB–SPR model has the potential to be a valuable tool for managers and other stakeholders of data-poor and small-scale fisheries. Given the importance of these fisheries to such a large number of people and nations, it is hoped that the LB–SPR methodology goes some way to addressing the significant problem of assessing and managing the world’s data-poor and small-scale stocks.
References


R Development Core Team (2012). R: A language and environment for statistical computing.


Appendices
A Biological parameters of the 123 species used in the meta-analysis (Chapter 2)

The table below contains the biological parameters and references for the 123 species used in the meta-analysis. Types of species are those identified in Chapter 2.

Growth model is 1) von Bertalanffy, 2) Schnute, 3) Gompertz, and 4 and 5) generic logistic curves.

Reproduction model is 1) Size/age-fecundity model from literature, 2) reproductive output proportional to biomass of individual or cohort, or 3) reproductive output assume independent of size.

* k not applicable for growth model, ** Length-weight is polynomial regression.

Numbers of species for each Type and Taxa are shown in parentheses.
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<th>$L_{50}$ (mm)</th>
<th>$k$ (y$^{-1}$)</th>
<th>$M$ (y$^{-1}$)</th>
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<th>Growth model</th>
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B Extended derivations for Chapter 3

This appendix provides the full derivations and supporting equations for the analytical models presented in Chapter 3. The headings in this appendix correspond directly to the headings of Chapter 3.

Number of animals at age in terms of $M/k$

Substituting $M = \frac{-\ln(0.01)}{t_{max}}$ and $x = \frac{M \ln(1-L_x)}{k \ln(0.01)}$ and simplifying gives:

$$\hat{N}_x = e^{(\frac{-\ln(0.01) M \ln(1-L_x)}{k \ln(0.01)} t_{max})} = e^{(\ln(1-L_x) \frac{M}{k})} = \left(1-L_x\right)^{\frac{M}{k}} \quad (B.1)$$

Relative biomass at age and length in terms of $M/k$

The relationship between fish length and weight ($W$) is often well described by:

$$W_t = a L_t^b \quad (B.2)$$

where $a$ is a scaling coefficient which varies between species and the exponent $b$ is usually close to 3 for most species. Standardised weight is then given as:

$$W_t = \frac{W_t}{W_\infty} = \frac{a L_t^b}{a L_\infty^b} = L_t^b \quad (B.3)$$

and weight at standardised age $x$ is:

$$\tilde{W}_x = \tilde{L}_x^b \quad (B.4)$$

An analytical solution to calculate the standardised length at which biomass is at a maximum ($L_{opt}$) can be found by differentiating $B_x = (1-L_x)^{\frac{M}{k}} L_x^b$ with respect to $L$ and setting
equal to zero:

\[
\frac{dB}{dL} = 0
\]

\[
(1 - \bar{L})^M \frac{d}{dL} \bar{L} + \bar{L}^b \frac{d}{dL} (1 - \bar{L})^M = 0
\]

\[
(1 - \bar{L})^M b \bar{L}^{b-1} - \bar{L}^b \frac{M}{k} (1 - \bar{L})^{\frac{M}{k}-1} = 0
\]

\[
\left[\bar{L}^{b-1}\right] \left[ b - \bar{L} \left( b + \frac{M}{k} \right) \right] \left[ (1 - \bar{L})^{\frac{M}{k}-1} \right] = 0 \quad (B.5)
\]

which solved for \( \bar{L} \) gives two solutions: 0 and \( \frac{b}{\frac{F}{M} + b} \) when \( b \) \& \( \frac{M}{k} > 0 \). Calculating the second derivative confirms that \( \frac{b}{\frac{F}{M} + b} \) is the maximum of the function, so:

\[
\bar{L}_{\text{opt}} = \frac{b}{\frac{F}{M} + b} \quad (B.6)
\]

and:

\[
L_{\text{opt}} = L_{\infty} \frac{b}{\frac{F}{M} + b} \quad (B.7)
\]

### Estimating SPR from \( \frac{M}{k} \), \( \frac{F}{M} \) & \( \frac{L_{\infty}}{L_{\infty}} \) with simple assumptions

If all size classes are fully selected by the fishery, then the number of individuals at each standardised age \( x \) and length \( \bar{L}_x \) in the fished state can be calculated by simply replacing \( \frac{M}{k} \) with \( \frac{F}{M} \):

\[
\text{Total Egg Production}_{\text{Fished}} = f \sum B_{x}^{\text{Fished}}
\]

\[
= f \sum N_{x}^{\text{Fished}} \bar{W}_x
\]

\[
= f \sum (1 - \bar{L}_x) \frac{\bar{W}_x}{\bar{L}_x}
\]

\[
= f \sum (1 - \bar{L}_x) \left( \frac{\frac{F}{M} + \frac{M}{k}}{\frac{F}{M} + \frac{M}{k}} \right) \frac{\bar{L}_x^b}{\bar{L}_x}
\]

\[
= f \sum (1 - \bar{L}_x) \left( \frac{\frac{F}{M} [\frac{F}{M} + 1]}{\frac{F}{M} + \frac{M}{k}} \right) \frac{\bar{L}_x^b}{\bar{L}_x}
\]

for \( x_m \leq x \leq 1 \) \quad (B.8)

### Fished length composition in terms of \( \frac{M}{k} \) & \( \frac{F}{M} \)

The probability of a fish in the fished state being greater than length \( \bar{L} \) is:

\[
\Pr\{\bar{L} \geq \bar{L}\} = \frac{N_x}{N_c}
\]

\[
= \frac{(1 - \bar{L})^M + \frac{F}{M} + \frac{M}{k} (1 - \bar{L}) - \frac{M}{k}}{(1 - \bar{L})^M + \frac{F}{M} + \frac{M}{k} (1 - \bar{L}) - \frac{M}{k}}
\]

\[
= \frac{(1 - \bar{L})^M + \frac{F}{M} + \frac{M}{k} (1 - \bar{L}) - \frac{M}{k}}{\bar{L}_c^M}
\]

for \( \bar{L}_c \leq \bar{L} \leq 1 \) \quad (B.9)
and so:

\[
G(\tilde{l})_{\text{Fished}} = \Pr\{\tilde{L} \leq \tilde{l}\} \\
= 1 - \left( \frac{(1 - \tilde{l}) \frac{M}{F} + \frac{F}{M} (1 - \tilde{L}_c) \frac{M}{F}}{(1 - \tilde{L}_c) \frac{M}{F}} \right) \\
\text{for } \tilde{L}_c \leq \tilde{l} \leq 1 \quad (B.10)
\]

This equation can also be re-written in terms of \( \frac{Z}{M} \):

\[
G(\tilde{l})_{\text{Fished}} = 1 - \left( \frac{(1 - \tilde{l}) \frac{M}{F} + \frac{F}{M} (1 - \tilde{L}_c) \frac{M}{F}}{(1 - \tilde{L}_c) \frac{M}{F}} \right) \\
= 1 - \left( \frac{1 - \tilde{l}}{1 - \tilde{L}_c} \right)^{\frac{Z}{F}} \quad \text{for } \tilde{L}_c \leq \tilde{l} \leq 1 \quad (B.11)
\]

The predicted proportion of individuals in length class \( i(P_i) \) can be calculated from Equation 27:

\[
P_i^{\text{Fished}} = \begin{cases} 
1 - \left( \frac{(1 - \tilde{l}_{i+1}^{lo}) \frac{M}{F} + \frac{F}{M} (1 - \tilde{L}_c) \frac{M}{F}}{(1 - \tilde{L}_c) \frac{M}{F}} \right) & \text{if } i = 1 \\
\left( \frac{(1 - \tilde{l}_{i+1}^{lo}) \frac{M}{F} + \frac{F}{M} (1 - \tilde{L}_c) \frac{M}{F}}{(1 - \tilde{L}_c) \frac{M}{F}} \right) - \left( \frac{(1 - \tilde{l}_{i}^{lo}) \frac{M}{F} + \frac{F}{M} (1 - \tilde{L}_c) \frac{M}{F}}{(1 - \tilde{L}_c) \frac{M}{F}} \right) & \text{if } 1 < i < I \\
\left( \frac{(1 - \tilde{l}_{I+1}^{lo}) \frac{M}{F} + \frac{F}{M} (1 - \tilde{L}_c) \frac{M}{F}}{(1 - \tilde{L}_c) \frac{M}{F}} \right) & \text{if } i = I
\end{cases}
\]

where \( I \) is the number of length classes, and \( \tilde{l}_{i}^{lo} \) is the lower bound of length class \( i \).

**Incorporating variation in length-at-age**

Using the simplifying assumption that individual growth is described by the von Bertalanffy equation, and that the sole source of variability in length-at-age is caused by a normally distributed \( L_\infty \), then the length-at-age \( (L_x) \) can be standardised to the expected \( L_\infty \) (\( E[L_\infty] \); i.e., the value typically thought of as the \( L_\infty \) of the stock):

\[
L_x' = \frac{L_x}{E[L_\infty]} = \frac{L_\infty (1 - e^{-kT_{\text{max}}})}{E[L_\infty]} \quad (B.13)
\]
The expected standardised length-at-age $x$ is then:

$$E[\tilde{L}_x] = \frac{E[L_\infty] \left(1 - e^{-kxT_{\text{max}}}ight)}{E[L_\infty]} = 1 - e^{-kxT_{\text{max}}} = 1 - 0.01 \left(\frac{x}{\bar{X}}\right) \quad (B.14)$$

and the variance of length-at-age $x$ is:

$$\sigma_{\tilde{L}_x}^2 = \frac{\sigma_{L_\infty}^2 E[\tilde{L}_x]^2}{E[L_\infty]^2} \quad (B.15)$$

from which the standard deviation is:

$$\sigma_{\tilde{L}_x} = \text{CV}_{L_\infty} \left(\frac{E[\tilde{L}_x]}{E[L_\infty]}\right) = \text{CV}_{L_\infty} \left(1 - 0.01 \left(\frac{x}{\bar{X}}\right)\right) \quad (B.16)$$

The probability distribution of length at standardised age $x$ is then:

$$p(\tilde{l}) = \frac{1}{\sigma_{\tilde{L}_x} \sqrt{2\pi}} e^{-\left(\frac{(\tilde{l} - E[\tilde{L}_x])^2}{2\sigma_{\tilde{L}_x}^2}\right)} \quad (B.17)$$

If there are $I$ length classes and $\tilde{l}_i$ is the mid-point of length class $i$, then the probability of a fish at standardised age $x$ being in length class $i$ can be given by:

$$P_{x,i} = \begin{cases} 
\frac{\phi \left(\frac{\tilde{l}_i - E[\tilde{L}_x]}{\sigma_{\tilde{L}_x}}\right)}{\frac{\tilde{l}_i - E[\tilde{L}_x]}{\sigma_{\tilde{L}_x}}} & \text{if } i = 1 \\
\phi \left(\frac{\tilde{l}_i - E[\tilde{L}_x]}{\sigma_{\tilde{L}_x}}\right) - \phi \left(\frac{\tilde{l}_{i-1} - E[\tilde{L}_x]}{\sigma_{\tilde{L}_x}}\right) & \text{if } 1 < i < I \\
1 - \phi \left(\frac{\tilde{l}_{I-1} - E[\tilde{L}_x]}{\sigma_{\tilde{L}_x}}\right) & \text{if } i = I
\end{cases} \quad (B.18)$$

where $\phi$ is the standard normal cumulative density function.
C Population dynamics model for Chapter 5

Operating Model

The abundance, $N$, of animals at age $a$ in time $t$ and given by:

$$N_{a,t} = \begin{cases} R_t & \text{if } a = 0,1 \\ N_{a-1,t-1} e^{Z_a} & \text{if } 1 < a \leq a_{\text{max}} \end{cases}$$  \hspace{1cm} (C.1)

where both $a$ and $t$ are in quarter-annual time-steps (i.e., $a = 1$ is the age of an animal at the beginning of its fourth month of life), $R_t$ is the recruitment at time $t$, $Z_a$ is the total mortality for age-class $a$, and $a_{\text{max}}$ is the maximum age. Total mortality at age is given by:

$$Z_a = M + S_a F$$  \hspace{1cm} (C.2)

where $M$ is the quarterly instantaneous natural mortality rate (assumed independent of age and size), $S_a$ is the selectivity at age $a$, and $F$ is quarterly instantaneous rate of fishing mortality. Maximum age (in quarters) was calculated by:

$$a_{\text{max}} = \frac{-\ln(0.01)}{M}$$  \hspace{1cm} (C.3)

The catch-at-age ($C_a$) was calculated using the Baranov equation:

$$C_{a,t} = \frac{F_a}{Z_a} N_{a,t} (1 - \exp^{-Z_a})$$  \hspace{1cm} (C.4)

The Beverton–Holt stock–recruitment relationship with multiplicative lognormal error was used to generate new recruits for the population at the beginning of the first two quarters ($Q$) of each year:

$$R_t = \begin{cases} \frac{S_B t - 2}{\delta + \rho S_B t - 2} \exp^{\varepsilon_t - (\sigma_t^2/2)} & \text{if } Q = 1, 2 \\ 0 & \text{if } Q = 3, 4 \end{cases}$$

where $S_B t$ is the spawning stock biomass at time $t$, $\delta$ and $\rho$ are parameters of the stock–recruit function, and $\varepsilon_t$ is the recruitment residual at time $t$ that is normally distributed $N(0, \sigma_t^2)$, where $\sigma_t$ is the standard deviation. The $\delta$ and $\rho$ parameters of the stock–recruit function were reparametrized in terms of steepness ($h$), which is defined as the fraction of the virgin recruitment ($R_0$) obtained the spawning biomass is 20% of the unfished spawning
biomass (i.e., $0.2SB_0$).

**Length, weight, maturity and selectivity curves**

Maturity was assumed to be size-dependent, and was modelled with the two-parameter logistic function:

$$\text{Mat}_l = \frac{1}{1 + e^{-\ln(19)(l - L_{50})}}$$

where $\text{Mat}_l$ is maturity at length $l$, and $L_{50}$ and $L_{95}$ are lengths at 50% and 95% maturity respectively. Maturity-at-length was converted to maturity-at-age ($\text{Mat}_a$):

$$\text{Mat}_a = \int_{l=0}^{l=\infty} \text{Mat}_l \frac{1}{\sigma_{L_a} \sqrt{2\pi}} e^{-\frac{(l-L_{a})^2}{2\sigma_{L_a}^2}}$$

where $\sigma_{L_a}^2$ is the variance of length at age $a$.

For most cases, selectivity was assumed to be asymptotic and size dependent, and was modelled by replacing $L_{50}$ and $L_{95}$ in Equation C.5 with the lengths at 50% and 95% selectivity ($L_{S50}$ and $L_{S95}$). The sensitivity of the model to dome-shaped selectivity was also examined. For these cases, selectivity-at-length ($S_l$) was modelled as a two-sided curve:

$$S_l = \begin{cases} 
    e^{-\frac{(l-L_1)^2}{2s_1^2}} & \text{for } l < L_1 \\
    e^{-\frac{(l-L_2)^2}{2s_2^2}} & \text{for } l \geq L_1 
\end{cases}$$

where $L_1$, $L_2$, $s_1$ and $s_2$ are the mean and standard deviations of the two normal curves. Selectivity-at-length was converted to selectivity-at-age ($S_a$) in the same manner as Equation C.6.

Growth was modelled with the three-parameter von Bertalanffy function:

$$L_a = L_\infty \left(1 - e^{-k(a-t_0)}\right)$$

where $L_\infty$ is asymptotic length, $k$ is the growth coefficient, and $t_0$ the theoretical age when length is zero. Variation of length-at-age was assumed to be normally distributed, with variance increasing with increased mean length:

$$\sigma_{L_a}^2 = \sigma_{L_\infty}^2 \left(1 - e^{-k(a-t_0)}\right)^2$$

$$\sigma_{L_\infty} = CV_{L_\infty} L_\infty$$

Spawning stock biomass was calculated as:

$$SB_t = \sum_a N_{a,t} \text{Mat}_a W_a$$
where \( W_a \) is weight at age \( a \), which was calculated as:

\[
W_a = \alpha L_a^\beta
\]  

(C.12)

where \( \alpha \) and \( \beta \) are constants. Egg production at age \( a \) was assumed to be proportional to weight:

\[
E_a \propto \text{Mat}_a W_a
\]

(C.13)

**Calculation of static SPR**

The static SPR was calculated following Goodyear (1993), by calculating the ratio of the average lifetime production of eggs per recruit \( (EP) \) at equilibrium for the fished and unfished states, assuming no density-dependent suppression of maturation or fecundity:

\[
\text{SPR} = \frac{EP_{\text{Fished}}}{EP_{\text{Unfished}}}
\]  

(C.14)

where

\[
EP_{\text{Fished}} = \sum_a E_a e^{-Z_a a} E_a
\]

for \( 0 < a \leq a_{\text{max}} \)  

(C.15)

and

\[
EP_{\text{Unfished}} = \sum_a E_a e^{-Ma}
\]

(C.16)

**Generation of length composition**

An age-length transition matrix (Hilborn and Walters, 1992) was constructed from the assumptions of mean length-at-age and variation of length-at-age, where the probability of an individual at age \( a \) being in length class \( i \) is given by:

\[
P_{i,a} = \left\{ \begin{array}{ll}
\phi \left( \frac{l_{i+1}^{lo} - L_a}{\sigma_i} \right) & \text{if } i = 1 \\
\phi \left( \frac{l_{i+1}^{lo} - L_a}{\sigma_i} \right) - \left( \frac{l_i^{lo} - L_a}{\sigma_i} \right) & \text{if } 1 < i \leq I \\
1 - \left( \frac{l_i^{lo} - L_a}{\sigma_i} \right) & \text{if } i = I 
\end{array} \right.
\]

(C.17)

where \( \phi \) is the standard normal cumulative distribution, \( l_i^{lo} \) is the upper bound of length class \( i \), and \( I \) is the total number of length classes. The age-length probability matrix was modified for the expected age-length distribution of the catch \( (p) \) to account for the selectivity-at-length by multiplying the age-length transition matrix by the selectivity at length class \( i \) \( (S_i) \):

\[
p_{i,a} = P_{i,a} S_i
\]

(C.18)
The age-length transition matrix for the catch was standardised so that the probability of an individual in the catch at age $a$ being in one of the $I$ length classes was 1:

$$
\hat{p}_{i,a} = \frac{p_{i,a}}{\sum_a p_{i,a}} 
$$

(C.19)

The length composition of the catch ($N_i$) was then constructed by multiplying the vector of catch-at-age by the transpose of the matrix $\hat{p}$:

$$
N_i = C_a \hat{p}^T
$$

(C.20)
D Simulation model to estimate $L_\infty$ from length composition of the catch

D.1 Introduction

Chapter 3 demonstrated that, at equilibrium and assuming no variation in length-at-age, the relationship between $L_\infty$ and the maximum observed length ($L_{\text{max}}$) is determined by the $\frac{M}{k}$ ratio (see Equation 3.5). For example, very few individuals of a species with high $\frac{M}{k}$ (e.g., > 2.5) would be expected to reach $L_\infty$ and $L_{\text{max}}$ is likely to be considerably less than $L_\infty$. On the other hand, species with low $\frac{M}{k}$ are expected to reach $L_\infty$ relatively early in life, and assuming variation in length-at-age, a considerable proportion of the population may be observed at lengths greater than $L_\infty$. Additionally, the exploitation history of a stock will also influence the observed $L_{\text{max}}$, as typically large fish are removed from the population first.

The length-based SPR model requires an estimate of the $\frac{M}{k}$ and $L_\infty$ of the stock. Unless the stock is very lightly fished, or unfished, there is little information on the $\frac{M}{k}$ ratio in the length composition of the stock, and this parameter must be estimated via other means (e.g., meta-analysis, expert judgment, or biological studies; see Chapter Chapter 2). However, given an estimate of $\frac{M}{k}$, the length composition of the catch does provide some information on the possible values of $L_\infty$. For example, if $\frac{M}{k}$ is believed to be quite high, $L_\infty$ would be expected to be considerably larger than the observed $L_{\text{max}}$. Conversely, if $\frac{M}{k}$ was believed to be low, it may be reasonable to estimate $L_\infty$ at or near $L_{\text{max}}$. The development of suitable rules-of-thumb to estimate the parameters from the length composition is an important area for further research. This Appendix presents the methods and R code for a simple simulation model that predicts $L_\infty$ from the expected length composition of the catch. This model was used in Chapter 5 to provide empirical estimates of $L_\infty$ from the observed length structure.

D.2 Methods

The model uses the derivations presented in Chapter 3 to link the expected size composition with the $\frac{M}{k}$ ratio and the level of exploitation ($\frac{F}{M}$). Following the methods outlined in Chapter 3, an age-based model (with an arbitrary time-scale) was used to generate the length frequency data. The expected relationship between the upper quantiles (95 and 99%) of the length distribution to the asymptotic length was then used to estimate $L_\infty$ from the observed length data.
The algorithm to estimate the relationship between the maximum observed size in the catch and the $L_\infty$ parameter requires five input parameters: $\frac{M}{k}$ and $CV_{L_\infty}$ which are both assumed to be known, $\frac{F}{M}$ which is estimated by the LB–SPR model, length at knife-edge selectivity ($L_c$), and $L_\infty$ which is in a relative scale, and can be set to any arbitrary value.

Assume $\dot{M}=0.05$ (in an arbitrary time-scale; see Chapter 3), then the von Bertalanffy growth parameter (again in an arbitrary time-scale) can be calculated as:

$$\dot{k} = \frac{\dot{M}}{M_k}$$ (C.1)

Similarly, the relative fishing mortality ($\dot{\hat{F}}$) is calculated as:

$$\dot{\hat{F}} = \frac{F}{M}$$ (C.2)

Following Chapters 2 and 3, the maximum age is calculated by:

$$A_{max} = \frac{-\log(0.01)}{\dot{M}}$$ (C.3)

The relative growth function for length-at-age ($L_a$):

$$L_a = L_\infty \left(1 - \exp\left(-kA\right)\right)$$ (C.4)

and the standard deviation of length-at-age is:

$$\sigma_{L_a} = CV_{L_\infty} L_a$$ (C.5)

Selectivity is assumed to be knife-edge ($S_a$):

$$S_a = \begin{cases} 0 & \text{if } L_a < L_c \\ 1 & \text{if } L_a \geq L_c \end{cases}$$ (C.6)

The vector of total mortality at age is then:

$$\dot{Z}_a = \dot{M} + (S_a \dot{\hat{F}})$$ (C.7)

The equilibrium population age structure was calculated by:

$$N_a = \begin{cases} R_0 & \text{if } a = 1 \\ N_{a-1} \exp(-\dot{Z}_{a-1}) & \text{if } a > 1 \end{cases}$$ (C.8)

where $R_0$ is the original number of recruits, set at some arbitrary high number. The catch-at-age was calculated with the Baranov equation:

$$C_a = \frac{\dot{F}_a}{\dot{Z}_a} N_a \left(1 - e^{-\dot{Z}_a}\right)$$ (C.9)
An age-length transition matrix (Hilborn and Walters, 1992) was constructed from the assumptions of mean length-at-age and variation of length-at-age, where the probability of an individual at age \( a \) being in length class \( i \) is given by:

\[
P_{i,a} = \begin{cases} 
\phi \left( \frac{l_{i+1}^{lo} - L_a}{\sigma_{la}} \right) & \text{if } i = 1 \\
\phi \left( \frac{l_{i+1}^{lo} - L_a}{\sigma_{la}} \right) - \left( \frac{l_{i}^{lo} - L_a}{\sigma_{la}} \right) & \text{if } 1 < i \leq I \\
1 - \left( \frac{l_{i}^{lo} - L_a}{\sigma_{la}} \right) & \text{if } i = I 
\end{cases}
\]

where \( \phi \) is the standard normal cumulative distribution, \( l_{i}^{lo} \) is the upper bound of length class \( i \), and \( I \) is the total number of length classes. The age-length probability matrix was modified for the expected age-length distribution of the catch \( (p) \) to account for the selectivity-at-length by multiplying the age-length transition matrix by the selectivity at length class \( i \) \( (S_i) \):

\[
p_{i,a} = P_{i,a}S_i
\]

The age-length transition matrix for the catch was standardised so that the probability of an individual in the catch at age \( a \) being in one of the \( I \) length classes was 1:

\[
\hat{p}_{i,a} = \frac{p_{i,a}}{\sum_i p_{i,a}}
\]

The length composition of the catch \( (N_i) \) was then constructed by multiplying the vector of catch-at-age by the transpose of the matrix \( \hat{p} \):

\[
N_i = C_a\hat{p}^T
\]

Finally, the 0.95% quantile of the length distribution was calculated, and divided by the \( L_\infty \) parameter. The resulting ratios were used to estimate the \( L_\infty \) of the stock for Scenarios 5 and 10 in Chapter 5 from the upper 95% quantile of the observed length structure of the catch.

The R Code below implements the algorithm described above.
D.3 R Code

```r
CalcRatios <- function(MK, CV, FM, L50, Linf=100) {
  # Function to generate random sample of length composition
  # and to estimate the relationship between Linf/Lmax and Mk, F/M and
  # L50/Linf.
  Mpar <- 0.05 # Can be set at any arbitrary low value. See derivations
              # in Chapter 3.
  kpar <- Mpar/MK
  if (!length(L50 > 0)) L50 <- 3/(MK+3) * Linf # If length at
  selectivity is unknown, assume that it is same as length-maturity,
  which is assumed to follow equation from Beverton 1992 (see
  Chapter 2 and 3)
  Fpar <- FM * Mpar
  MaxAge <- round(-log(0.01)/Mpar,0) # Define maximum age. See Chapter 2
              # and 3.
  Ages <- 1:MaxAge
  LenVec <- Linf * (1-exp(-kpar*Ages))
  LenSD <- LenVec*CV
  Sel <- rep(0, length(Ages))
  Sel[LenVec >=L50] <- 1
  FVec <- Fpar * Sel
  ZVec <- Mpar + FVec
  Num <- NULL
  Num[1] <- 1E6
  for (X in 2:length(Ages)) Num[X] <- Num[X-1] * exp(-ZVec[X-1])
  Catch <- NULL
  for (X in 1:length(Ages)) Catch[X] <- FVec[X] * Num[X] * (1-exp(-ZVec[X]))
  if (FM == 0) Catch <- Num
  LenVector <- 0:(LinL50 > 0)
  LenPropMatrix <- matrix(NA, nrow=length(LenVector), ncol=length(Ages))
  for (x in seq_along(Ages)) LenPropMatrix[,x] <- dnorm(LenVector,
                                                  LenVec[x], LenSD[x])
  apply(LenPropMatrix,2,sum) # check that all columns sum close to 1 if
  if (L50 > 0)
  LenPropMatrix[1:max(which(LenVector < L50)),] <- 0 apply(LenPropMatrix
  ,2,sum) # no longer sum to 1
  for (x in seq_along(Ages)) {
    if (sum(LenPropMatrix[,x]) > 0) {
      LenPropMatrix[,x] <- LenPropMatrix[,x]/sum(LenPropMatrix[,x])
    }
  }
  apply(LenPropMatrix,2,sum) # sum to 0 or 1
  Lengths <- Catch %*% t(LenPropMatrix)
  LenList <- NULL
  for (x in seq_along(Lengths)) LenList[[x]] <- rep(LenVector[x],
                                             Lengths[x])
  AllLens <- unlist(LenList)
  return(quantile(AllLens, c(0.95, 0.99, 1))/Linf) }
```

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D.4 Use of the model

For the scenarios in Chapter 5 where $\frac{M}{k}$ and $L_\infty$ were assumed to be unknown the above model was run to estimate $L_\infty$ from the length structure of the catch. The model was initially parameterised with the estimated $\frac{M}{k}$ and $\frac{F}{M} = 1$ (assuming that the stock quite heavily fished), and relative length at knife-edge selectivity ($\frac{S_{L50}}{L_\infty}$) was assumed to be 0.3. In subsequent years the model was parameterised with the estimate of $\frac{F}{M}$ and $\frac{S_{L50}}{L_\infty}$ from the previous year.