Prawn tales: A deep dive into the population biology and fisheries management of spot prawns (*Pandalus platyceros*) in British Columbia, Canada

by

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A thesis submitted in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

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Abstract

Marine invertebrates have long supported ecosystems and fed people in Pacific Canada. Today, marine invertebrates increasingly form the foundation of commercial fisheries in Pacific Canada, outpacing the scientific capacity to manage them. Despite their ubiquity, large populations, and broad dispersal as larvae, marine invertebrate populations can and do collapse. Some are sequential hermaphrodites whose complex life histories interact with fishery dynamics in poorly understood ways. This thesis examines the population biology and management of spot prawns (*Pandalus platyceros*) in British Columbia, a protandrous hermaphrodite targeted by a commercial trap fishery operating under a fixed escapement framework. In Chapter 2, I use a theoretical population model to show that variable fishing pressure on males can generate oscillating dynamics in the fishery length, a pattern consistent with commercial data. Limiting male harvest led to a more stable, longer annual fishery with some catch trade-offs. In Chapter 3, I conduct a field experiment that finds high post-release survival of spot prawns under immediate release and cool conditions. These results suggest release-based measures may be effective but depend on handling. In Chapter 4, I empirically assess spring escapement of spot prawn female spawners for three regions in BC. Drawing on fishery data and research survey data, I find that escapement routinely falls below management targets despite fishery data suggesting above-target escapement at fishery close. Post-fishery mortality rates were higher and more spatially variable than currently assumed, potentially reflecting elevated mortality, positively biased catch indices, or both. These findings underline risks of relying on fishery-dependent data and static targets. Together this work provides empirical estimates and analytical tools to support adaptive management by federal and First Nations governments, while illustrating how species-specific investigation of population biology can inform stewardship of growing invertebrate fisheries.

Preface

Versions of the three data chapters (Chapters 2, 3, and 4) included in this thesis are in preparation for submission to peer-reviewed journals. These chapters were collaborative projects and as such are written using the first-person ‘we’ pronoun.

Chapter 2, “This year’s males, next year’s spawners: Minimizing male harvest stabilizes fishery dynamics for a protandrous sequential marine hermaphrodite”, is in preparation for submission to Proceedings of the Royal Society B. This chapter was a collaboration with Dr. Micah Brush and Dr. Mark Lewis.

Chapter 3, “Back to life at depth: Post-release survival of trap-caught spot prawns (*Pandalus platyceros*) declines with increasing air exposure and temperature”, is about to be submitted to ICES Journal of Marine Science. This chapter was a collaboration with Kyra Ford, Jacob Houtman, and Dr. Mark Lewis.

Chapter 4, “Fishery-independent surveys suggest that spot prawn (*Pandalus platyceros*) spawner escapement in Pacific Canada often falls short of management targets”, is in preparation for submission to the Canadian Journal of Fisheries and Aquatic Sciences. This chapter was a collaboration with Dr. Andrew Bateman, Ken Cripps, Kyra Ford, Midori Nicolson, Dr. Christina Service, and Dr. Mark Lewis.

Generative artificial intelligence was not used for any aspect of the writing of this thesis and was not used for any original code or analysis produced in this thesis. Artificial intelligence (Claude models Opus 4.1 and Sonnet 4.5 from Anthropic) was used to support polishing and revising figures (Chapters 2, 3, 4), code debugging (Chapter 4), and table formatting (Chapter 3).

Dedication

In memory of Nik Radosevic and Billy Proctor, whose spirited
lives inspire me to squeeze the juice out of my own.

Acknowledgements

Reflecting on the many people who have supported this work in one way or another is extraordinarily humbling. An interesting and winding road with such good company. I am grateful to anyone who has had the patience to listen to me ramble about prawns over the years.

Thank you to my supervisor, Mark Lewis, for joining me down this rabbit hole and for teaching me so much. I came to you with a collection of ideas about spot prawns and a lot to learn about models. You gave me the space, funding, and encouragement to follow my interests. Thank you for fostering such a curious, generative, and kind research group. Thank you to Stephanie Green for stepping into a co-supervisory role when Mark moved to Victoria and for your enthusiasm and thoughtful feedback throughout my thesis. This work might not have got off the ground without the support of Dennis Rutherford, who agreed to join my committee over lunch in Nanaimo the first day we met. Thank you for helping me navigate the world of spot prawn stock assessment and for hanging in with me after retirement, I’m honoured to be your last professional commitment. Thank you to my external examiners, Rolf Vinebrooke and Will White, for taking the time to read my thesis and participate in its defense. I gratefully acknowledge funding support from Fisheries and Oceans Canada, the Natural Sciences and Engineering Research Council, the North Island Marine Mammal Stewardship Association, the Pacific Prawn Fishermen’s Association, Mitacs, the Musgamagw Dzawada̱’enux̱w Fisheries Group, and the Spirit Bear Foundation.

When I started my PhD, I was worried it might be lonely in the prawn world. Those fears were quickly assuaged by many prawn-y folks who supported this work with their expertise, curiosity, and good humour. Thank you to the prawn folks at DFO including Ken Fong, Andres Araujo, Kyle Krumsick, and Dillon Buerk. Thank you to J.O. Thomas for sending me off as a fishery observer for two years and teaching me the ins and outs of indexing prawns. Many of the ideas in this thesis began as conversations amongst observers – thanks to Doug Tallman, Sylvia Chow, Ficus Chan, and Angus Hunter for sharing your insights and encouraging me in this work. Thanks to Mike Atkins and the PPFA for your support. Many thanks to all the curious, thoughtful folks working on prawn boats for the questions, ideas, and knowledge you shared. Thanks especially to the Nadeau family, Guy Johnston, and Mark Urwin. And thanks to Richard

Michelson for teaching me how to set up prawn groundlines, showing me which knots to use, and encouraging me to just get out there and give ‘er a shot.

Who I am today as a researcher and human being is tremendously influenced by a cluster of islands and inlets off the northeast tip of Vancouver Island and the people I’ve met there. It has been a gift to work and spend time in Musgamagw Dzawada̱’enux̱w territories over the past 10 years. The Dzawada̱’enux̱w, Gwawa’enux̱w, K̠wikwa̱sutinux̱w, and Ha̱x’wamis peoples have stewarded their territories in the Broughton Archipelago and mainland inlets for thousands of years and continue to today. Thank you to Midori Nicolson and the Musgamagw Dzawada̱’enux̱w Fisheries Group for the time, trust, on-the-ground support, and knowledge you contributed to this work.

Ideas for this research percolated many years ago on Gilford Island. Thank you to Coady Webb for first introducing me to the quirks of spot prawns and their fishery and setting me on this path. Otherwise, I would probably have done a salmon PhD and bless ‘em but we’ll surely live without another one of those. Thank you to Salmon Coast Field Station for being the home base for much of this work. Thanks especially to Amy Kamarainen, Caroline Glass, Bogdan Kraft, and the SCFS board. Thanks to the dynamite field crew that first season: Kyra Ford, Kate Fleming, Kylie Milne, and Jay Speier. That was a lot of work and a lot of fun. Thanks to my mum, Cate, for packing a U-Haul to the brim with prawn gear with me and driving it up island. And thanks to everyone who lent a hand that summer: Julie Charbonneau, Rose Chisholm, Lilly Crosby, Sean Godwin, Rob Hummeny, Madeline Jarvis-Cross, Kate Medcalf, and Jess Williamson. Thanks to the field techs who braved blizzards and outflow winds to count prawns in the winter with me: Alana Coon, Deano Coon, Rob Humenny, Kyra Ford, Jessy Phillips, and Julia Smith. That was a lot of work and not always a lot of fun! A lot of boat and hydraulics logistics (mishaps) took place in Port McNeill. Thanks to the folks at Shop-Rite (Andrew, Keith, and Thor), Logan at Micron Machine Works, and Buddy at BOS for your expertise and good humour and for getting me out of many a pinch.

Billy Proctor lived his whole life in the Broughton and passed away this year. He was a curious, gentle person who maintained a sense of wonder about the world around him for 90 years. The depth and tenderness with which Billy interacted with his home waters and forests inspired many, including me. I first met him in 2016 as an undergrad who couldn't tell a pink fry from a chum. He gave me four sixty-foot boomsticks and held his tongue as I built two floats that I needed to run a field experiment. I am grateful for his company and wisdom over the years. And for his willingness to host my prawn operation in several of its iterations. Many a cold winter day prawning started with a morning visit to Billy and Buster.

Thank you to the Kitasoo Xai'xais Stewardship Authority for your support and for trusting me to work with your prawn data. The KXSA started running prawn surveys in their territories in the 1990s and showed me the ropes of running a prawn show off a small boat. Thanks to Ken Cripps and Christina Service for your logistical and funding support and for your expertise. Thanks to the folks who hosted me in Klemtu and brought me out to count prawns: Rebecca Benjamin-Carey, Nick Duncan, Ben Edgar, Julian Heavyside, Jaspreet Sahib, and Laurel Sleigh.

The University of Alberta, University of Victoria, and University of Bergen were my academic homes for various parts of my PhD. Thank you to Kim Schaerer, Tom Hantos, and Shelley Scott at UAlberta for keeping me safe and administratively on track. Thanks to Michelle and Laura in the UVic Biology department for hosting me and supporting me through the final years in Victoria and thank you to Dave Punzalan for knowing when a whiskey was what was needed. Katja Enberg graciously hosted me as a visiting student during an eight-month jaunt to Norway. Thank you to her and the rest of the Theoretical Ecology Group for welcoming me, for the many interesting discussions over lunch, and for convincing me that things-on-bread truly is the best lunch food. Thank you to the Lewis Research Group for being the most wonderful collection of curious, funny, and kind math biologists. It has been such a pleasure. Plenty of folks have made it a treat including Chris, Peter T., Micah, Evan, Kevan, Shan, Maria, Ferdi, Yueyang, Shibai, and many, many others. Akina, thank you for keeping me sane with our runs this fall – I looked forward to them every week. Kim Wilke-Budinski is the quiet anchor of the LRG who makes the wheels turn. Kim, thank you so much for your kindness and support from the beginning.

My friends humoured a lot of prawn talk and told me when it was time to take break and go on an adventure. Thanks to Tom Rapaport for picking me as your project partner in Grade 12 biology because you thought it'd bump your grade and subsequently becoming one of my closest friends through undergrad and after. Thanks to Peter Harrington for your friendship and the many adventures it has taken us on, including lots of fun bike and ski trips but also three trips to the emergency room. Thanks for being such a kind support for the many medical and existential mishaps of my PhD. I hope we get to go on many more outdoor adventures together and hopefully far fewer to the hospital. Thank you to Simon, Evgeni, and Cole for making those years in Edmonton lots of fun and to the river valley for its company during my rambles. Thank you, Andrew Bateman, for being such a wonderful mentor, colleague, debate adversary, and friend for many years. The last three and half years in Victoria have been a delight. Thanks to Rob Hummeny for your excellent company in discussion and adventure as my friend, roommate, field tech, and walk companion. And thanks to many other friends on the island – Jessy, Jay, Claire, Caroline, Bogdan, and Uli – for good times and good chats.

There aren't many scientists in my family. I probably do what I do because growing up my mum took me and my sister out into Stanley Park every day to muck about in puddles and wander around the forest. Thank you, Cate, for raising me with such love and encouragement and for imparting on me your inquisitive drive to ask questions, read books, and think critically about the world around you. Thank you to my dad, David, for always being interested in what I was up to and always being there to listen, encourage, and share sage suggestions on life and work. Despite being the elder child, I tend to find myself looking up to my sister Clare. She has been a wise and grounding presence in my life for so long and through so much. Thank you, Clare, for being my sister and for all your love in all its shapes throughout this life. Dylan, thank you for your love, humour, deep meandering discussions, and for not once asking me to stop talking about prawns. Finally, thank you to my cats, Dig and Gull, for being such excellent cats.

Table of Contents

List of Tables

List of Figures

Chapter 1.

General Introduction

1.1 The growth of marine invertebrate fisheries

The long-standing problem of understanding and managing exploited species includes challenges posed by complex life histories, climate variability, and multiscale social-ecological systems (Harley and Rogers-Bennett 2004; Pinsky et al. 2011; Malick et al. 2015). Expanding marine invertebrate fisheries face each of these complexities across the world (Anderson et al. 2011b; Boenish et al. 2022), including in Canada where they now represent the economic mainstay of Canadian fisheries on the Atlantic and Pacific coasts (Fisheries and Oceans Canada 2012). The history of Canadian commercial fisheries tracks parallel trajectories of rising dominance and subsequent depletion of Atlantic cod and Pacific salmon fisheries, followed by groundfish, and now the coast-to-coast boom of invertebrate fisheries (Perry et al. 1999; Anderson et al. 2008). Will there be a bust?

Evidence suggests that low-trophic level fisheries are vulnerable to boom-and-bust patterns (Pezzuto and Borzone 1997; Orensanz et al. 1998; Conand 2004; Kirby 2004; Berkes et al. 2006). Recent climate-mediated collapses of Gulf of Maine northern shrimp (Richards and Hunter 2021) and Bering Sea snow crab (Szulwalski et al. 2023; Litzow et al. 2024) underline that even highly abundant species are vulnerable to abrupt collapses. Shifting ecological processes at local and regional scales often, in aggregate, drive broader scale patterns, which in turn interact with social governance processes.

1.2 The fisheries governance context in Pacific Canada

Just as ecological processes span multiple scales, so too do fisheries governance processes and challenges arise when either aspect of a social-ecological system shifts. Fisheries, including for marine invertebrates, have played a critical role in Indigenous food systems for thousands of years and Indigenous governments and communities continue to steward and depend on marine invertebrate populations today (Augustine and Dearden 2014; Ban et al. 2017; Frid et al. 2023;

Salomon et al. 2023; Hayes et al. 2025). In Pacific Canada, the history of fisheries governance over the past almost 200 years is indelibly intertwined with the history of First Nations rights and title (Harris 2008). Fishing rights were central to the development of the First Nations reserve system in British Columbia which was premised on the assumption that First Nations were primarily fishing peoples and thus did not require large land bases (Harris 2008). This approach to First Nations land reserves was juxtaposed by colonial fisheries management approaches that limited First Nations food access and banned traditional fishing techniques as non-Indigenous commercial fisheries expanded through the late 1800s and through the 21st century. Over the last 20 years, with formal recognition of Indigenous rights to fish (*R. v. Sparrow* 1990; *R. v. Gladstone* 1996; *R. v. Van der Peet* 1996), fisheries governance processes have begun to address the need to manage fish populations subject to harvest (and stewardship) from multiple user groups and rightsholders.

Three trends have emerged in Pacific Canada marine invertebrate fisheries: increasing pressure on marine invertebrate fisheries (Perry et al. 1999), changing fisheries governance processes between the crown and First Nations (e.g., Fisheries and Oceans Canada 2021), and mounting uncertainties in the biology and management of marine invertebrate species (Anderson et al. 2008). While the historic details of fisheries governance might seem tangential to a technical thesis in biology, governance conflicts are frequently exacerbated in the presence of uncertainty, a connection which has, in part, motivated this research. The research questions we develop as applied scientists, and how we address them, benefit from thoughtful grounding in the historical context of the social ecological systems we seek to inform. Adapting fisheries management frameworks to suit new governance frameworks is extremely difficult in the absence of sufficient information on the biology and population dynamics of harvested species.

Common threads in the recent history of marine invertebrate fisheries and in the current governance context of fisheries in Pacific Canada also run through the story of the spot prawn trap fishery in British Columbia (BC), the focal topic of this thesis. The overarching goal of this research was to produce information using Western scientific approaches that could be generally useful to our understanding of spot prawn population biology and of their fishery. To that end, this research has been informed and supported by collaborative relationships with government scientists, fishery managers, and prawn harvesters. I have also aimed, through this research, to fill specific information needs of First Nations governments. Components of the research included in this thesis were conducted in collaboration with two organizations representing the stewardship interests of First Nations on the central coast of BC. The Musgamagw Dzawada̱'enux̱w Fisheries Group (MDFG) represents the fisheries and stewardship interests of the Musgamagw Dzawada̱'enux̱w peoples and the four tribes they belong to – the Dzawada̱'enux̱w (Kingcome Inlet), Ḵwikwa̱sut'inux̱w (Gilford Island), Ha̱x'wamis (Wakeman Sound), and Gwawa'enux̱w (Hopetown). Musgamagw Dzawada̱'enux̱w territories lie off the northeast tip of Vancouver Island, including the Broughton Archipelago and neighbouring mainland inlets. The Kitasoo Xai'xais Stewardship Authority (KXSA) provides technical advice and support for stewardship decision making by the Kitasoo Xai'xais community on the north central coast of BC. The Kitasoo Xai'xais Nation represents the Kitasoo and Xai'xais peoples with a community based in Klemtu on Swindle Island. Both the MDFG and the KXSA seek to inform their stewardship of spot prawn populations and fisheries in their territories, and this thesis research makes one contribution towards that end.

1.3 History, biology, and current challenges facing the spot prawn trap fishery

The history of the spot prawn (*Pandalus platyceros*) trap fishery in BC mirrors that of many high-value invertebrate fisheries (Prince and Hilborn 1998; Perry et al. 2002; Anderson et al. 2011b; Purcell et al. 2014). It followed a period of rapid expansion through the late 20th century and then a period of increasing commercial fishery efficiency alongside increasing measures to manage fishing effort (Fisheries and Oceans Canada 2025). The first record of a spot prawn fishery in BC dates to 1889 but the fishery began in earnest in the early 1900s and basic research on shrimp species in BC started in 1926 (Berkeley 1931). The commercial fishery operated on a small scale until the 1970s when it underwent a period of rapid expansion prompting the Canadian Department of Fisheries and Oceans (DFO) to develop a fixed escapement management framework known as the "Spawner Index" framework (Boutillier and Bond 2000). Since then, the fishery has been managed as a derby-style fishery, where the length of the commercial season varies annually, governed by how quickly a catch index of female spawner abundance crosses a fixed escapement threshold. The management framework has progressed to include license and trap limitations, length-based release measures, moderations on effort, and opening the commercial fishery no earlier than May, post egg release (Fisheries and Oceans Canada 2025). Perhaps the single most influential management shift was the implementation of a single daily haul rule in 2001 which drove an increase in fishery efficiency (Fig. 1.1). The length of the fishery has rapidly declined from most of the year in the 1990s to as short as 27 days in 2025 (Fig. 1.2) (Fisheries and Oceans Canada 2025).

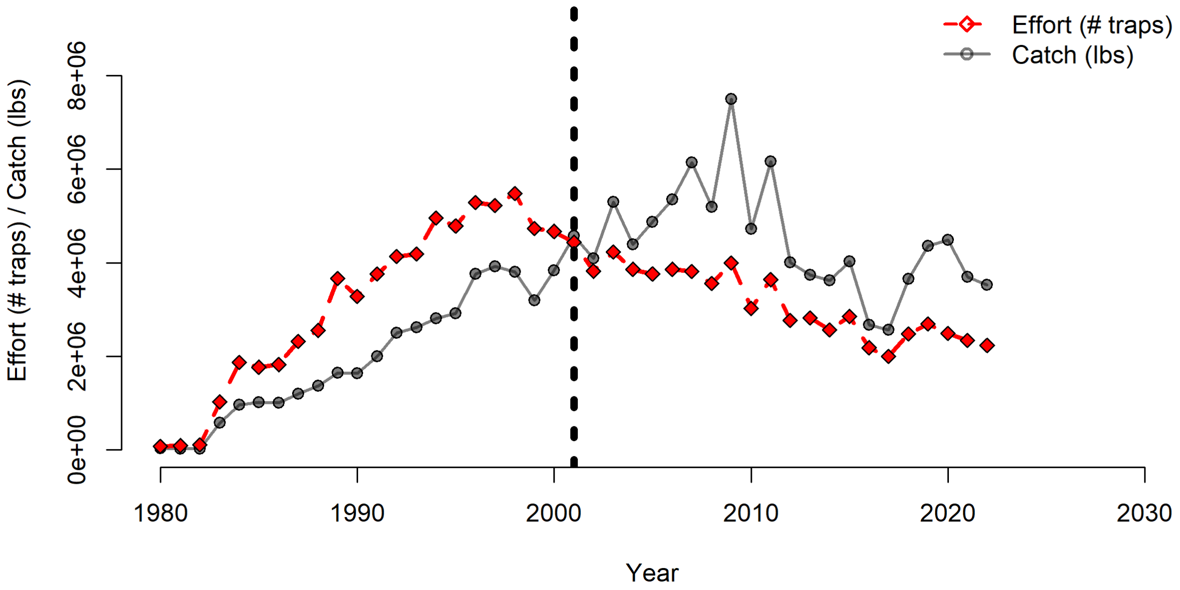

Figure 1.1 Trends in catch and effort in the commercial spot prawn fishery. Annual number of traps set and total reported catch from the commercial fishery across British Columbia. Data sourced from the Shellfish Data Unit at Fisheries and Oceans Canada.

Spot prawns are sequential protandrous hermaphrodites with a highly mobile larval dispersal stage followed by a relatively sedentary remaining life as adults. Their geographic range extends from Mexico up to Alaska (Lowry 2007) and as adults they inhabit depths of ~45-250 m (Bergstrom 2000; Lowry 2007). Juvenile spot prawns hatch from eggs immediately upon their release from brooding females circa March-April and begin their larval dispersal stage, settling in shallow water (10-15 m) two or three months later (Berkeley 1931; Butler 1964). Young prawns migrate from shallow nursey areas into deeper water where they continue to mature and subsequently reproduce as males (Marliave and Roth 1995). Spot prawns tend to inhabit rocky shelf type habitat as opposed to the flat muddy bottom habitat type inhabited by most other

Pandalid shrimp species (Berkeley 1931; Butler 1964). Most spot prawns transition from male to female at age three, although there is evidence in some Pandalid shrimp of early maturing females (Charnov and Anderson 1989; Bergstrom 1992). In BC, there is no reported evidence for early maturing female spot prawns. Mating between males and females occurs from the late summer through early fall and is direct, with males attaching spermatophores directly to the female abdomen and the female extruding eggs (Lowry 2007). The specific details of spot prawn mating systems (e.g., whether they form breeding aggregations) is not well understood. Females continue feeding as they brood eggs through the fall and into the spring when egg release occurs. In BC, the life span of spot prawns is thought to be four years – females are assumed to only spawn once and die shortly after egg release (Butler 1964). However, in Alaska there is evidence for repeat breeding in females (Kimker et al. 1996) and there is evidence that post-spawn females contain developing ova (Berkeley 1931). Experiments have also documented post-spawn females surviving to reproduce a second time (Prentice and Rensel 1977).

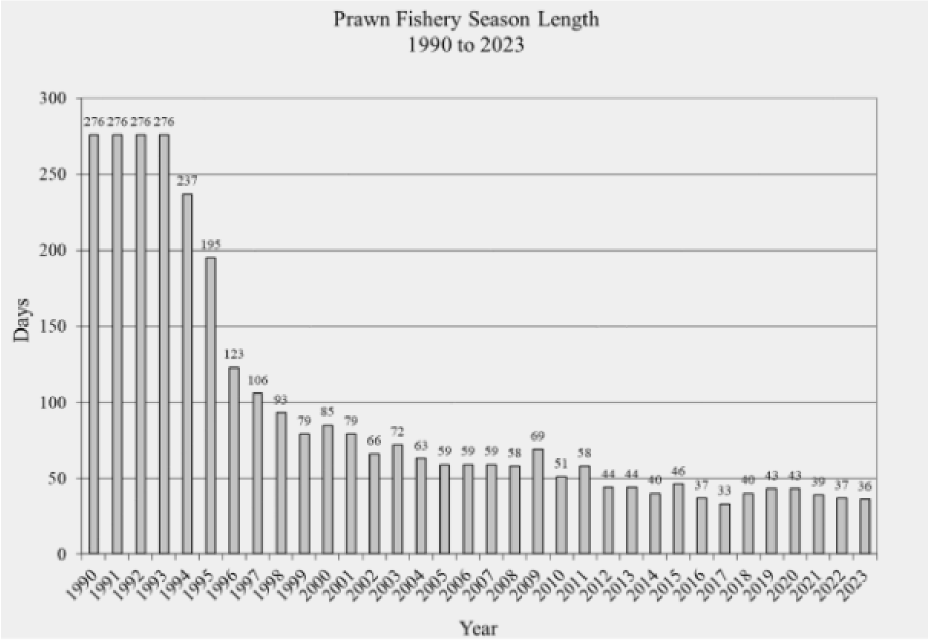

Figure 1.2 Length of the commercial spot prawn fishery in British Columbia from 1990-2023.

Figure sourced from (Fisheries and Oceans Canada 2025)

Previous research has investigated the mortality (Boutillier and Bond 2000), growth (Butler 1964; Kimker et al. 1996), and recruitment (Boutillier and Bond 2000; Smith 2014) of spot prawns in the northeast Pacific. Recent studies have illuminated potential mechanisms for sex change in spot prawn (Levy et al. 2020, 2021) and numerous studies have dug into the evolutionary dynamics of sex change in other Pandalid shrimps (Charnov 1979; Charnov and Anderson 1989; Charnov and Groth 2019). In BC, there has been relatively sparse research attention devoted to spot prawns and their commercial fishery over the last several decades following the initial development of the management framework (Boutillier 1987; Boutillier and Bond 2000). Two graduate students investigated rockfish bycatch (Favaro et al. 2010, 2014) and the Spawner Index management system (Smith 2014), providing important contributions to our understanding of the fishery. Many questions remain.

Many knowledge gaps persist in our understanding of the biology of spot prawns in BC. They include whether and how mortality varies over time and space, the specifics of their mating dynamics, and the spatial structure and connectivity of populations in BC. Important management uncertainties persist including survival post catch-and-release, consequences of stage-specific harvest, and the relationship between spawner escapement at time of fishery closure and survival to reproduce as females the following spring. A third category of uncertainty is in our measurements of the system including, for example, the relationship between catch indices and the underlying population dynamics. Across uncertainties, there is a clear need for data collected outside of the commercial fishery. I will not answer each the questions I introduce above, which feasibly could occupy an interested biologist for a career or two. I will, however, make contributions to each of the three categories of uncertainty and collate or collect fishery-independent data from three regions across the BC coast.

1.4 Tools for understanding population and fisheries dynamics

I confront the research questions in my thesis using theoretical models, field experiments, and hierarchical statistical models. These tools each offer their own unique insights.

1.4.1 Field experiments

Field experiments facilitate testing specific hypotheses in a controlled but realistic setting. Experiments and population models ask questions at distinct but mutually informative levels. Models can be useful to determine the necessary information to understand population-level dynamics. Once identified, specific uncertainties can be addressed at a mechanistic level through various empirical methods including experiments. Empirical estimates can then inform future modelling work – connecting individual level processes to population level dynamics is a central motivation for many ecologists.

1.4.2 Dynamical population models

Theoretical dynamical models are mathematical tools describing how systems change over time, capturing how current conditions determine future states through equations that can reveal patterns in complex systems (Caswell 2001; Otto and Day 2007). They are used across many fields, from physics to economics to ecology. Dynamical population models are especially useful in ecology when the purpose is to understand emergent behaviour, often in contexts that include non-linear dynamics describing scenarios where growth rates depend on population size (i.e., density dependence). They have been applied to fisheries problems for over 100 years (Baranov 1918) and most fisheries modelling studies still rely on equations developed long ago (e.g., Baranov 1918; Ricker 1954; Schnute 1977; Beverton and Holt 1993).

Theoretical population models are useful because they can be analytically tractable, allowing for more general insights, or they can be investigated through numerical methods to understand specific scenarios. They force us to explicitly state our assumptions about how we think a system might work (through equations) and they provide a method to pose and pursue “what if?” questions, exploring unrealized states in the systems we study. Fisheries ecologists often confront the practical realities of the time and expense required to address abundant knowledge gaps and thoughtfully constructed theoretical models can be one powerful way to prioritise empirical research. What are the consequences of uncertainty in one parameter versus another? If we make this assumption or that one, does it matter? Addressing such questions empirically is not always possible or practical and theoretical population models have proved a valuable tool in fisheries science, including to understand the population dynamics of marine invertebrates.

Ecologists have drawn insights into the population dynamics of marine invertebrates and their fisheries using theoretical models to investigate metapopulation persistence (Botsford et al. 1994), the consequences of stage-selective harvest (Botsford 1995), mechanisms underlying density dependence (Lundquist and Botsford 2011), and the fishery implications of hermaphroditic life histories (e.g., Armsworth 2001; Alonzo and Mangel 2004; Alonzo et al. 2008; Easter and White 2016; Easter et al. 2020). Stage-structured models have shown that targeting large, highly fecund individuals can lead to population collapse even when total harvest rates appear sustainable (Birkeland and Dayton 2005). Metapopulation models have demonstrated the importance of larval connectivity in maintaining regional population stability (Botsford 2001) and work on sequential hermaphroditism found that size-selective fishing can create severe sex ratio imbalances, reducing reproductive success (Armsworth 2001). Models of density dependence have identified recruitment bottlenecks as key regulatory mechanisms in many marine invertebrate populations (Lundquist and Botsford 2011). Ultimately, theoretical models usually generate new hypotheses and research questions that are well addressed by confronting model predictions with empirical data within a statistical framework (Hilborn and Mangel 1997). This iterative process of theory development and statistical validation (or rejection) has advanced both our fundamental understanding of marine invertebrate population dynamics and our ability to manage their fisheries sustainably.

1.4.3 Hierarchical statistical models

Confronting questions (often posed as models) with data is fundamental to most scientific pursuits. Partitioning variance in ecological systems is a tricky task. Ecology is a uniquely observational discipline and thus a different kind of statistics is needed to partition sources of variance including process variance (uncertainty in biological processes), observation variance (uncertainty in measurements), and structural uncertainty in the model itself. Fortunately, the range of available statistical tools has rapidly expanded since Baranov's time, and ecologists are increasingly able to meet the complexity of their systems with appropriately complex models. Hierarchical models, that explicitly account for data structure at multiple levels, have become a critical tool to partition and understand sources of variance in ecological systems including fisheries.

In this thesis, I employ each of these approaches to address related questions to do with the population and fisheries dynamics of spot prawns in British Columbia, Canada.

1.5 Overview of thesis

My thesis comprises three connected investigations. In my second chapter, I developed a discrete-time stage-structured model for the dynamics of spot prawn populations including a sub-model for the fishery dynamics. I was motivated by the uncertainty in our understanding of spot prawn population biology and in our understanding of how the current fishery interacts with their unique hermaphroditic life history. A relatively simple population model that could be used to explore "what if" questions, in and beyond this thesis, was clearly needed at this point in the development of the fishery. The question I address with the population model (what are the consequences of fishing the males in a protandrous hermaphroditic fishery?) was motivated, in part, by many conversations I had with commercial fishermen on the fishing grounds during the two years (2020-2021) I spent working as an at-sea fishery observer.

One relevant uncertainty that emerged from my second chapter was whether prawns survive the process of being captured and released, as that underlies the effectiveness of release-based management measures currently used to prevent overfishing male spot prawns. In my third chapter, I conducted a field experiment to evaluate post-release survival of trap-caught spot prawns across a range of air exposure and air temperature. Post-release survival is an increasingly recognized uncertainty in fisheries management (Davis 2002), including for the spot prawn fishery. How seriously release-based management measures should be considered as a tool in the spot prawn fishery depends on how effective those measures are at protecting individuals from commercial and recreational fisheries.

Finally, in my fourth chapter, I use fishery-independent population surveys to confront the Spawner Index management framework with data. The results of my second chapter were most sensitive to uncertainty in survival rates, and I revisit this uncertainty by estimating post-fishery survival for three regions on the Pacific coast of Canada. This analysis is the first time post-fishery mortality has been empirically estimated for the spot prawn fishery in BC in 25 years and it produces the first empirical assessment of regional variation in post-fishery spawner dynamics.

Chapter 2.

This year's males, next year's spawners: Minimizing male harvest stabilizes fishery dynamics for a protandrous sequential marine hermaphrodite

2.1 Introduction

Across the world, marine invertebrate fisheries are on the rise, in terms of total catch as well as the growth of new fisheries (Anderson et al. 2011b; Boenish et al. 2022). Canada is no exception, where invertebrates now represent the highest value fisheries on both the Atlantic and Pacific coasts (Fisheries and Oceans Canada 2012; DFO 2023). While marine invertebrates have been a stable, integral part of local food systems for thousands of years (e.g., Augustine and Dearden 2014), the expansion of commercial invertebrate fisheries is relatively recent. Driven by many factors including growing markets (Purcell et al. 2014), declines in higher trophic level fisheries (Pauly et al. 2001; Rogers-Bennett and Juhasz 2014), and increases in abundance thought to be connected to predator release (Myers and Worm 2003; Baum and Worm 2009), the growth of invertebrate fisheries comes with risks and opportunities warranting attention.

For over 20 years, researchers have noted the risks of 'gold rush' invertebrate fisheries including serial depletion (Orensanz et al. 1998; Anderson et al. 2011a; Eriksson and Byrne 2015), unreliable indices of abundance (Prince and Hilborn 1998), and life histories that make them vulnerable to overfishing (Uthicke et al. 2009). Recent decades have also seen notable invertebrate collapses including most Alaskan crab and shrimp fisheries in the 1990s (Litzow et al. 2013), the Gulf of Maine shrimp fishery in the early 2010s (Richards and Hunter 2021), and the high-profile collapse of Bering Sea snow crab in 2021 (Szulwalski et al. 2023). Each story has its nuance but abrupt collapses in invertebrate fisheries often occur when high fishing pressure is accompanied by abrupt shifts in climate and/or trophic interactions (Harley and Rogers-Bennett 2004; Litzow et al. 2024). More generally, there is building evidence that certain mixes of fishery management, life history traits, and environmental variability increase collapse risk (Harley and Rogers-Bennett 2004; Essington et al. 2015; Pinsky and Byler 2015; Siple et al. 2019).

The same life history traits that pose risks may also confer resilience. For example, species with short generation times may be more vulnerable to collapse when fishery management can't pivot quickly enough to track productivity changes (Hilborn et al. 2004; Pinsky and Byler 2015) but such species might also recover more readily so long as there is sufficient juvenile recruitment, often aided by pelagically dispersing larval stages (Jamieson 1993), though persistence depends on how populations are connected (Hastings and Botsford 2006a). Uncertainty abounds and science lags (Anderson et al. 2011b). There is a clear need for research that attempts to understand how marine invertebrates, the people who fish them, and the institutions that manage them interact.

To complicate the matter, many marine invertebrates are also hermaphrodites, spending part of their life as males before or after transitioning to or from female. A growing body of literature recognizes the importance of accounting for hermaphroditic life histories in fisheries management (e.g., Armsworth 2001; Alonzo and Mangel 2004; Alonzo et al. 2008; Easter and White 2016). Harvested hermaphroditic fishes are usually but not always (see for example Bauer 2006) sequential, transitioning from one sex to the other part way through their lives. When size and age correlate with sex, as is the case for sequential hermaphrodite fish, it is important to evaluate the impact of fisheries on their population and evolutionary dynamics (Benvenuto et al. 2017). For example, size-selective fisheries can lead to shifts in sex ratios and mate limitation for protogynous (female first) species (Alonzo and Mangel 2004). The persistence of harvested protogynous hermaphrodites can depend on sex change cue and mating mechanism (Easter and White 2016). Protogyny is the most studied form of hermaphroditism in fish (Kuwamura et al. 2020), where transition is often governed by social factors such as the death of a dominant male and mating is typically non-random (Benvenuto et al. 2017). In contrast, many harvested marine invertebrates are protandrous hermaphrodites, transitioning from male to female. For these species, mating is often random and size-at-transition is often fixed at a constant proportion of maximum length (e.g., Charnov and Skúladóttir 2000; Allsop and West 2003) with some evidence that it may be genetically fixed (Marliave et al. 1993). While the full suite of factors and mechanisms governing sex change in protandrous invertebrates is not resolved, there is evidence in pandalid shrimps that the frequency of early maturing females fluctuates, at a population level, in response to the age structure of the population, suggesting some level of plasticity in sex change timing (Charnov 1979; Charnov and Anderson 1989; Charnov and Groth 2019). Whether and how pandalid shrimp assess their status within a group accurately, given that they are not known to form breeding aggregations, has not been thoroughly investigated. An interesting case study in evolutionary theory, pandalid shrimp are also the subject of many important fisheries across the world, including fisheries for spot prawn (*Pandalus platyceros*) across the northeast and northwest coastlines of the Pacific Ocean.

Spot prawns (also known as ‘spot shrimp’) are protandrous sequential hermaphrodites, beginning their lives as males before transitioning and completing their lives as females (Fig. 2.1). Their range on the Pacific coast of North America stretches from Mexico to Alaska and they are found as adults at depths of ~45-250 m (Lowry 2007). Generally, spot prawns begin their lives as pelagic larvae spending 2-3 months in the water column before settling in shallow water as immature males (Marliave and Roth 1995) and migrating deeper as they grow. Unlike other *Pandalus* shrimp, spot prawns are typically found in rocky shelf-type habitat and are less readily captured in bottom trawls along flatter bottoms (Fisheries and Oceans Canada 2024). After spending one or two breeding seasons as males, spot prawns transition to and complete their lives as reproductive females fertilized directly by males in the late summer/early fall. Females brood eggs through the winter months until larvae hatch in the spring circa March-April. The specifics of spot prawn life history vary spatially and ample uncertainty remains with respect to life span, growth, and natural mortality. For example, in Alaska, tagged spot prawns have been recaptured as females in their third breeding season (Kimker et al. 1996) and variation in growth appears to follow latitudinal clines. The relationship between growth and age is not well characterized, largely due to the practical challenge of aging moulting invertebrates (Becker et al. 2018). This study focuses on the spot prawn fishery in British Columbia (BC) where their lifespan is thought to be four years with males transitioning to females in the final year of their life (Butler 1964).

Like many commercial invertebrate fisheries, the spot prawn trap fishery in BC has tracked a dynamic history marked by rapid growth over the past several decades. Beginning in southern BC in the early 1900s, the fishery began to expand quickly in the 1970s which led to the development of a fixed escapement management system introduced in 1979 (Fisheries and Oceans Canada 2024). The fishery is a trap fishery, where fishers set strings of baited traps (typically ~50 traps per string) which soak overnight before being hauled, processed, and reset the following day. Unlike other spot prawn fisheries in Alaska, Washington, and Oregon, the commercial spot prawn fishery in BC is managed as a derby-style fishery based on female catch-per-unit-effort (CPUE) rather than allocated quota. In its current form, managers open the fishery in early May after most egg-bearing females have released their brood. Fishery observers collect stage-structure data from commercial boats including trap-level counts of males, transitioning individuals, and females. Government science staff use these data to produce in-season estimates of the 'Spawner Index', calculated as the sum of the 'transitionals' and females per trap (identified via reproductive appendages on their swimming legs), corrected for trap and bait type, and string-level average Spawner Indices are evaluated within Pacific Fishery Management Area Subareas (PFMAS). Fishery managers close subareas to fishing as the Spawner Index nears or crosses some fixed escapement target assumed to correspond to the spawner population necessary to ensure sufficient spawning females remain the following spring when larvae hatch (Fig. 2.2). Closure decisions are holistic (and somewhat enigmatic), taking into consideration Spawner Index but also fishing effort (number of boats), nearby closures, the rate of decline of the Spawner Index, etc. (Dillon Buerk, *personal communication*, 2023). As more subareas close, boats become concentrated in fewer regions until a coastwide closure is announced.

Multiple measures to manage catch and effort accumulated through the 1980s and 1990s culminating in a major shift in management in 2001 that introduced a single daily haul rule which is thought to have incentivized increased efficiency amongst fishers. Today the fishery is managed with the Spawner Index framework as well as measures to manage male harvest (minimum mesh size, minimum carapace length) and manage effort (trap limits, limited fishing hours). The length of the fishery has declined from over 60 days in the early 2000s to as short as 27 days in 2025. With a management framework reliant on catch data, increasing commercial and non-commercial fishing pressure, and sparse stock assessment science – the last published evaluation of the stock assessment framework was over 20 years ago (Boutillier and Bond 2000) – there is a need to investigate the dynamics of spot prawns, of the fishery, and of how the two interact. Particularly, there is a short-term need to identify opportunities to stabilise the rapidly shortening length of the fishery and minimise risk of collapse.

As the spot prawn fishery has intensified, several factors appear to have driven higher fishing pressure on males. In earlier years, fishers have reported that buyers often only accepted a small proportion of 'mediums' (smaller prawns, typically all or mostly males). Because they were substantially less valuable per kilogram than the larger prawns, there was little incentive to continue fishing a spot where the catch was dominated by males (Phil Burgess, *personal communication*, 2023). As the fishery developed, the relative value of smaller prawns has trended higher both in the international frozen market and as a result of growing local markets which often buy spot prawns live or frozen in mixed size tubs (Mark Urwin, *personal communication*, 2023). Additionally, fishers and fishery observers alike have noted a sense of 'grinding a spot down' even when catch is marginal due to limited options for alternative spots to move. In theory, subareas should close in these scenarios if the Spawner Index is low, but increasing efficiency in the fishery (Rossi et al. 2023) might lead to non-trivial fishing pressure in the interlude between data collection and regional closures. Furthermore, although mesh size and minimum carapace length requirements protect the smaller males, there is no formal mechanism to manage to a fixed escapement target for males as well as spawners. We emphasize that these observations are anecdotal and the perspectives of those involved in the fishery certainly vary. Nonetheless, it is critical to listen to observations from the fishing grounds and the concept of stage-selective harvesting pressure as a destabilizing factor in invertebrate population dynamics is not new (Botsford 1995).

Theoretical models have provided fundamental insights into marine invertebrate population dynamics (Quinn et al. 1993; Botsford 1995; Higgins et al. 1997; Hastings and Botsford 2006a). Stage-structured models facilitate insights into the persistence and stability of marine invertebrate populations (Botsford 1995) and have been applied to understand the role of larval dispersal in connectivity and metapopulation dynamics (Botsford et al. 1994; Hastings and Botsford 2006b). These models have shown how fishery harvest can destabilize population dynamics and the importance of carefully considering age structure (Botsford and Wickham 1978). While such models have been developed and thoroughly explored for many species like Dungeness crab (Botsford and Wickham 1978; Higgins et al. 1997), red sea urchin (Quinn et al. 1993), and other commercially important marine invertebrates in the Pacific Northwest, there has been relatively sparse attention devoted to the intricate life history of spot prawns and their unique fishery in BC (though see Smith 2014; Rossi et al. 2023).

In conjunction with our understanding of the population dynamics of fished species, a question arises: what are the consequences of varying escapement of male spot prawns in the BC commercial trap fishery? The larger size class of males (hereafter referred to as 'mature males') targeted by the commercial fishery largely represent the following year's spawners (transitionals and females). It follows intuitively that mature male fishery dynamics in a given Subarea one year might carry over to the spawner fishery dynamics the following, particularly if there is limited adult migration. For example, consider a year when the starting spawner population size is high. Assuming a constant harvest rate, it takes longer for the Spawner Index to cross the fixed escapement threshold, the Subarea stays open for longer, and the males in the population are subject to a longer fishing period. The remaining mature males transition in the following spring and next year's commercial fishery opens with at a lower starting spawner population size. This in turn leads to a shorter fishery, lower cumulative fishing pressure on mature males, leaving more to transition to spawners and culminating in a feedback loop (Fig. 2.3) between fishery and population dynamics that we might expect to drive variability in the length of the fishery at local scales.

In this paper, we draw on theoretical population models and empirical data to investigate whether harvesting males drives variability in the length of the spot prawn trap fishery in BC. Our focus on this phenomenon is guided by on-the-ground observations, the availability of broad scale data to assess observational evidence for this hypothesis, and the ability to explicitly compare alternative scenarios and sets of assumptions with theoretical population models to better understand potential mechanisms and uncertainties. We investigate whether there is evidence for this proposed feedback loop and assess the potential of alternative management approaches to stabilise the fishery length. We discuss these results in the context of potential trade-offs between fishery stability and total catch. Our goal through this study is two-fold: first, to investigate a specific phenomenon in the spot prawn fishery and second, to develop a relatively simple population model that can be extended to pursue the many questions that abound for the spot prawn fishery in BC.

We pursued two lines of inquiry into the interaction between spot prawn life history and the fishery management framework in BC. The first, and primary, approach involved developing a stage-structured population model with a tailored fishery sub-model to compare alternative management regimes through simulation. This allowed us to address whether status quo management could, in theory, drive oscillating dynamics in the fishery length. The nature of the theoretical model also allowed us to evaluate how the contrast in management regimes was influenced by varying levels of survival and harvest rate. The second line of inquiry built on the theoretical foundation to ask whether there is observational evidence for oscillations in the commercial fishery length using spectral analysis. Together these two lines of inquiry demonstrate that variable male harvest can and may drive oscillating dynamics in the length of the commercial spot prawn fishery.

2.2 Methods

First, we outline the methods for constructing a model for spot prawn population and fishery dynamics. We then describe how we parameterized the model and the set of alternative scenarios we investigated through simulation. We follow with the methods for the analysis of commercial fishery length data.

2.2.1 Developing a population model with annually varying fishery dynamics

To model the population dynamics of spot prawn and their fishery management in British Columbia, we developed an age-structured, discrete time population model that tracks five life stages year-to-year. Here, we start by defining a simple annual model without fishing dynamics (which we used to define the stable stage distribution in the absence of fishing) before outlining our approach to incorporating a seasonal commercial fishery sub-model capturing the nuances of the management context in BC.

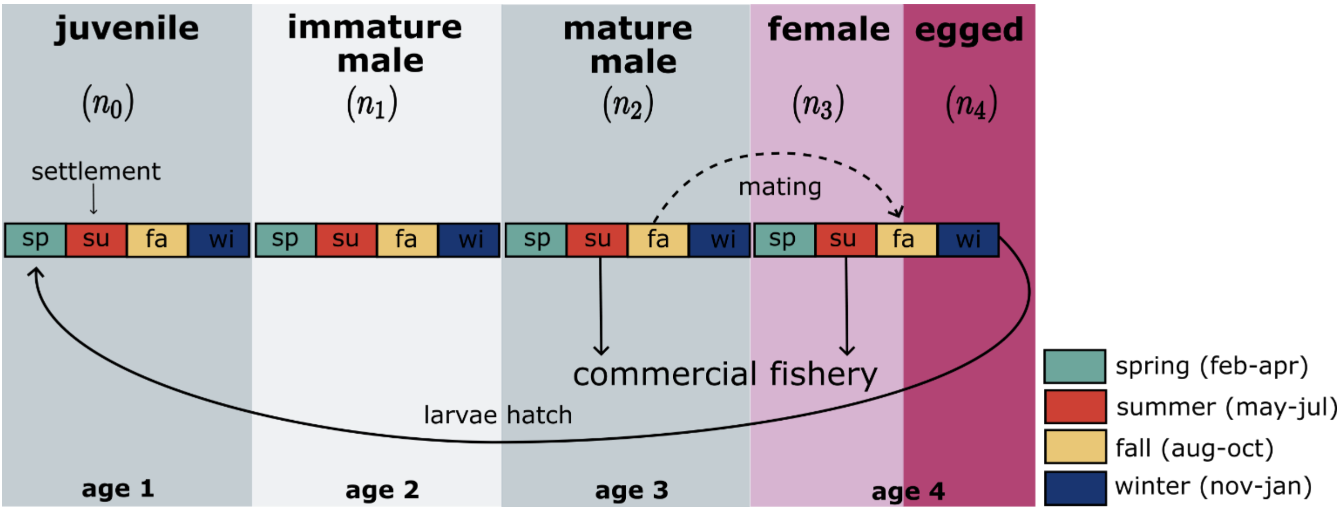

Figure 2.1 Schematic figure visualising the annual (panels) and seasonal (coloured boxes) population dynamics of hermaphroditic spot prawns subject to commercial fishery harvest.

Unfished annual population model

To describe spot prawn population dynamics in the absence of fishing, we defined an annual age-structured population model that tracks five stages from year t to year $t + 1$: juveniles (n_0), immature males (n_1), mature males (n_2), females (n_3), and egged females (n_4). The census time for the model is February, just before larvae hatch from egged females. There are no non-egged females, n_3, in the population because all reproductive females are egg-bearing at this time of year and the mature males have yet to begin transitioning to female. The female stage is an ephemeral stage, lasting for just a portion of the year (Fig. 2.1), but to keep notation consistent, we include it in the description of the simple annual model:

$$n_0(t+1) = \underbrace{R\big(n_4(t)\big)}_{\textbf{recruitment}}, \tag{1.1}$$

$$n_1(t+1) = G_0 n_0(t), \tag{1.2}$$

$$n_2(t+1) = G_1 n_1(t), \tag{1.3}$$

$$n_3(t+1) = 0, \tag{1.4}$$

$$n_4(t+1) = G_2 n_2(t)\,\underbrace{P_b\big(n_1(t)\big)}_{\substack{\textbf{fertilization}\\ \textbf{probability}}}. \tag{1.5}$$

Individuals transition into the immature and mature male stages and survive with probability G_0 and G_1 respectively (Eqs. 1.2 and 1.3). The $n_4(t)$ stage is populated by individuals who transition from male to female and survive (G_2) and will subsequently become egg-bearing.

Recruitment into the juvenile stage class (Eq. 1.1) is defined as a function of the egged females in the previous year with fecundity δ eggs-per-female. In principle, recruitment can take multiple forms. In the absence of evidence for overcompensation in spot prawn, for this study we assume that recruitment follows Beverton-Holt dynamics, which captures compensatory density dependence (Beverton and Holt 1993),

$$R\big(n_4(t)\big) = \frac{\alpha\delta n_4(t)}{1 + \beta\delta n_4(t)}, \tag{2}$$

where α represents juvenile survival in the absence of density dependence and β represents density-dependent survival during the settlement process (when you might expect competition to occur).

A mating function, $P_b\big(n_1(t)\big)$, describes the probability of fertilization during the length of the breeding season, τ, as a function of immature males (who will transition to and reproduce as mature males in the summer of year t) and a pair-forming rate, σ:

$$P_b\big(n_1(t)\big) = 1 - e^{-\sigma n_1(t)\tau}. \tag{3}$$

See Appendix A for further details regarding the mating function.

The annual population model (Eqs. 1.1-1.5) describes the fishery-independent dynamics of spot prawns and is relatively simple. Modelling the dynamics of the simple annual model produces the steady states of the stages in the absence of fishing, which we use as initial conditions for the simulations of the dynamics including fishery harvest (details below). To explore the interaction between population and fishery dynamics, we extend the model to include a seasonal commercial fishery sub-model.

Annual population model with fishery mortality

The commercial trap fishery for spot prawns in BC is unique in its timing and management and investigating applied questions to do with the fishery requires developing an appropriately nuanced model. We start by including a fishery mortality term in the original population model for the two susceptible stage classes, mature males and females:

$$n_0(t+1) = \underbrace{R\big(n_4(t)\big)}_{\textbf{recruitment}}, \tag{4.1}$$

$$n_1(t+1) = G_0 n_0(t), \tag{4.2}$$

$$n_2(t+1) = G_1 \quad \underbrace{F}_{\substack{\textbf{fishery}\\ \textbf{mortality}}} \quad n_1(t), \tag{4.3}$$

$$n_3(t+1) = 0, \tag{4.4}$$

$$n_4(t+1) = G_2 \underbrace{P_b\big(n_1(t)\big)}_{\substack{\textbf{fertilization}\\ \textbf{probability}}} \quad \underbrace{F}_{\substack{\textbf{fishery}\\ \textbf{mortality}}} \quad n_2(t). \tag{4.5}$$

We initially define fishery mortality generally, as a constant source of mortality, much the way we define the other survival terms. This approach would be reasonable if the fishery were managed such that a fixed proportion of the population was harvest each year. However, the commercial spot prawn fishery varies year-to-year, and thus we redefine fishery mortality to be $F\big(n_3(t)\big)$, a function of the female population at the start of the fishery season. Defining this function, which depends on an ephemeral stage class only populated for a subset of the year, requires that we refine our simpler annual model to appropriately capture seasonal fishery dynamics.

Seasonal population model with annually varying fishery dynamics

To define fishery mortality at the appropriate seasonal (and interannually varying) scale, we must define a seasonal version of the simpler annual model (Fig. A.2). We begin by making a simplifying assumption that males are not a limiting factor to fertilization and that $P_b\big(n_1(t)\big) = 1$. This assumption is supported so long as the male population is even moderately abundant and the pair-forming rate, σ, is not low (Fig. A.1). This revises Equation 4.4 to,

$$n_4(t+1) = G_2 \underbrace{F\big(n_3(t)\big)}_{\substack{\textbf{fishery}\\ \textbf{mortality}}} n_2(t). \tag{5}$$

We define a version of the model comprised of four seasons: Spring (P, February through April), Summer (S, May through July), Fall (F, August through October), and Winter (W, November through January). The seasons are delineated to approximately align with points in the year when data are collected through both fishery-dependent or -independent sampling.

In the following equations, we use superscripts to indicate season for the population variables, with P for Spring, S for Summer, F for Fall, and W for Winter. For example, $n_0^P(t)$ refers to the individuals in the juvenile stage class at the start of the spring season in year t. A given year starts at the beginning of the spring season with individuals in the juvenile ($n_0^P(t)$), immature male ($n_1^P(t)$), mature male ($n_2^P(t)$), and egged female ($n_4^P(t)$) stages.

In principle, survival probabilities could vary depending on stage and season (hence the subscripts in Eqs. 4.1-4.5 above), but there is limited information on spot prawn survival and so we assume constant survival with respect to stage and season. To simplify notation, we drop the additional stage-specific notation in following equations and adopt $\bar{G}$ to denote seasonal survival (see Appendix for details of converting from annual survival, G, to seasonal survival, $\bar{G}$). The change in the population from the beginning of the spring to the start of the summer season is described as,

$$n_0^S(t) = \delta \bar{G} n_4^P(t), \tag{6.1}$$

$$n_1^S(t) = \bar{G} n_0^P(t), \tag{6.2}$$

$$n_2^S(t) = \bar{G} n_1^P(t), \tag{6.3}$$

$$n_3^S(t) = \bar{G} n_2^P(t), \tag{6.4}$$

$$n_4^S(t) = 0. \tag{6.5}$$

The set of equations above describe survival of egged females ($\bar{G}$) and the release (with fecundity, δ eggs-per-female) of pelagic larvae (Eq. 6.1), the transition of juveniles to immature males (Eq. 6.2), the transition of immature to mature males (Eq. 6.3), the transition of mature males to females (Eq. 6.4), and the death of last year's reproductive females after releasing their eggs (Eq. 6.5). The seasonal model tracks five stage classes across each season and its key biological and fishery events (Fig. A.2).

A key season for the focus of this study is the Summer season, during which the commercial fishery occurs. During the summer season, individuals are present in the juvenile, immature male, mature male, and female stages. No egged females are present yet, as breeding is assumed to occur during the Fall season. From the start of Summer to the start of Fall, the population changes as follows:

$$n_0^F(t) = \underbrace{r\left(n_0^S(t)\right)}_{\substack{\textbf{recruitment}\\\textbf{function}}}, \tag{7.1}$$

$$n_1^F(t) = \bar{G}n_1^S(t), \tag{7.2}$$

$$n_2^F(t) = \underbrace{f\left(n_3^S(t)\right)}_{\substack{\textbf{fishery}\\\textbf{mortality}}}\bar{G}n_2^S(t), \tag{7.3}$$

$$n_3^F(t) = \underbrace{f\left(n_3^S(t)\right)}_{\substack{\textbf{fishery}\\\textbf{mortality}}}\bar{G}n_3^S(t), \tag{7.4}$$

$$n_4^F(t) = 0. \tag{7.5}$$

This set of equations describe density-dependent recruitment as larval juveniles settle (Eq. 7.1), survival of immature males (Eq. 7.2), and survival of the two commercially vulnerable stage classes – mature males (Eq. 7.3) and females (Eq. 7.4). We use lowercase to distinguish the recruitment and fishery functions in the seasonal model from those in the annual model (the formulation is slightly different between the two models to ensure they map directly to one another).

The key event during the Summer season, and the focus of this study, is the commercial fishery. To explore the dynamics of alternative management scenarios, we include a fishery sub-model, represented by the function, $f\left(n_3^S(t)\right)$, which captures commercial harvest of mature males (Eq. 7.3) and females (Eq. 7.4),

$$\underbrace{f\left(n_3^S(t)\right)}_{\substack{\textbf{fishery}\\\textbf{mortality}}} = \exp\left(-\overbrace{h}^{\substack{\textbf{weekly}\\\textbf{harvest rate}}} \cdot \overbrace{w\left(n_3^S(t)\right)}^{\substack{\textbf{fishery length}\\\textbf{(weeks)}}}\right). \tag{8}$$

The mature male and female populations at the end of the summer season are a function of both natural and fishery mortality. The magnitude of fishery mortality depends on the size of the female population at the start of the Summer season (Eq. 8, Fig. 2.2). A key feature of the fishery sub-model is that the length of the fishery, in number of weeks, is allowed to vary annually – this detail is crucial to be consistent with the spot prawn fishery in British Columbia (Fisheries and Oceans Canada 2024) and to investigate the central question of this study. The annual length of the fishery, $w\left(n_3^S(t)\right)$, depends on the size of the female population at the start of the Summer and how long it takes for the female population to reach a fixed escapement target, n_3^{target}, which represents the target number of females at the end of the fishery and does not vary year-to-year. Rearranging Eq. 8, we can solve for the number of weeks the fishery can stay open without crossing the fixed escapement target (the female population size at which the fishery closes),

$$w\left(n_3^S(t)\right) = -\frac{\ln\left(\frac{n_3^{\text{target}}}{n_3^S(t)}\right)}{g+h}. \tag{9}$$

The continuous time natural mortality rate, g, can be calculated from the seasonal survival probability, G. The weekly harvest rate, h, is defined to correspond to low, moderate, or high annual harvest (see Appendix for full details of the fishery sub-model parameterization and simulation steps). We assume that mature males and females experience equivalent rates of harvest during the commercial fishery.

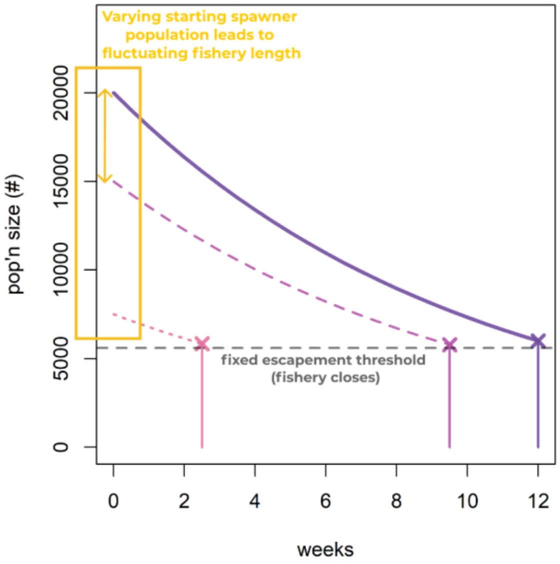

Figure 2.2 Schematic of the spot prawn fishery management approach.
The foundation of the approach is to close the fishery when the spawner population (as measured by an index of the spawner abundance) crosses a fixed escapement threshold. Variation in the initial spawner population at the start of the commercial fishery season leads to a variable length fishery.

After the Summer season, the seasonal model tracks individuals in each stage through the Fall and Winter seasons. The population status at the end of Winter in year t is equivalent to the population status at the start of the Spring season in year $t + 1$. The full seasonal model, mapped from the start of Spring in year t to the following Spring in year $t + 1$ is broadly equivalent to the annual model introduced in Eq. 4.1-4.5 with the exception that fishery mortality is defined as a constant mortality source, F, in the annual model as opposed to the more detailed fishery function just described for the seasonal model. The full derivation of the seasonal model can be found in the Appendix, and the Spring-to-Spring formulation of the seasonal model (the version of the model used in our simulations described below) can be summarized as,

$$n_0^P(t+1) = \bar{G}^3 \underbrace{r(\bar{G}\delta n_4^P(t))}_{\substack{\textbf{recruitment}\\ \textbf{function}}}, \delta n_4^P(t), \tag{10.1}$$

$$n_1^P(t+1) = \bar{G}^4 n_0^P(t), \tag{10.2}$$

$$n_2^P(t+1) = \bar{G}^4 \underbrace{f\left(n_3^S(t)\right)}_{\substack{\textbf{fishery}\\ \textbf{mortality}}} n_1^P(t), \tag{10.3}$$

$$n_3^P(t+1) = 0, \tag{10.4}$$

$$n_4^P(t+1) = \bar{G}^4 \underbrace{f\left(n_3^S(t)\right)}_{\substack{\textbf{fishery}\\ \textbf{mortality}}} n_2^P(t). \tag{10.5}$$

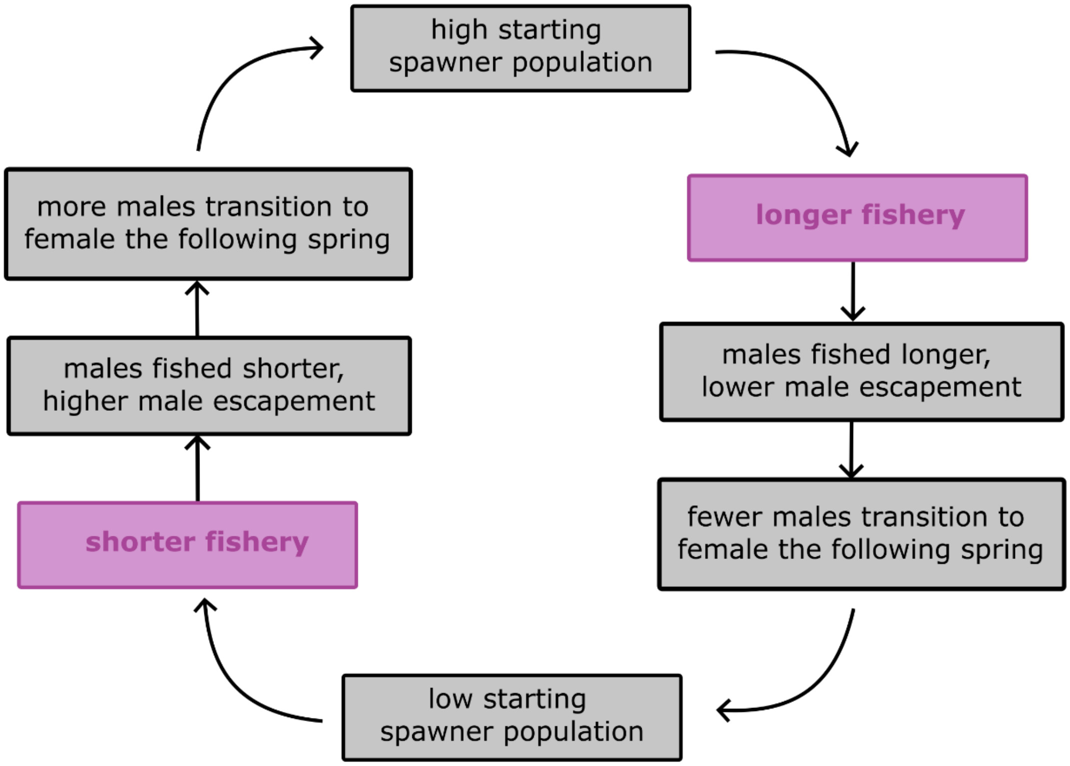

Figure 2.3 Schematic description of hypothesized feedback loop between male harvest and fishery length.

1.2.2 Assessing consequences of male harvest scenarios through simulation

We parameterized and simulated the seasonal population model to investigate the consequences of alternative harvest and survival scenarios and to assess the influence of male harvest on fishery dynamics. We drew on a combination of estimates from previous research and unpublished data (Table 2.1, see Appendix A for full details of parameterization). We set parameter values for seasonal survival, $\bar{G}$, based on previously estimated natural mortality rates (Boutillier and Bond 2000) and we drew on harvest rate estimates from commercial fishery data (Rossi et al. 2023). We parameterized the model for simulation with the spatial scale of a PFMA Subarea in mind because that is the scale at which in-season closure decisions are implemented. Subareas vary in their exact size but are on the order of ~5-30 km^2.

Our analysis focused on two main harvest regimes: male and female harvest (status quo) and a female-only harvest regime, illustrating the hypothesis that harvesting males destabilizes fishery dynamics. Within those two management scenarios, we considered variation in two parameters:

survival probability ($\bar{G}$) and harvest rate (h), chosen to investigate how the contrast between harvest regimes is influenced by harvest and survival conditions. We considered ‘low’, ‘medium’, and ‘high’ parameter values for each focal parameter, which resulted in nine scenarios (e.g., high survival/high harvest) for each of the two management options. For survival, we defined ‘medium’ survival as the average estimate from (Boutillier and Bond 2000) and defined ‘low’ and ‘high’ survival as the lower and upper range of the reported estimates. We chose parameter values for h based on the range of annual harvest rates estimated in (Rossi et al. 2023, see Appendix A for full details).

For each combination of management regime, survival, and harvest rate, we conducted both deterministic and stochastic simulations. For the version of the simulations that included environmental stochasticity, we simulated recruitment as occurring with lognormal annual variability. We applied bias correction (subtracting $\frac{\sigma^2}{2}$ from the normal deviate) to ensure that mean recruitment in stochastic simulations matched the deterministic expectation. Larvally dispersing juveniles at the start of the Summer season settle and experience density-dependent recruitment competition with some environmental stochasticity,

$$r\left(n_0^S(t)\right) = \frac{\alpha n_0^S(t)}{1 + \beta n_0^S(t)} e^{\epsilon}, \tag{11.1}$$

$$\epsilon \sim \mathrm{N}\left(-\frac{1}{2}\sigma^2, \sigma^2\right). \tag{11.2}$$

We initiated the age classes for each simulation at their unfished stable state and tracked the population, fishery length, and fishery catch dynamics for 50 years (see Appendix A for details of calculating fishery catch). We evaluated two alternative management frameworks: “status quo” management (harvesting males and females) and “no male harvest” management (only fishing the females). For each management scenario, we evaluated all combinations of three survival estimates (low, average, and high), three harvest rates (40%, 60%, and 80% annual commercial harvest), and three levels of recruitment variation (CV = 0.2, 0.3, and 0.4). This resulted in a total of 54 simulation scenarios. We focus on the results for the CV=0.2 scenario in the main text but include the accompanying results for the other recruitment scenarios in Appendix A.

We compared fishery dynamics across scenarios by assessing differences in the mean fishery length and the variation in fishery length. To capture differences in variability, we calculated the coefficient of variation for the fishery length (CV, the standard deviation divided by the mean). To assess catch tradeoffs between scenarios, we calculated annual stage-specific fishery yield (landed biomass, see Appendix A for details) and, for each combination of harvest level and survival, we calculated the relative change in 10-year rolling catch between the status quo and no-male-harvest management approaches.

Table 2.1 Table of model parameters, parameter values, and literature sources.

Parameter	Description	Units	Estimate	Range	Source
δ	Fecundity	eggs-per-female	2,700	Fixed	DFO research survey data, see Appendix
α	Recruitment function steepness	settlers-per-juvenile	0.3	Fixed	Chosen to approximate high juvenile mortality expected at this stage, within the range of previous estimates for marine invertebrates (White et al. 2014)
β	Strength of density dependence	juveniles^{-1}	0.0000013	Fixed	Chosen to produce moderate compensatory density-dependence (~1 settled recruit per 20 m^2, based on typical Subarea size)

$\bar{G}$	Seasonal survival	dimensionless	0.803	0.694 – 0.900	Boutillier and Bond 2000 (converted from annual natural mortality rate)
g	Weekly natural mortality rate	week^{-1}	0.01692	0.02808 – 0.00808	Boutillier and Bond 2000 (converted from annual natural mortality rate)
h	Weekly harvest rate	week^{-1}	0.1360 (0.60 proportional harvest per year)	0.0740 – 0.2544 (0.40-0.80 harvest per year)	Rossi et al. 2023.
$w\left(n_3^S(t)\right)$	Fishery length	weeks	Variable; calculated annually within simulation.		
σ^2	Variance in recruitment	dimensionless	$\sigma^2 = \ln(1 + \mathrm{CV}^2)$ Where CV = 0.2	See Appendix for CV = 0.3 and 0.4 scenarios	Set to consider a reasonable range of CV based on the literature, life history, and spatial scale
n_3^{target}	Female escapement target	number-of-females	35% of stable fall female starting population in absence of fishery	Fixed	
b_i	Stage-specific weight during summer season	grams	$b_{n_2^S} = 26$ g $b_{n_3^S} = 35$ g	Fixed	DFO research survey data, see Appendix

2.2.3 Assessing observational evidence for oscillating fishery length in commercial data

To assess whether there is observational evidence for oscillating dynamics in the length of the commercial spot prawn fishery at a local scale, we conducted a spectral analysis of timeseries' of annual fishery length. Spectral analysis takes time series data and decomposes it into different frequency signals with associated amplitudes (Platt and Denman 1975). From this information, we evaluated the dominant frequency and calculated the average wavelength. We calculated the average cycle length (in years) in the fishery length data, which provided the period over which fishery length is oscillating. We assembled 295 timeseries, each associated with a DFO Pacific Fishery Management Area Subarea (PFMAS) in British Columbia. For a given subarea, the time series tracked the annual length of the commercial fishery season (in weeks), as interpreted from the number of weeks with reported commercial landings. We used commercial logbook data provided by the Invertebrate Data Section at DFO and filtered for subareas with a minimum of 10 years of data.

To account for the persistent declining trend in the fishery length over time, we de-trended each time series before calculating the Fast Fourier Transform. We used a locally weighted scatterplot smoothing (LOWESS) technique to estimate and subtract the trend component, which we implemented through the 'pracma' package in R (Borchers 2023). For each detrended time series, we calculated the Fast Fourier Transform (FFT) to obtain a spectrum of the amplitude of different frequencies in the time series. We determined the dominant frequency of the time series as the frequency with the highest magnitude and converted from frequency to wavelength to determine the associated dominant cycle length (in years). We calculated spectra for each time series and visually assessed the dominant cycle length across subareas.

2.3 Results

The no-male-harvest management scenario resulted in a longer, less variable fishery relative to status quo management regardless of harvest rate or survival (Figs. 2.4, 2.5). The variability in the status quo fishery was largely driven by damping oscillations in the deterministic population dynamics of mature males which disappear in the no-male-harvest scenario (Fig. 2.6). The qualitative difference between management scenarios was consistent regardless of recruitment stochasticity, although fishery dynamics were generally more variable when recruitment stochasticity was high (Fig. A.14). Our analysis of fishery length data found some observational support for the hypothesis that male harvest may drive oscillations in the sub-area fishery length with a period length of two years (e.g., Fig. 2.7). Time series length ranged from 17-25 years with an average length of 24.5 years. Across the 295 subareas evaluated, the most common dominant cycle length was ~2 years after accounting for the persistent declining trend across subareas (Fig. 2.8). Other common dominant cycle lengths included ~6 years, ~8 years, and ~11 years.

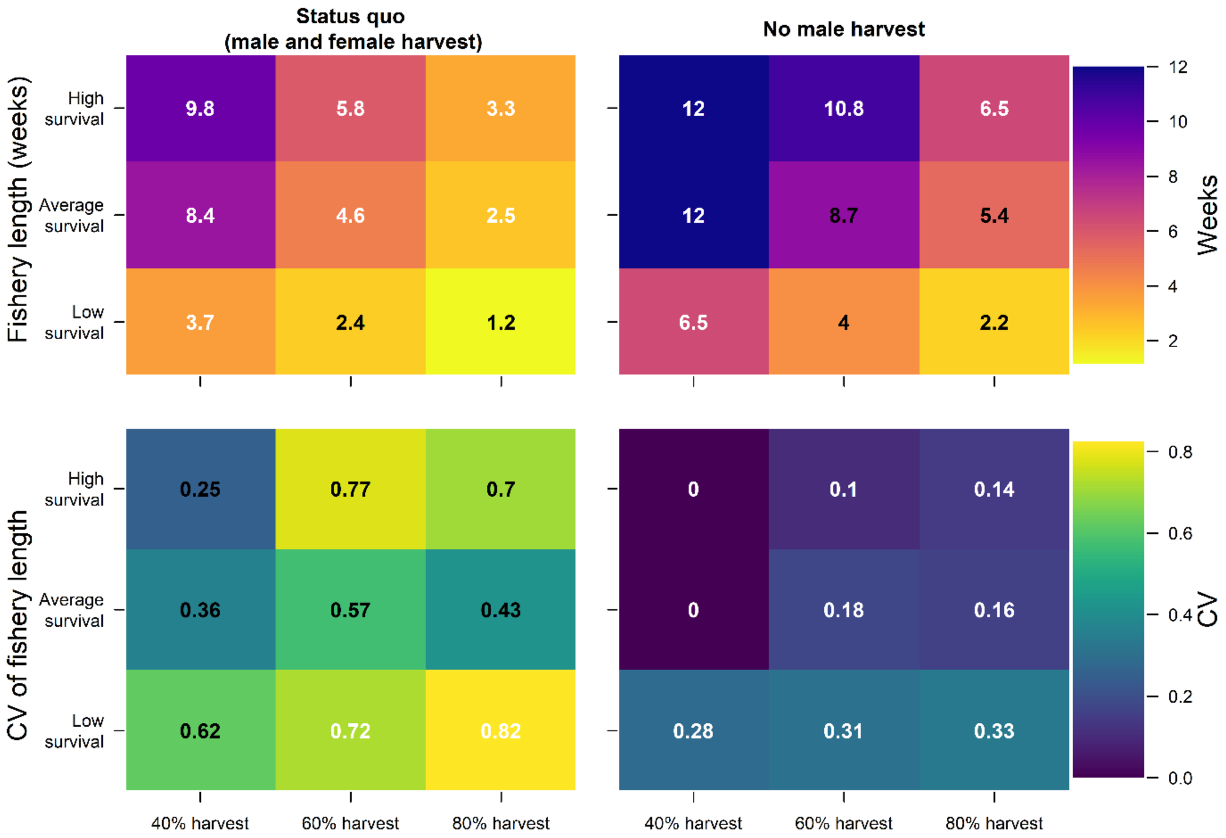

Figure 2.4 Heatmap of fishery length and variation across simulation scenarios. Average length of fishery (top) and coefficient of variation of fishery length (bottom) for two management scenarios (status quo, left and no-male-harvest, right) and across the simulated range of survival and harvest rates. This figure visualizes results for population dynamics when the coefficient of variation in recruitment is 0.2 (see Appendix A for recruitment CV=0.3 and 0.4 scenarios). In general, the fishery is longer and less variable under the no-male-harvest management scenario, at high survival, and at low harvest.

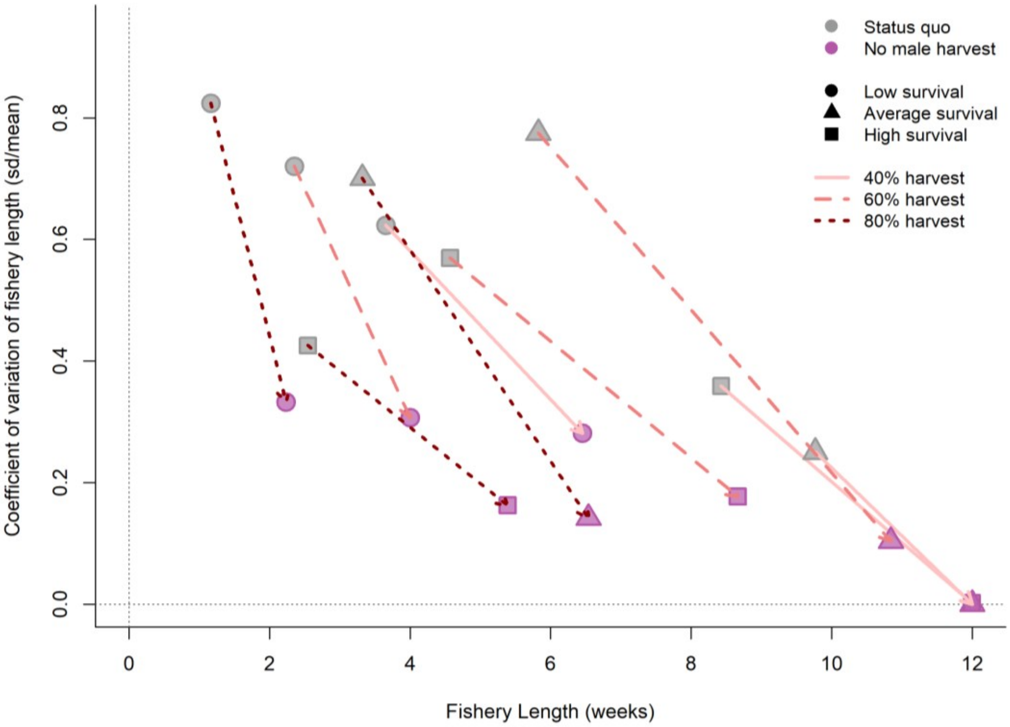

Figure 2.5 Scenario-specific shifts in fishery length and variation.

Arrows depict the shift from status quo to no-male-harvest management regime. Note that for one scenario (average survival, low harvest), the fishery length stabilizes at the maximum length regardless of management approach and thus the points are overlapped at (12, 0).

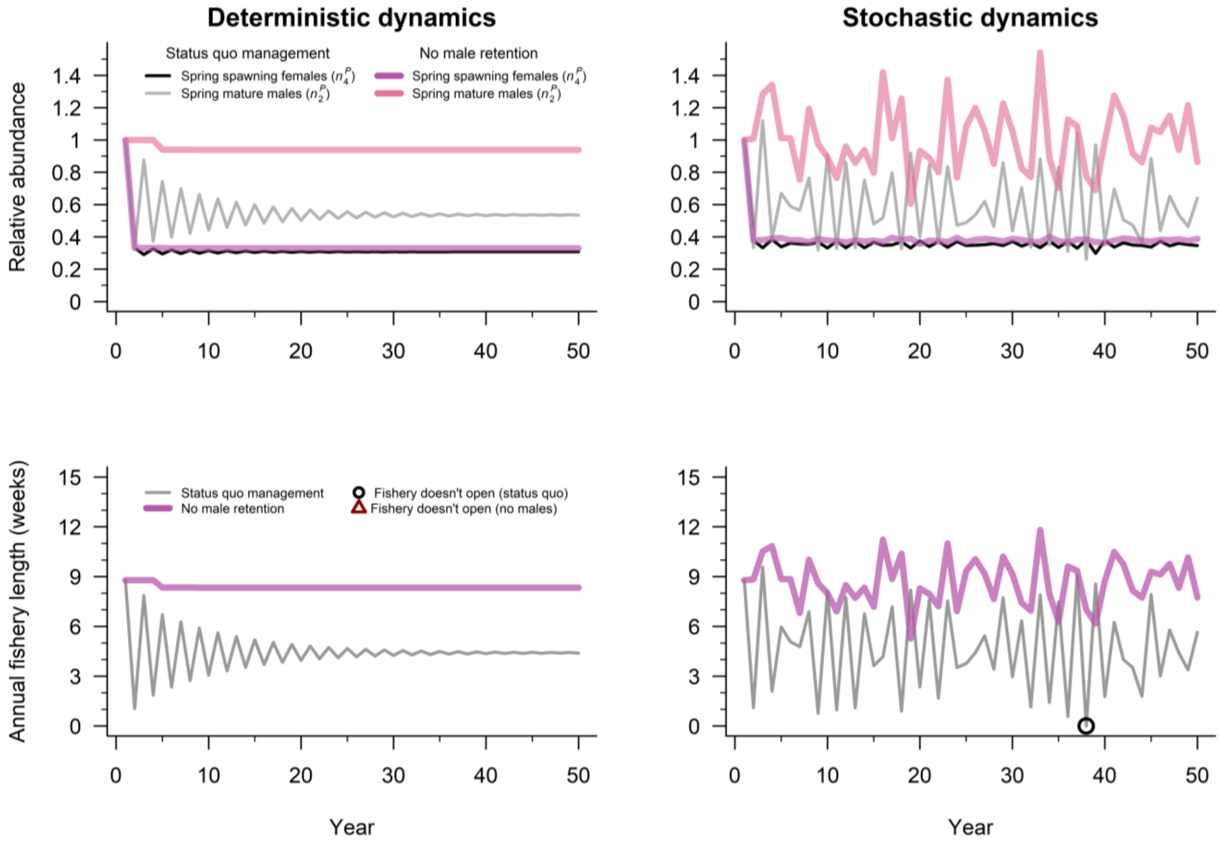

Figure 2.6 Comparing population and fishery length dynamics between status quo and no-male-harvest management scenarios.

Panels visualize deterministic (left column) and stochastic (right column) dynamics for average survival and 60% harvest parameter scenario. Top row visualizes the population dynamics of mature males ($n_2^P(t)$) and egged females ($n_2^P(t)$) at the start of the Spring season. Bottom row visualizes the annual fishery length dynamics. Abundance dynamics are scaled relative to the initial stage-specific population size (the unfished steady state). Grey and black lines visualize dynamics under status quo management whereas light pink and dark pink lines indicate dynamics under the no-male-harvest scenario.

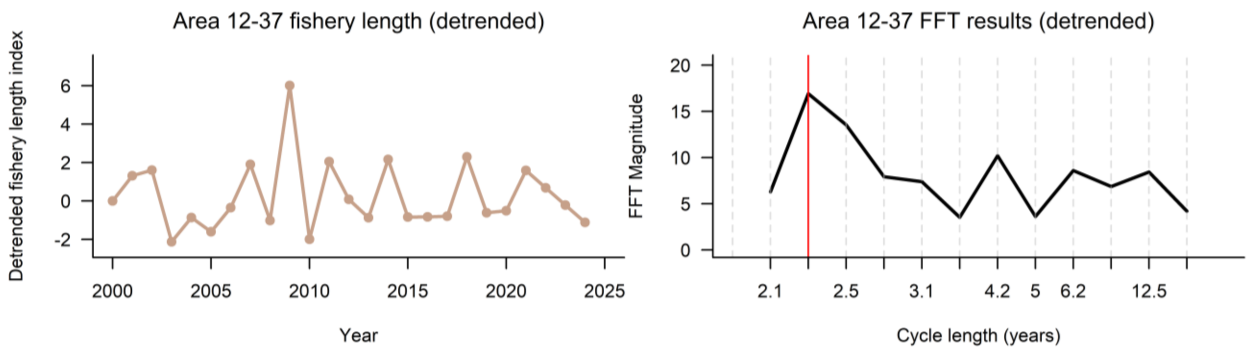

Figure 2.7 Example of a time series of annual fishery length and cycle length spectrum for a Subarea in DFO Area 12.

Raw fisheries length time series are detrended to account for the persistent declining trend in the length of the fishery. Red line denotes the dominant cycle length (~2.3 years), the distribution of which is visualised in Figure 2.8.

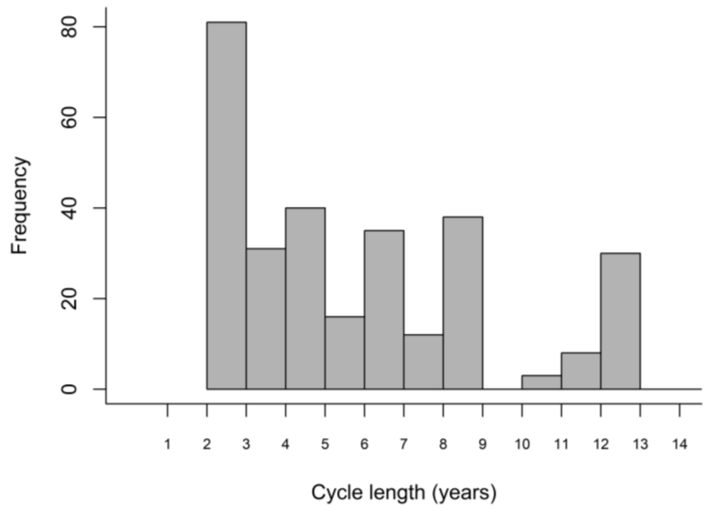

Figure 2.8 Histogram of frequencies of dominant cycles in fishery length dynamics across 295 Pacific Fishery Management Area Subareas in British Columbia.
For a given Subarea, we evaluated the dominant cycle length (years between peaks) describing the oscillations in annual fishery length.

Simulated fishery length dynamics were most sensitive to changes in survival, although harvest rate and recruitment variation also resulted in differences between scenarios (Fig. 2.9). In general, higher survival resulted in a longer, more stable fishery under both management scenarios. When survival was low, the difference between management approaches was often the difference between a short but consistently open fishery and a population which frequently did not meet the simulated threshold for opening the fishery (Fig. 2.9, though this result should be interpreted qualitatively given that in practice, populations are not assessed prior to the commercial opening). Regardless of management or harvest scenario, low survival resulted in highly variable fishery dynamics (Fig. 2.5). When survival was high and the harvest rate was low, the length of the fishery stabilized at the maximum possible length within the constraints of the modelling framework (12 weeks, Fig. 2.8). Higher harvest rates generally resulted in a shorter average fishery but had variable effects on the stability of the fishery length. For example, under status quo management, 80% harvest led resulted in lower variability than the 60% harvest scenario (see Discussion for potential mechanism).

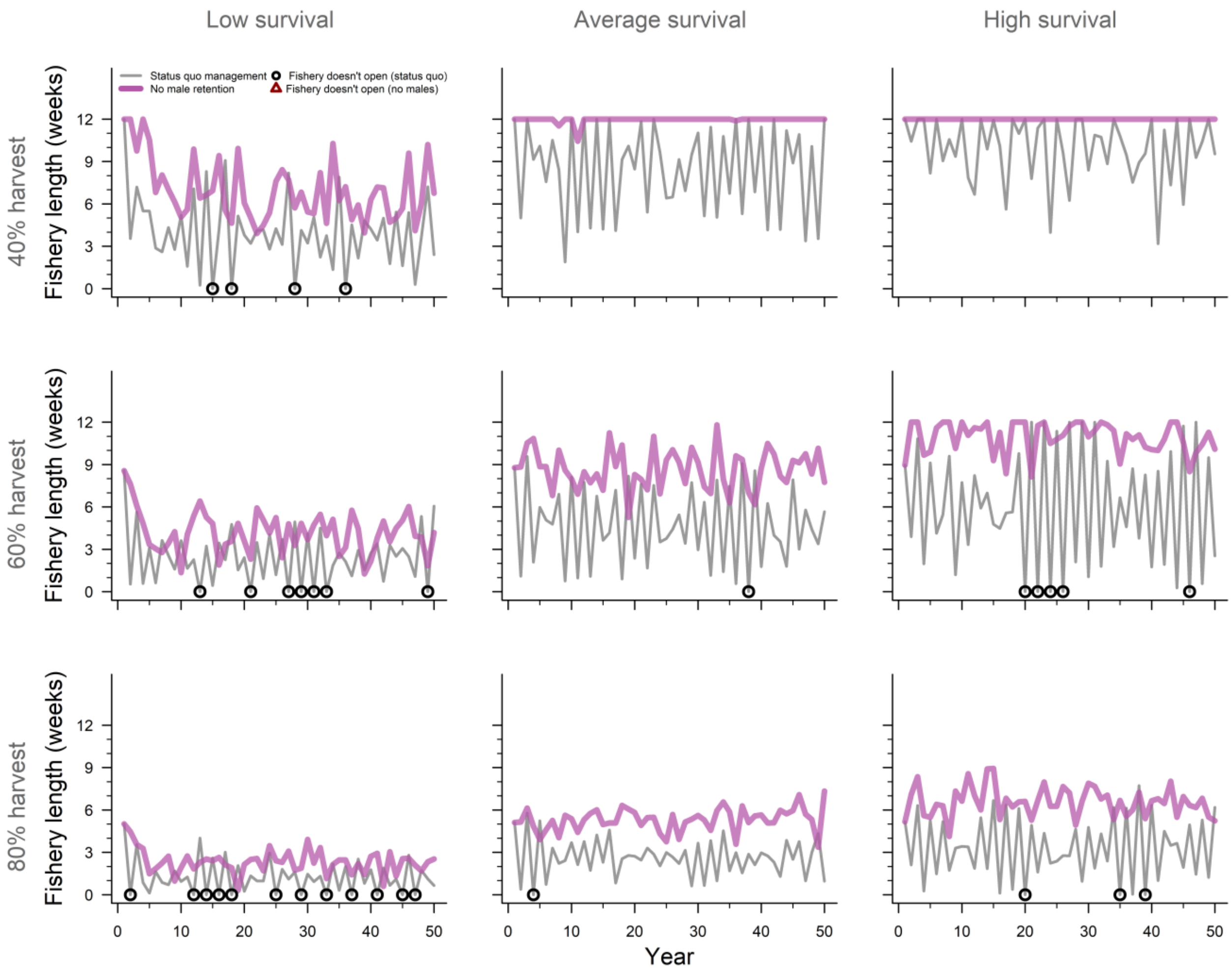

Figure 2.9 Fishery length dynamics under status quo management and the no-male-harvest scenario across survival and parameter values.

Rows represent different harvest scenarios (from low to high). Columns represent different survival scenarios (from low to high). Black circles (status quo) and red triangles (no-male-harvest) indicate years in which the fishery did not open because the female population at the start of the commercial season (Summer) was below the fixed escapement target.

Changing the magnitude of recruitment variation increased variability but did not qualitatively change the differences between the status quo and no-male-fishery scenarios (Figs. A.13-A.16). For clarity we constrain the main text figures and bulk of our Discussion to the simulations conducted for CV=0.2. A no-male-harvest management approach resulted in a longer, less variable fishery regardless of CV but there were some quantitative differences in the dynamics under different CV values (Figs. A.8, A.9). For low survival, higher variation in recruitment resulted in a longer but more variable fishery length (Figs. A.13, A.14). Across survival and harvest levels, higher recruitment variation led to a higher frequency of years where the fishery did not open (the female population at the start of the summer was below the fixed escapement target) (Fig. A.8, A.9).

The longer, more stable fishery associated with no-male-harvest management was accompanied by catch tradeoffs in our simulations. In general, foregoing male harvest led to higher female catch but lower total catch relative to status quo management (Fig. 2.10). This was true both in terms of average annual catch and in terms of the average rolling 10-year total catch (hereafter referred to as ‘long-term catch’). Long-term total catch decreased by ~0-50% under no-male-harvest management relative to status quo whereas long-term female catch increased by ~100-200%. The catch tradeoff was lowest at high survival and high harvest rates, although survival had a stronger effect than harvest (Fig. 2.10). Regardless of recruitment stochasticity, high survival and harvest consistently led to the lowest catch tradeoff but the relative outcomes for low and average survival scenarios depended on recruitment CV (Figs. A.17, A.18).

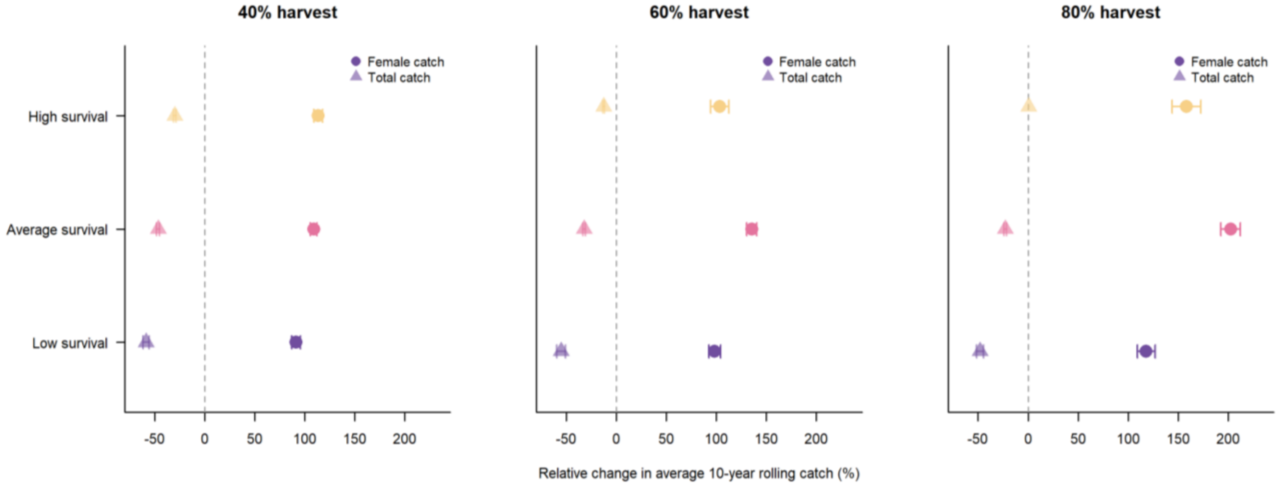

Figure 2.10 Average change in long-term catch from no-male-harvest scenario relative to status quo scenario across different survival rates and harvest rates.
Across scenarios, total catch is lower under the no-male-harvest scenario, but female catch is higher. For each scenario, we visualize two catch indices: female catch and total catch (females plus males). Long-term catch was estimated as the rolling 10-year total catch and the percent change was estimated as the percent-change in the average 10-year rolling total. Points represent the mean percent change and bars represent the standard deviation.

2.4 Discussion

Evidence suggests that the interaction between life history and fishery management drives variability in the spot prawn fishery in British Columbia and we found that variable annual escapement of male spot prawns from the commercial fishery may contribute to a shorter, more variable annual fishery. Our approach focused on an observed pattern and drew on empirical information as well as constructing a tailored theoretical population model to better understand one potential driver of variability in the spot prawn fishery. The results, interpreted carefully within the context of the assumptions they rely on, may be useful to fishery managers seeking options to ease the intensity of the present-day fishery. A longer, less variable fishery season would probably come with a trade-off in total catch though a detailed bioeconomic analysis would be needed to be confident in the exact trade-offs.

Fishery length is more variable under status quo management because males are subject to uneven harvesting pressure year-to-year which drives oscillations in the abundance of mature males and associated abundance of females the subsequent year (Fig. 2.3). In the absence of male harvest, the incoming spawner population stabilizes and thus the length of the fishery stabilizes. Because the overall mortality of mature males is lower (no harvest), the stable starting spawner population is also higher and thus the fishery dynamics stabilize at a longer annual fishery. Simulations of the deterministic version of our population model suggest that the feedback loop between male harvest and fishery length leads to damping oscillations which stabilize under the no-male-harvest management scenario (Fig. 2.6). These damping oscillations occur because the structure of the model doesn't allow the starting summer spawner population to return to or surpass its initial size once the feedback loop initiates. In other words, the shorter fishery that results from a small starting spawner population relieves that year's cohort of mature males, but not so much that the following year's starting spawner population is as large as at the start of the simulation. As a result, the magnitude of the oscillations dampens over time. Higher survival and higher harvest rates both tended to increase the magnitude of the oscillations in mature male abundance and fishery length (Fig. A.12). Simulations of just the deterministic dynamics provide insight into the mechanism for the harvest-induced variability, and the influence of different factors on that variability. Adding environmental stochasticity at the juvenile recruitment stage removed the dampening and led to persistently variable dynamics, but the qualitative difference between harvest scenarios remained (Fig. 2.6). For low and average survival scenarios, the variability in fishery length was similar or lower under 80% harvest than 60%. Although initially this may seem counterintuitive, it follows that higher harvest rates lead to a shorter overall fishery but also lower male harvest which may act to stabilize the fishery overall in a similar manner to the no-male-harvest scenario.

Several factors likely contribute to the variability in dominant cycle length we found through the analysis of fishery length data. In reality, the ‘true’ fishery length dynamics may be closer to a mix of the two binary scenarios we consider. Our simulation study assumed no adult immigration or emigration, an assumption which is probably more or less reasonable depending on the specific subarea. Because the spot prawn management units (PFMA Subareas) were originally delineated for wild salmon management, they vary widely in size from most of an inlet to a small bay. They also vary bathymetrically (e.g., gradually sloped bay vs. the steep shelves of many inlets or fjords) and in their tidal dynamics. Subareas that experience higher male immigration year-to-year may be less likely to experience the two-cycle feedback loop driven by male harvest in the absence of immigration. In those cases, cycles might be driven more by the generation time of the species (~4 years) which could be why we also see a high frequency of dominant cycle lengths at four, eight, and twelve years. The constraints of the management framework and observation error likely also contributed to variability in the fishery length. Closure decisions are typically made twice per week during the fishery but only evaluate subareas for which there are observer data. Delays in data and imperfect information adds variability that we do not account for in our simulations. It is also possible that the two-cycle dynamics predicted from variable male escapement may be more common in the latter part of the time series than the earlier part of the time series when there may have been less incentive or pressure to maximize male harvest. Nonetheless, the prominent peak at 2 years in the frequency distribution of the real data suggests that the male harvest feedback loop is at play in at least some subareas and the intensifying nature of the fishery means that this dynamic may only become more important.

We set out to construct a relatively simple population model to investigate the general differences between two fishery scenarios while maintaining sufficient realism to be confident in the relevance of our results, which required several assumptions and simplifications. In various parts of our modelling framework, we assume temporally fixed parameters. For example, we assume that survival is constant within and between years (though we investigate the influence of different survival values), and we assume a constant harvest rate within the fishery and year-to-year. Our modelling framework allows, in principle, for stage- and season-specific survival but there is very little empirical information to inform what those values should be. Indeed, even the available estimates of annual survival are highly uncertain and based on a single study from over 20 years ago that focused on one region in southern BC (Boutillier and Bond 2000). The stabilizing effect of the no-male-harvest scenario was present regardless of survival; however, the magnitude of the effect on fishery length, variability, and the catch trade-off all depended on survival. Uncertainty in survival (a.k.a. natural mortality) is a common problem in fisheries (Maunder et al. 2023) and there are clear consequences to assuming constant survival through space or time (Johnson et al. 2015; Punt et al. 2021).

For simplicity, we assumed a constant weekly harvest rate in our simulation both within the year, between years, and between stages. In reality, the weekly harvest rate in the commercial fishery has likely increased over time with the development of the fishery and increasing efficiency, which may be one factor driving the declining trend in the length of the fishery (Rossi et al. 2023). Although we do not capture this within a given simulation, our exploration of a range of weekly harvest rates captures the shorter annual fishery that results from higher weekly harvest rates (as the escapement threshold is reached sooner). Given the brevity and intensity of the fishery, we suggest that the assumption of constant weekly harvest rate within-fishery is reasonable. Our population model is age-structured without a length-based component, and we assume that mature males and spawners are both fully selected for in the fishery and captured at the same rate. This is likely a simplification, but in the absence of length data from the commercial fishery, we felt it was justified. If, for example, only a proportion of mature males are selected for by the commercial fishery, we might expect a more moderate destabilizing effect from harvesting males.

Two factors – a maximum fishery length constraint and no adult immigration – add important context to the results of our investigation, particularly when connected to their application for fisheries decision making. We constrained the maximum fishery length to 12 weeks and assumed no adult immigration into the population between years. The maximum fishery length constraint was a function of the seasonal structure of our model, but it is also substantially longer than the actual length of the commercial fishery over the past 25 years – the last 12-week coastwide fishery was in 2000 and the fishery has been less than 9 weeks long since 2001. At the level of subarea, the scale on which our model operates, the fishery can be much shorter depending on the region. The different combinations of survival, harvest, and recruitment stochasticity that we consider could be thought of as representing different potential subarea ‘profiles’ with the coastwide fishery dynamics as a sort of composite of hundreds of subareas, each with their own population and environmental characteristics. Our simulated fishery length hit the 12-week constraint when the spawner population did not cross the escapement threshold within that timeframe. This occurred when survival was high and the harvest rate was low or moderate. This probably does capture real scenarios for highly productive or underexploited subareas that close when the coastwide closure occurs, but not because that specific subarea had fallen below the escapement threshold. Nonetheless, the imposed constraint leads to artificially low fishery length variability (Fig. 2.4) that should not be overinterpreted.

Because we focused on the subarea-level dynamics, we did not allow for adult immigration into the population. This is likely a reasonable assumption for many subareas (a study in Alaska recaptured tagged adult prawns within <2 km of their tagging site, Kimker et al. 1996) but may not be the case for some subareas where oceanographic and/or bathymetric factors lead to higher adult movement. It is hard to say for sure how adult movement would change our results – male immigration might buffer the harvest-induced oscillations, emigration might amplify them, or the combination might just add another source of stochasticity.

We explore the binary contrast in fishery scenarios with and without male harvest, but in practice there is likely a spectrum of management interventions that would support a longer, more stable fishery. Indeed, connecting this study to potential applications includes contextualizing specific results in the nuances of the ecology and management that our model necessarily simplifies. We note that the goal of this study was not to provide precise estimates of absolute population metrics nor was it to provide a management prescription – we acknowledge that fishery decision-making is multi-faceted and rarely hinges on one point of view or source of information. Rather, we sought to construct a relatively simple population model that described the general system dynamics and allowed for comparison of alternative scenarios.

Completely eliminating male harvest from the spot prawn fishery would be difficult to implement but the key intervention is to manage male escapement more proactively and this could be achieved with tools that already exist. For example, using the in-season stage structure data collected by fishery observers to generate a ‘male index’ which could inform in-season closure decisions alongside the spawner index or increasing the minimum mesh size or the minimum retention size to lower the effective male harvest. It may be counterintuitive to focus on limiting male catch (and increasing female catch) given that the goal of this fishery (and many others) is to prevent overfishing of females. The scenarios we explore do not, in principle lead to lower female escapement (the escapement target remains constant across scenarios). Assuming that management achieves escapement targets, which we acknowledge as a major assumption, female catch is higher because the fishery is waiting to fish the male population until they transition. It also buffers the younger male stage to other uncertain sources of non-commercial harvest and natural mortality. Such trade-offs are particularly relevant when maximizing profit is not the sole objective among other objectives such as the long-term longevity of a fishery or managing populations to buffer uncertain impacts of climate change (Samhouri et al. 2025).

The full scope of bioeconomic implications of foregoing or minimizing male harvest in the BC spot prawn fishery will depend on many factors including market fluctuations, fisher-specific operating costs, and size-based pricing. The no-male-harvest scenario resulted, on average, in a longer and less variable commercial. This potential benefit comes with trade-offs in fishery catch which we superficially assess in terms of landed biomass (Fig. 2.10). Foregoing males may lead to lower overall catch but higher landed value, depending on market conditions and the relative price of females and males. Future work could more thoroughly explore the economic and ecological trade-offs associated with alternative management approaches. Local markets are becoming increasingly higher value than international markets but cannot absorb the same volume of product (Mark Urwin, *personal communication,* 2023). Other trade-offs of a longer fishery include more drawn out direct ecological impacts of the fishery, a higher potential for marine mammal bycatch (Brown and Niedzwecki 2020), and higher costs associated with implementing the fishery observer program.

Our work demonstrates the value of tailored but relatively simple population models applied to fisheries problems, an approach shared by many investigations into the dynamics of fished invertebrates (e.g., Botsford et al. 1994, 2014; Botsford 1995; Higgins et al. 1997; Hastings and Botsford 2006) and hermaphroditic species (Armsworth 2001; Alonzo and Mangel 2004; Alonzo et al. 2008; Easter and White 2016; Easter et al. 2020). Previous research found that single-sex harvest can have destabilizing effects on the population dynamics of marine invertebrates (Botsford 1995), which could be interpreted as a contrast to our finding that foregoing male harvest stabilized fishery dynamics for spot prawn. Some of this contrast is likely due to the details of this specific study system and the fact that the BC spot prawn fishery manages males and females differently, leading in principle to higher variability in male escapement than female escapement. It also may have to do, at least in part, with the fact that spot prawns are invertebrates *and* protandrous hermaphrodites.

While we included a mating function in our model, we focused on the case where males are not a reproductively limiting factor. It is well established that accounting for sex-changing life histories in fisheries management is important but it is also well-documented that it is difficult to assess impacts without information on the fundamental biology of a given species (Alonzo et al. 2008). To understand how depletion might impact sex change and/or mating dynamics, we must first understand the basic drivers of sex change and the details of hermaphroditic mating systems. Uncertainty in mating functions has been previously highlighted (Easter and White 2016) and points to a fruitful direction for future research, including in the case of spot prawn.

By linking male harvest dynamics to fishery instability in a protandrous hermaphrodite, this study extends theoretical understanding of how sequential hermaphroditism interacts with stage-selective fishing pressure and suggests that the consequences of harvesting the non-targeted sex may be underappreciated in hermaphroditic fisheries. Developing a tailored but relatively simple population model, as we have done here, provides a framework for further investigation of future questions regarding the biology and management of spot prawns.

Chapter 3.

Back to life at depth: Post-release survival of trap-caught spot prawns (*Pandalus platyceros*) declines with increasing air exposure and temperature

3.1 Introduction

Marine invertebrate fisheries are growing faster than any other group of fisheries in the world, with catches increasing by six-fold since 1950 and unique harvested taxa doubling (Anderson et al. 2011b). Within that growth, decapod crustacean fisheries are growing faster than any other major group of marine invertebrates (Boenish et al. 2022). Despite the pace of expansion, invertebrate fisheries receive relatively less scientific and stock assessment attention (Berkes et al. 2006; Anderson et al. 2008; Chen 2021). This attention is pivotal to stewarding marine invertebrate populations because they play important ecosystem roles (e.g., Eddy et al. 2017) and because this trend may be an example of 'fishing down the food web' (Pauly et al. 1998; Pinsky et al. 2011) which is accompanied by risks to ecosystems and the human communities that depend on them. The global pattern of expanding invertebrate fisheries is mirrored on the Pacific coast of Canada where declining finfish fisheries have led to a redistribution of effort towards invertebrate fisheries (Perry et al. 1999) including the spot prawn fishery in British Columbia (BC).

Spot prawns (*Pandalus platyceros*) are sequential protandrous hermaphrodites, beginning their lives as males before transitioning to and reproducing as females. In BC, they are thought to live for four years (Butler 1964). In the spring, brooding females release hatched eggs which spend 2-3 months in a larval dispersal stage before settling and developing as juveniles in shallow waters (Marliave and Roth 1995). Spot prawns spend ~2.5 years as males before transitioning to females. They breed in the late summer through early fall and females brood eggs through the winter before releasing them the following spring. Timed to begin after most brooding females have released their eggs, the commercial spot prawn fishery is the largest shrimp fishery in BC.

With annual landed values of $33.5-39 million (DFO 2019), this commercial fishery supports over 250 licenses alongside a growing recreational fishery. While most shrimp fisheries are conducted by trawl, with accompanying concerns for their negative ecosystem impacts (Andrew and Pepperell 1992), the prawn-by-trap fishery represents a rare example of a relatively low-impact shrimp fishery (Boutillier and Bond 2000). The commercial fishery is managed as a derby style fishery, where in-season closures are implemented based on the average number of females-per-trap (the ‘Spawner Index’, Boutillier and Bond 2000) to ensure sufficient spawning females for the subsequent year. An additional management measure was introduced in 1985, implementing a minimum size limit of 30 mm carapace length. Since then, the size limit has increased to 33 mm and commercial traps must comply to a minimum mesh size. These size-based measures are designed to protect the small males in the population who will fertilize females then transition and reproduce as females in subsequent years. Furthermore, the year-round recreational fishery mandates that egged females must not be retained. Despite numerous release-based management measures, the survival of released prawns is not well understood.

Quantifying discard mortality – “the mortality of fish actively released by fishermen after capture” (ICES 2004) – is a necessary component of appropriately accounting for direct and indirect sources of mortality in fisheries. Although it may be challenging, estimating discard mortality rates is imperative to assessing the benefit of management rules such as length limits or catch-and-release regulations. For example, relatively low discard mortality rates can impede meeting fishery yield objectives and undermine the utility of minimum length limits (Coggins et al. 2007). Studies investigating discard mortality can also reveal opportunities to make targeted adjustments to fishing methods or management frameworks that produce substantial improvements in incidental mortality. For example, discard mortality differs depending on the season (Giomi et al. 2008), sorting and handling methods (Mérillet et al. 2018), and fishing methods (Musyl et al. 2009). Sometimes the goal is to simply account for discard mortality in fishery management frameworks, but there can also be opportunities to make practical adjustments to minimize mortality. Discard mortality estimates can rarely be generalized and are context dependent. Just as the growth of invertebrate fisheries has lagged that of finfish fisheries, so too has the research investigating discard mortality. Many studies focus on mortality associated with trawl fisheries (Hill and Wassenberg 1990; Evans 1994; Giomi et al. 2008;

Mérillet et al. 2018; Boussarie et al. 2020) though there is some research into the discard mortality for several trap fisheries (DiNardo et al. 2002; Grant 2003; Lorenzon et al. 2013). In the northeast Pacific region, extensive research exists on incidental fishing mortality of Pacific salmon (Patterson et al. 2017) but there are relatively few studies estimating discard mortality associated with any of the invertebrate trap fisheries. Such investigations are particularly urgent as both commercial and non-commercial (recreational and First Nations) fisheries grow (DFO 2023).

To address the uncertainty in post-release survival of spot prawns caught in trap fisheries, we conducted an *in-situ* field experiment that evaluated the influence of air exposure, air temperature, and carapace length on the probability of survival after release. Briefly, we collected spot prawns by trap and subjected them to a range of air exposure treatments before ‘releasing’ them in traps with closed openings such that they could not escape. We reset these traps in the same location they were collected and after approximately 24 hours we rehauled the traps and assessed survival and condition. We drew on previous work (Stoner 2012) to inform our condition assessment as an indirect measure of long-term mortality. In this paper, we outline the details of the experimental and statistical methods we use to assess post-release survival and discuss the results amidst the local management context as well as the broader context of post-release survival in fisheries generally.

3.2 Methods

Designing a realistic and logistically tractable experiment is one of the central challenges associated with evaluating post-release survival in a fisheries context. Ideally, the capture mechanism, post-capture treatment, and release environment should resemble the conditions of the relevant fishery. Directly replicating fishery conditions is complicated by equipment limitations, the need to count and track individuals subjected to experimental treatments, and the need to recapture individuals post-release to assess survival. We aimed to design a field experiment that would yield reasonable post-release survival estimates while working within the logistical and scientific constraints necessary to generate those estimates.

Simply put, our field experiment involved collecting prawns by trap and subjecting them to varying periods of air exposure (Fig. 3.1). We 'released' prawns by setting them down in strings of traps with closed openings, which we rehauled the following day to assess survival and condition. We conducted 23 experimental trials between May 22, 2022 and June 28, 2022 in the Broughton Archipelago, British Columbia, Canada (Fig. 3.2). A given experimental trial consisted of three components conducted over three days: (1) setting and hauling traps for specimen collection, (2) conducting the experiment exposure and release, and (3) processing prawns at the end of the experiment to assess survival and condition. Each trial took 3-4 days to complete (the string of traps to initially collect prawns fished for 24-48 hours). In the subsections below, we describe the methods for each of the three components of a trial followed by the statistical methods for our analysis.

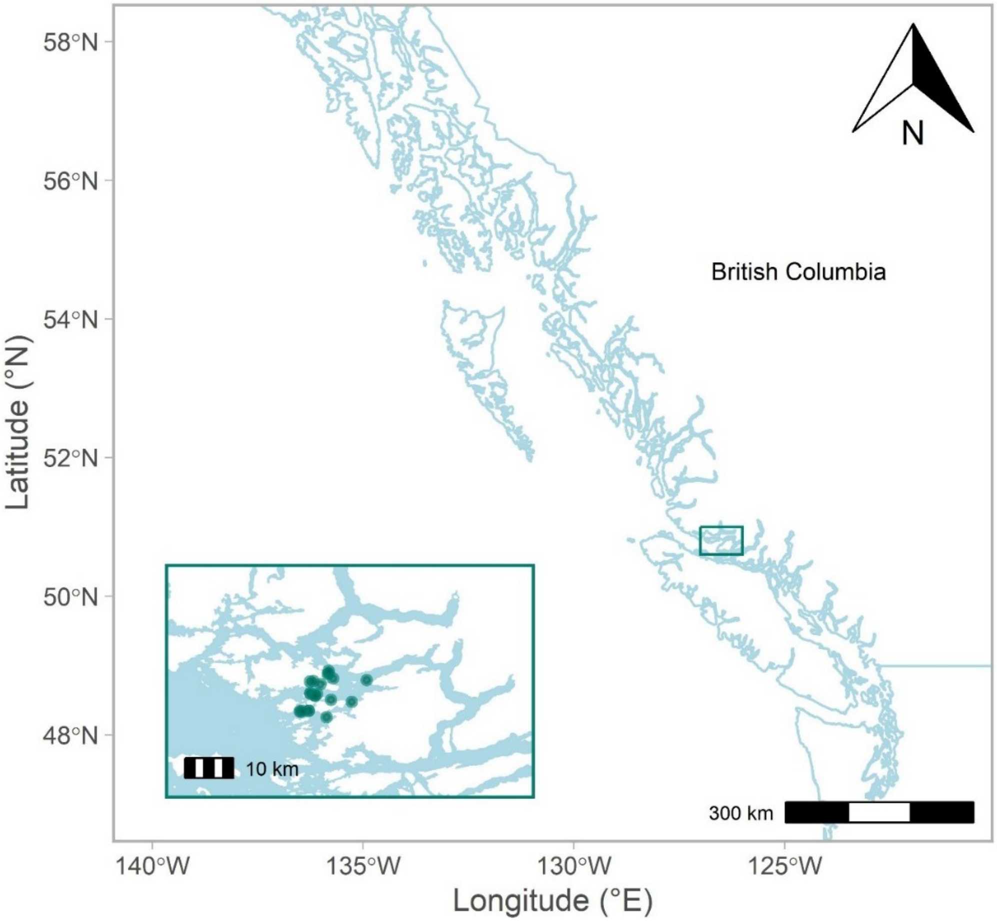

Figure 3.1 Map of study area in British Columbia off the northeast tip of Vancouver Island. Points reflect experimental set locations. All experimental trials were conducted in Musgamagw Dzawada̱'enux̱w territories near Gilford Island in the Broughton Archipelago.

2.2.1 Field methods

Setting traps for field collection

To collect prawns for a given trial, we set a string of 10 prawn traps (76 cm tapered stainless steel tapered round traps with 1.9 cm mesh) baited with pellets (Taplow Feeds Commercial Prawn & Crab Bait) within a target depth range (55-110 meters) that aligns with the approximate depth range targeted by commercial and recreational fisheries. Depending on weather conditions and logistics, the string of traps fished for 24-48 hours before we hauled the traps and began the experimental trial. On the day the trial began, at the trap setting site, we collected air temperature, water temperature (at 0 m and 10 m depths), and water salinity (at 0 m and 10 m depths) measurements using a YSI (YSI Pro30). During some of the trials, the YSI was broken, and we collected temperature and salinity data using a thermometer and refractometer respectively. We hauled the string of traps using a hydraulic pot hauler (10” Hydro-Slave hanging pot hauler powered by 5.5 hp hydraulic power unit). During trap hauling, as each trap came on the boat, we released any bycatch and emptied the remaining prawns into a small square white bin (10 L, 213 mm x 255 mm x 290 mm) with drilled holes that allowed water to flow through. We placed each white bin in a large fish tote (66 cm x 48 cm x 63.5 cm inside dimensions) filled with seawater (~200 L). This method ensured that until the trial began, prawns experienced minimal air exposure (10-15 seconds as trap was emptied into white bin). Part way through the field experiment (Trial 11 onwards, Table 3.1), a freshet caused the salinity of surface seawater to decline below 20 ppt. To maintain consistent salinity conditions, we began pumping seawater from below the freshet layer (i.e., >1 m below the surface) using a hydraulic pump and measuring salinity within the tote to ensure it remained >24 ppt.

Conducting experimental exposure and release

After hauling all traps, we assessed how many prawns to assign to each treatment (minimum 35 per treatment, maximum 70 per treatment to minimize density-dependent effects). We haphazardly assigned prawns to one of four or five treatments: ‘immediate release’ or air exposures of 30, 60, 90, or 120 minutes. In trials where the number of prawns was a limiting factor, we did not include the 120-minute treatment.

To implement the ‘immediate release’ treatment in an experimentally tractable manner, we hung prawns off the research vessel in a weighted mesh drawstring bag (2.5 cm mesh, approximately 20 L volume) approximately 20 m below the surface of the water. This mimicked quick release while still allowing for the final ‘release’ of prawns from all treatments together in one string of traps at the end of the trial. We counted out the appropriate number of individuals, used forceps to place a coloured orthodontic ligature tie on the base of the rostrum, and placed each prawn in the mesh bag which was submerged in a 20 L bucket of seawater. Once all prawns had been banded for the ‘immediate release’ treatment, we cinched the mesh bag and attached it to a weighted line hanging off the boat to a depth of ~20 m.

To begin the air exposure treatments, we removed the remaining white bins from the fish tote all together such that all prawns became air-exposed at the same time. We started a timer for the first treatment (30 minutes) and dispensed the appropriate number of prawns to each bin, distributing haphazardly by size. For trials with fewer prawns, we allotted one bin per treatment (e.g., ~35 prawns per bin) and for trials with more prawns, we allotted two bins per treatment (e.g., two bins, each with ~35 prawns). For the duration of the treatment time, we kept the bins under the canopy of the boat such that they received no direct sun exposure or direct precipitation. The spatial arrangement of the bins was haphazard with respect to treatment. Choosing different colours for different treatments (the exact colour varied trial to trial), we applied coloured bands to the rostrum of each individual prawn. After the given treatment time elapsed, we emptied the banded prawns of one band colour into a weighted mesh bag and clipped it to the hanging line such that it descended to hang with the other treatment bags at ~20 m.

At the end of the final treatment (90 minutes or 120 minutes), we placed the final group of prawns in a mesh bag hung off the side of the boat, so all treatments experienced the process of being lowered and raised in a mesh bag. Finally, we raised all the bags at the same time and distributed the prawns from all treatments across six baited prawn traps with the tunnels tied shut, preventing any prawns from escaping. To avoid confounding treatment effects with trap effects, we distributed some prawns from each treatment to each trap such that traps contained a mix of all treatments (the coloured bands facilitated mixing prawns without losing information on treatment). Once prawns had been distributed, we closed the traps and reset the string of six traps in the same location and depth they had been hauled from initially. For each trial, we recorded the length of time it took from the trial ending (mesh bags coming out of water) to the final trap hitting the water during re-setting.

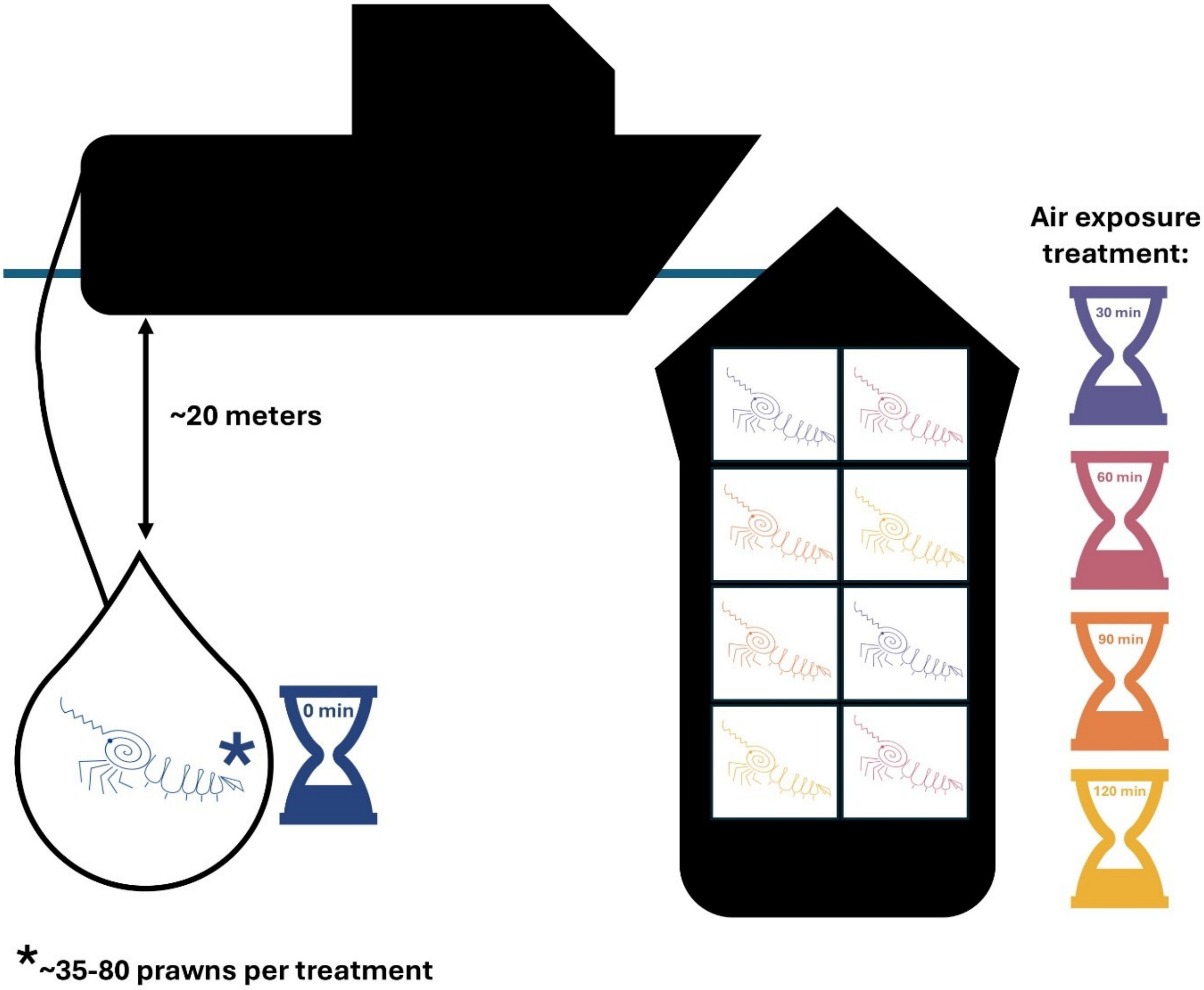

Figure 3.2 Schematic illustration of experimental set-up.
Prawns in the 'immediate release' treatment were hung in a mesh bag approximately 20 m below boat while the air exposure treatments were conducted. Prawns in air exposure treatments ranging from ~30-120 minutes out of water were held on the deck in containers (1-2 containers per treatment). At set time increments, prawns of a given treatment were 'released' by transferring them to a mesh bag which was hung off the boat until the end of the final time treatment.

Evaluating post-release prawn survival and condition

Approximately 24 hours after we conducted the experimental treatment, we hauled the string of traps containing the 'released' prawns. We followed the same procedure as at the beginning of the experiment, collecting temperature and salinity measurements before hauling the string and placing the contents of each trap into a white square bin which we kept in the seawater-filled fish tote.

After hauling, we emptied one square bin (i.e., one trap's worth of prawns) at a time into a sampling tray and collected the end-of-trial data. For each individual prawn, we recorded their band colour, life stage (juvenile, male, transitional, female, egged female, or spent female), and their carapace length as well as whether they were alive, dead, or scavenged. We considered a prawn dead if their gill filaments were not moving at all (i.e., the individual was no longer breathing). A 'scavenged' prawn referred to an individual that was dead and missing some body parts. We returned dead and scavenged prawns to the ocean. As they were counted and measured, alive prawns were transferred from the sampling tray to a mesh bag submerged in a 20 L bucket of seawater. After processing a single trap, the mesh bag of live prawns was hung off the boat at 20 m to maintain the prawns as close to their initial condition as possible.

After collecting survival data for all traps, we assayed each live prawn for a suite of ten reflex behaviours (Table B.2), based on the approach outlined in (Stoner 2012) that developed a set of ten reflex behaviours in spot prawns that cumulatively predicted long term survival in the lab. Processing one trap's worth of prawns at a time, we assessed each prawn for how many of the ten reflex behaviours they displayed, resulting in a cumulative score from 0-10. Here, a score of zero indicates a prawn that is alive but displays no other behaviours (poor condition) and a score of ten indicates a prawn that is alive and displays all assessed reflex behaviours (good condition). After we finish assessing the reflexes of the live prawns, we remove their nose band and return them to the ocean.

2.2.2 Statistical methods

We structured our analysis to estimate the probability of survival and to test the hypothesis that the probability of survival varies with varying air exposure, air temperature, and carapace length. To evaluate this hypothesis, we used generalized linear mixed-effects models (GLMMs) that accommodate the hierarchical structure of the experiment and the non-linear distribution of the data. We took a model selection approach to assess which combination of the three focal covariates and their two-way interactions (i.e., models that represented reasonable biological hypotheses with interpretable interaction effects) was most parsimonious.

Data cleaning

In some cases (488 of 5053), we excluded data from prawns for which either treatment group or carapace length was unknown. A small portion of the prawns (273) lost their coloured band during the release stage of the experiment (Table 3.1) and could not be assigned to a treatment group. We considered the possibility that small prawns may have been more likely to lose their band. To ensure we would not confound our results, we compared the size distribution of these prawns to that of the prawns that retained their band (Fig. B.3). There was a statistically significant difference between the two groups (T=3.25, *p*=0.0013), however the difference was very small (1 mm, 3%). We therefore excluded these individuals from the final dataset. We excluded an additional 215 prawns that had damage on their carapace such that we could not measure length accurately.

Model structure

To appropriately capture the error structure of the response data, which consisted of values of either 0 (dead or scavenged) or 1 (alive), we fit a GLMM with a binomial error structure such that the survival outcome, $Y_{i,j}$ for prawn i in trial-trap combination j follows a Bernoulli distribution:

$$Y_{i,j} \sim \text{Bernoulli}(p_{i,j}) \tag{1}$$

In this case, $p_{i,j}$is the probability of survival and the linear model is specified, for example, as:

$$\text{logit}(p_{i,j}) = \beta_0 + \beta_1 \text{Treatment}_i + \beta_2 \text{Temperature}_i + \beta_3 \text{Length}_i + \theta_j \tag{2}$$

The β terms represent estimated parameter coefficients and θ_j is a normally distributed random effect on the intercept to account for the shared variation within a trap of a given trial due to factors such as set depth, trap orientation and handling, etc. We fit a suite of 18 candidate models representing biologically reasonable combinations of treatment, air temperature, carapace length, and their two-way interactions (Table 3.2). To assess relative model support, we calculated the Bayesian Information Criterion which penalizes model likelihood according to its complexity (number of parameters). We used BIC rather than AIC for model selection for its stronger penalty against complexity, which aligned with our aim to assess the relative strength of alternative drivers of survival rather than to maximize predictive accuracy of overall survival probability (Aho et al. 2014). We selected the most parsimonious model as that with the lowest BIC value, although we considered all models with ΔBIC < 10 to have moderate support (Burnham et al. 2011). Given that we were interested in interpreting the parameter effects themselves (rather than prioritizing predictive accuracy through model-averaged predictions), we generated model predictions from the model with the lowest BIC value. We conducted all analyses in version 4.5.1 of R (R Core Team 2025) using Laplace approximation to estimate the maximum likelihood, which we implemented using the 'lme4' package (Bates et al. 2015).

2.3 Results

The 23 experimental trials included 5,052 prawns encompassing juvenile through female life stages (Fig. B.2). Due to the timing of the experimental period, we did not have access to egged or spent females to include in the experiment. The majority of the prawns were male or transitional stage and prawn carapace length ranged from 18.0 mm to 52.4 mm (Fig. 3.3). Air temperature varied throughout the experimental season with trials conducted in climates from 10.7ºC to 25ºC. We attempted to maintain high salinity conditions which required pumping water from below the freshwater layer during the freshet event that occurred midway through the experimental period. The seawater that we kept prawns in during the experiment ranged from 24.5 ppt to 31.4 ppt, with the exception of two trials which we did not include in the final analysis (trial 11, 21.5 ppt during end-of-trial processing and trial 12, 14.0 ppt during end-of-trial processing).

The post-release survival of spot prawns declined with increasing length of air exposure (Figs. 3.4, 3.5) and with increasing air temperature (Figs. 3.4, 3.6). Of the models we fit to determine the best predictors of prawn survival probability, the model including two interaction effects – an interaction between treatment and temperature and between temperature and length – was best supported by BIC (Table 3.2). The interaction terms suggest that survival probability declines more quickly with time out of water at higher air temperatures and that smaller prawns survived relatively better than larger prawns at low but not high air temperatures (though note that the effect size for the latter interaction was small, see Fig. B.1). There was no definitively clear top model, with reasonable support for five models which all fell within 10 ΔBIC of the top model (Burnham et al. 2011). The treatment-temperature interaction effect was common across all five top models.

Table 3.1 Trial data for 23 trials conducted on post-release survival of spot prawns in the Broughton Archipelago, BC.

Air temperature and salinity measurements were taken at the start of each trial set-up. Salinity was measured from the sea surface or, for trials 13-23, from the seawater-filled tote that prawns were held in during trap hauling. Two trials, 11 and 12, were not included in the analysis due to a freshet event that subjected prawns to extremely low salinity conditions while held in fish tote during trap hauling (see *Methods* for full details). During trial 8, we 'gained' 5 prawns, likely due to miscounting at the start of the trial.

	Start-of-trial								**End-of-trial**		
			Number of prawns						**Number of prawns**		
Trial No.	**Air temp (°C)**	**Sal-inity (ppm)**	**'Immediate' release**	**30 min**	**60 min**	**90 min**	**120 min**	**Total**	**End total**	**Lost**	**No band**
1	12.9	31.2	80	76	81	80	0	317	274	43	44
2	12.9	29.9	37	55	55	55	0	202	188	14	24
3	15.2	30.4	40	78	79	82	0	279	257	22	26
4	10.7	31.3	60	60	63	60	0	243	215	28	22
5	13	28.6	40	40	40	40	0	160	153	7	10
6	14.1	31.3	36	36	35	35	0	142	104	38	4
7	14.3	31.4	50	50	50	50	50	250	209	41	17
8	12.8	30.3	70	70	70	70	0	280	285	-5	14
9	13.6	26.2	39	39	39	39	0	156	117	39	9
10	15.5	30	54	54	54	54	54	270	201	69	24
11											
12											
13	12	24.5	56	56	56	56	0	224	212	12	6
14	12.3	26	30	30	30	30	0	120	108	12	3
15	11.9	27.5	70	70	70	70	70	350	295	55	3
16	13.5	30	70	70	70	70	70	350	348	2	15
17	14.3	29	60	60	60	60	60	300	272	28	11
18	11.5	25.6	70	69	70	70	70	349	344	5	12
19	17.8	25.1	70	70	70	70	70	350	309	41	7
20	25.7	25.4	70	70	70	70	70	350	345	5	10
21	22.2	24.7	44	44	44	44	0	176	176	0	5
22	25.4	25.4	70	70	70	70	70	350	343	7	4
23	18.7	25.9	60	60	60	60	60	300	297	3	3

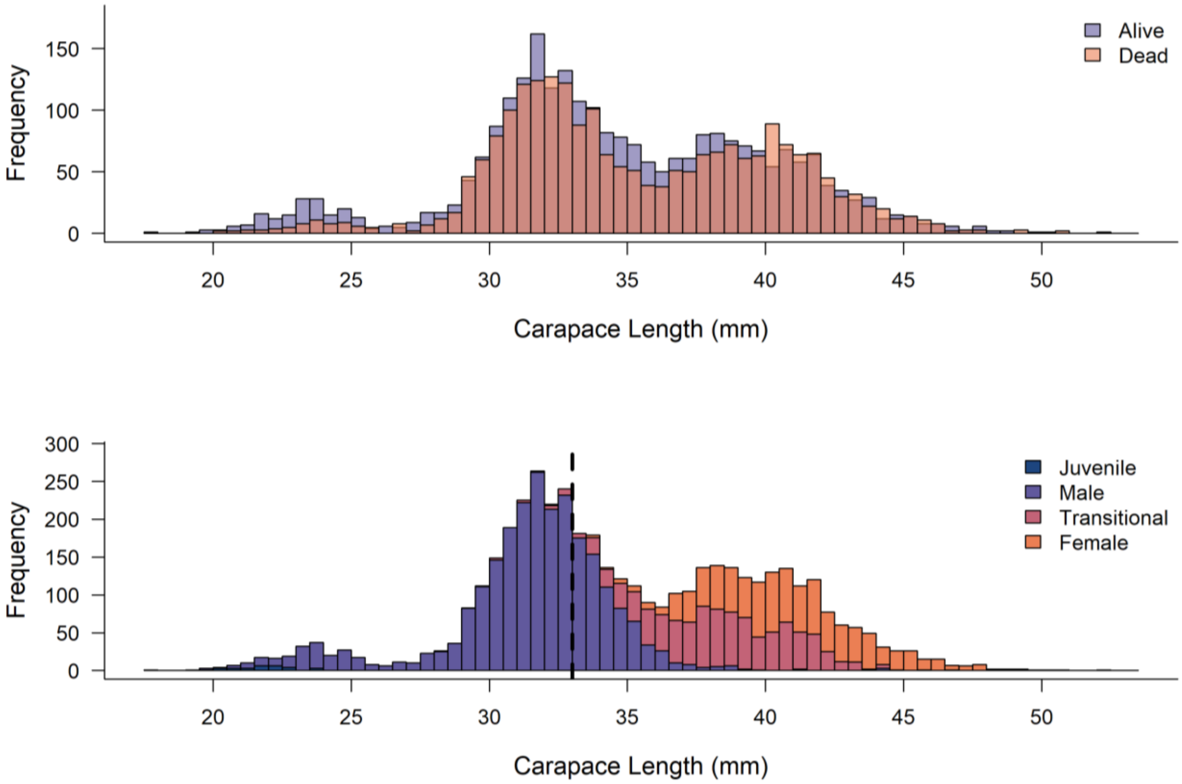

Figure 3.3 Length distributions of prawns at end of trial by survival (top panel) and by stage (bottom panel).

Dashed line indicates minimum size threshold (33 mm) implemented in the commercial fishery

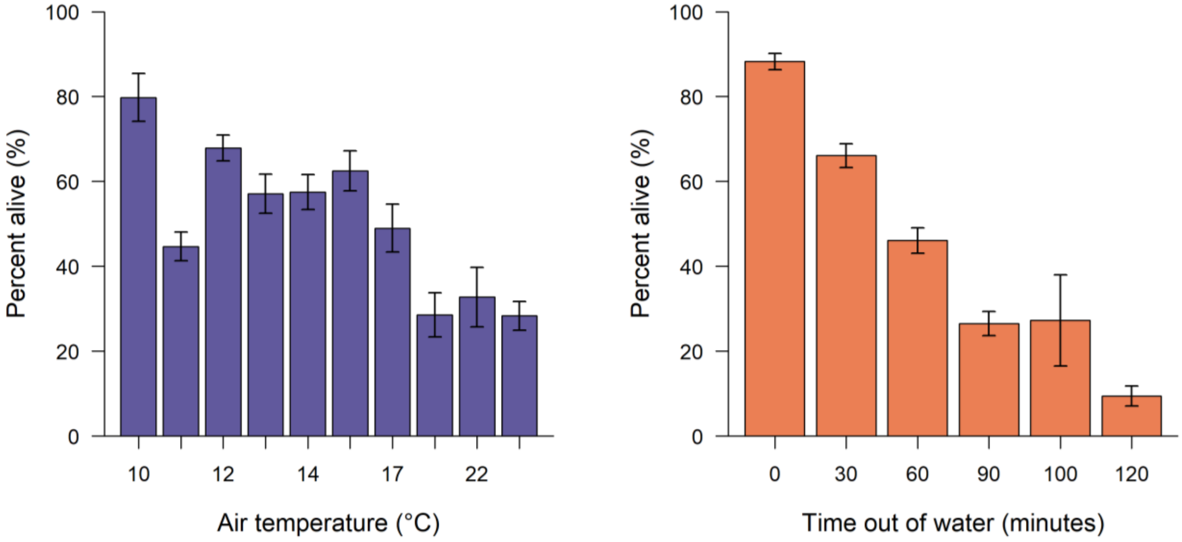

Figure 3.4 Raw survival data (% prawns alive at end of trial) by air temperature and time out of water.

Each bar plot shows the mean trial-level percent survival for given temperature or treatment and 95% confidence intervals.

Table 3.2 Model selection statistics from generalised mixed-effects models fit to post-release survival data for spot prawns.

Models included combinations of three fixed effects: duration of air exposure (treatment), air temperature during exposure (temperature), and carapace length (length). All models included a random effect on the intercept for trial-trap number. Models with interaction terms include all lower-order effects and all models include an intercept term. Differences in the Bayesian Information Criterion (BIC) relative to the top model are listed under ΔBIC; w_i indicates the model weight (the proportion of model support attributed to a given model).

Rank	Model	ΔBIC	w_i	Cumulative w_i
1	Treatment x Temperature + Temperature x Length	0	0.73	0.73
2	Treatment x Temperature + Length	2.4	0.22	0.95
3	Treatment x Temperature	6.4	0.03	0.98
4	Treatment x Temperature + Treatment x Length + Temperature x Length	8.1	0.01	0.99
5	Treatment x Temperature + Treatment x Length	9.1	0.01	1
6	Temperature x Length + Treatment	31.9	0	1
7	Length + Treatment + Temperature	32.4	0	1
8	Treatment + Temperature	37.5	0	1
9	Treatment x Length + Temperature	38.5	0	1
10	Treatment x Length + Temperature x Length	39.4	0	1
11	Treatment + Length	70.4	0	1
12	Treatment x Length	76.6	0	1
13	Treatment	77.4	0	1
14	Temperature + Length	1470.7	0	1
15	Temperature	1477.1	0	1
16	Temperature x Length	1477.7	0	1
17	Length	1508.1	0	1
18	Intercept only	1516.3	0	1

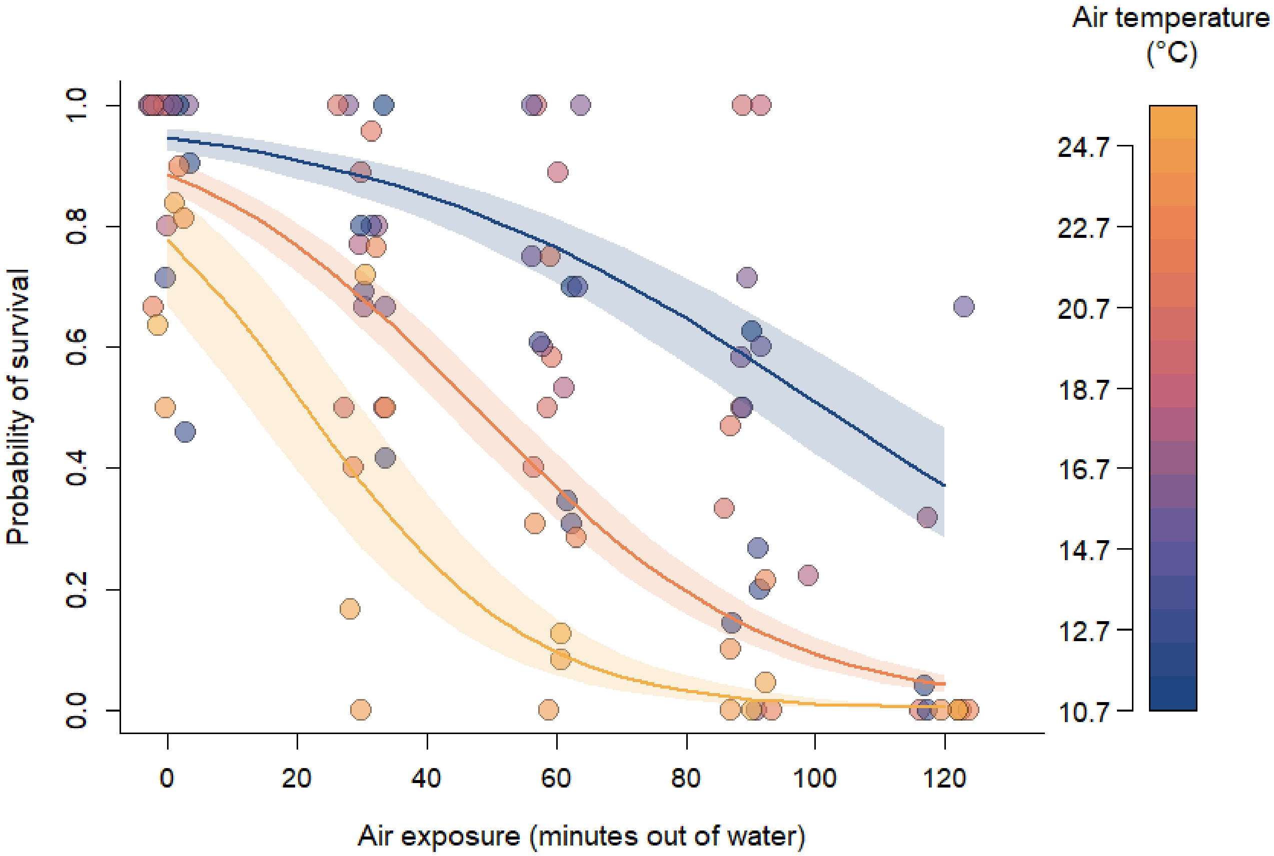

Figure 3.5 Estimated probability of survival across varying periods of time out water (0-120 minutes) and air temperature, holding prawn size constant (32 mm).

Curves reflect model-predicted probability of survival across three air temperatures: 10°C (top), 18°C (middle), and 26°C (bottom). Plotted points (horizontally jittered to distinguish amongst points) represent the raw data, summarised as trial-level mean survival proportions of prawns within the 31-33 mm size range.

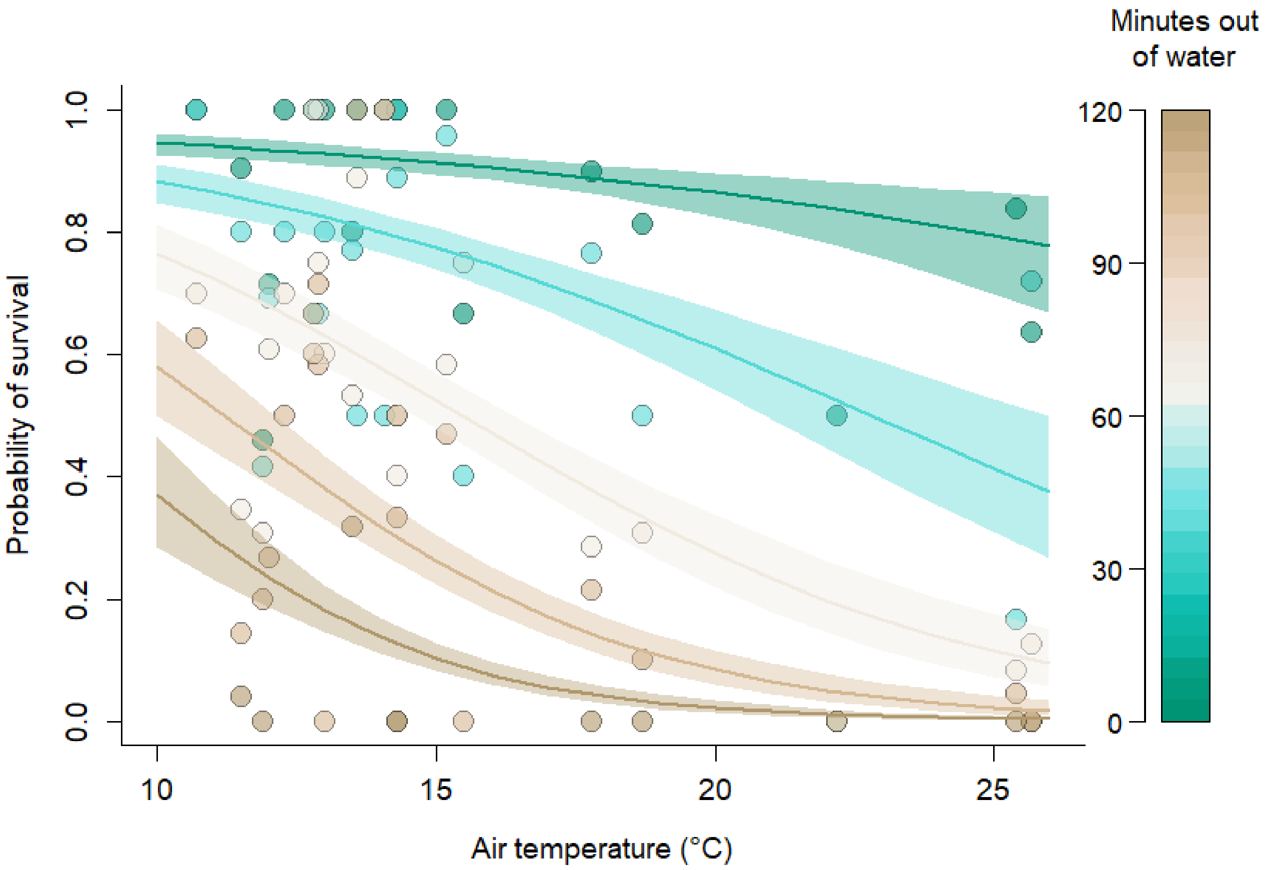

Figure 3.6 Estimated probability of survival across the range of air temperatures encompassed in the experiment (10-26°C) and across air exposure treatments, holding prawn carapace length constant (32 mm).
Curves reflect model-predicted probability of survival across five air exposure treatments (top to bottom): 'immediate release', 30 min, 60 min, 90 min, and 120 min. Plotted points represent the raw data, summarised as trial-level mean survival proportions of prawns within the 31-33 mm size bin.

Predictions from the top model suggest that 32 mm prawns in the 'immediate release' treatment have a 95% survival probability in cool conditions (10°C, 95% C.I. = 93-96%, Table B.1), which declines to 80% in hot conditions (25 °C, 95% C.I. = 70-87%). This represents a typical scenario for the commercial fishery where traps must be sorted as they are hauled and prawns under 33 mm must be released. Under cool conditions and when immediately released, smaller prawns (22 mm, the median length for juveniles) are predicted to survive at a slightly higher probability (97%, 95% C.I. = 95-98%) than larger prawns (40 mm, the median length for transitionals and females) are predicted to survive (92%, 95% C.I. = 88-94%) but this relationship reversed at hot temperatures, for which larger prawns are predicted to have a higher survival probability than small prawns (75-90% for 40 mm prawns compared to 56-85% for 22 mm prawns). For a median length male prawn (32 mm), mean predicted survival probability falls below 50% after 101 minutes out of water in cool conditions (10 ºC) and after 24 minutes in hot conditions (26 ºC).

The mean reflex score (number of reflex behaviours present, of ten assessed behaviours) for surviving prawns declined with increasing air exposure and ranged from 8.3 for surviving prawns from the 90-minute air exposure treatment to 9.3 for surviving prawns from the 'immediate release' treatment (Fig. 3.7).

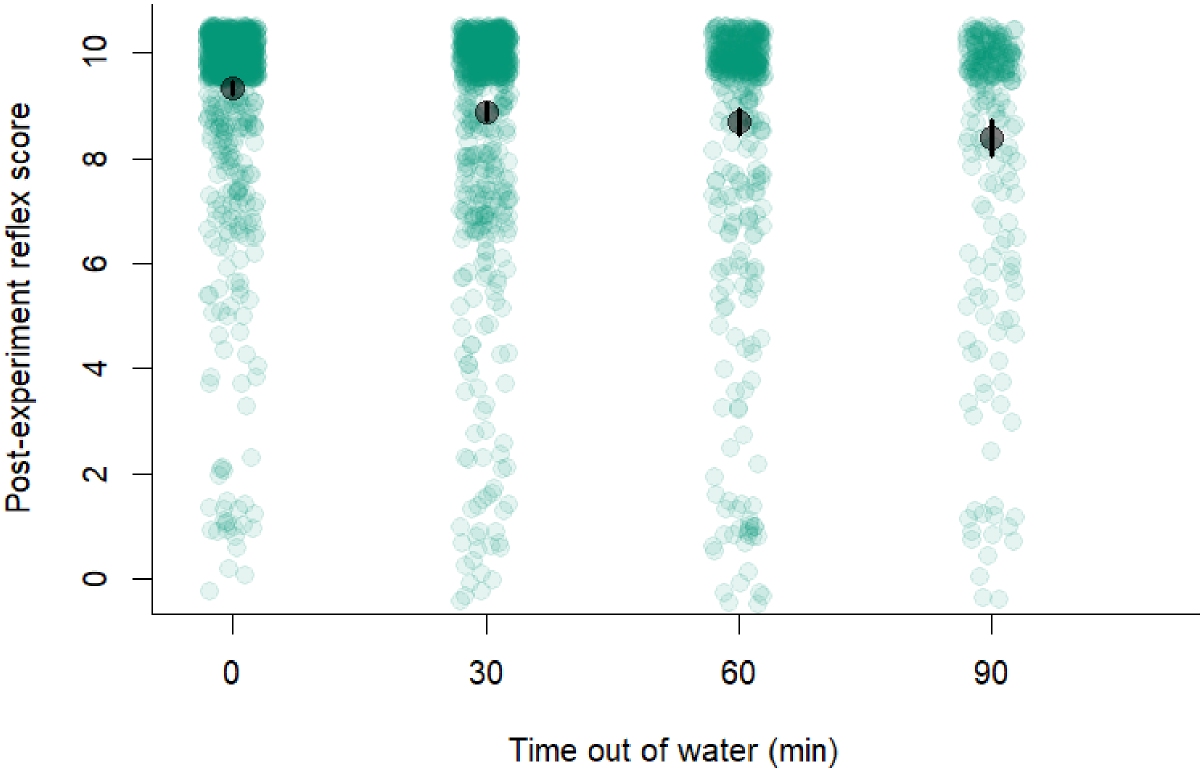

Figure 3.7 Distribution of post-experiment reflex scores (0-10) for surviving prawns from each air exposure treatment.

A reflex score of 0 indicates no reflex behaviours present (poor condition) and a reflex score of 10 indicates the full set of reflex behaviours are present (excellent condition). Teal points represent individual prawn scores. The black points and segments indicate the treatment specific mean reflex score and 95% confidence interval.

3.4 Discussion

Prawns like to be cold
Release them lickety split
Back to life at depth

Summarized in the haiku above, evidence from this field experiment suggests that spot prawns are best-positioned to survive trap-capture and release when they are returned to water immediately and are handled in cool air temperatures. In cool weather (~10ºC), we estimated survival probability as high as 97%, depending on length of air exposure, but this dropped quickly with increasing warmth and no prawns survived two hours of air exposure in >25ºC weather. Although we did not track survival longer than 24-hours post-release, our assessment of reflex behaviours suggested that the majority of surviving prawns were in good condition, indicating possible longer-term survival (Stoner 2012). Discard mortality in fisheries is an increasingly acknowledged and investigated uncertainty (ICES 2004; Basti et al. 2010; Wilson et al. 2014; Patterson et al. 2017), but it is relatively less well understood for fished invertebrates and, as far as we are aware, this is the first assessment of post-release survival of spot prawns and one of few direct assessments of post-release mortality in trap-capture invertebrate fisheries (c.f. DiNardo et al. 2002; Grant 2003). The broad results of our experiment are generally consistent with previous studies on the discard mortality of other marine invertebrates, including the strong influences of air exposure and temperature on post-release survival (Van Tamelen 2005; Giomi et al. 2008; Urban 2015).

While we expected that spot prawns would fair less well out of water for long periods of time in hot weather, we were surprised by the relatively high survival of individuals released immediately and the high reflex scores for surviving prawns, regardless of air exposure treatment. We use the discussion below to situate our results within the context of previous work, highlight several limitations and caveats, connect our results to the management context in Pacific Canada, and suggest directions for future investigation. Directly comparing post-release survival estimates between studies is challenging; the range of species, fishing methods, and experimental conditions precludes apple-to-apple comparison. However, our study results connect generally to the existing literature on three factors governing post-release survival: physiology, environmental conditions, and capture and handling methods.

First, physiologically, we might expect species without swim bladders that are adapted to large vertical migrations to survive capture-and-release more readily than more physiologically vulnerable species. Invertebrate species, such as Dungeness crab, which experience intertidal environments during their lives appear to survive at higher rates after release (Yochum et al. 2017). Although spot prawns are not adapted to direct air exposure, they settle as juveniles in shallow water (Marliave and Roth 1995) and are known to make nightly diel vertical migrations throughout the water column (Barr 1970). These migrations may confer a baseline physiological tolerance for a broader range of depths. Furthermore, spot prawns and other fished invertebrates do not have swim bladders and thus do not suffer the same barotrauma experienced by, for example, rockfish (Jarvis and Lowe 2008). Multiple studies have investigated the metabolic responses of fished invertebrates to capture and air exposure, primarily focusing on desiccation and its associated impacts (e.g., Vermeer 1986). Because spot prawns and other crustaceans require water flow across their gill filaments for proper respiration, desiccation through air exposure leads to a number of metabolic impacts including a shift to anaerobic respiration and the accumulation of toxic metabolites (Vermeer 1986). While we did not directly measure the metabolic response of spot prawns in this experiment, declining metabolic function is a likely path to mortality for individuals in the longer air exposure treatments. The large negative effect of air temperature on survival is most clearly explained by the increase in desiccation rates of exposed prawns, emphasizing the influence of seasonality and other environmental factors on post-release survival.

Environmental conditions were an important predictor of post-release survival and the speed at which it declined with increasing air exposure. Air temperature was a covariate in the five top models comprising 100% of the cumulative model support by BIC (Table 3.2) with a pronounced effect on the shape of the drop-off in survival probability with increasing air exposure (Fig. 3.6). On the hottest days (26ºC), survival dropped off quickly with air exposure, falling to ~10% estimated probability of survival after an hour out water compared to ~80% estimated probability of survival on a cool day (10ºC). This result is consistent with previous invertebrate-focused studies that have found a strong effect of seasonality (Giomi et al. 2008; Lorenzon et al. 2013; Mérillet et al. 2018) and is intuitive given the influence of heat on desiccation rate and associated metabolic function. We expected that smaller prawns might survive less well than larger prawns due to their higher relative surface area and possibly faster desiccation rates (Vermeer 1986), but survival was higher at smaller sizes and our top model included a negative interaction effect between temperature and carapace length. While this might be a true ecological effect, it is possible that the difference in survival across size is at least in part an artifact of the experiment itself. The sample size of small juvenile prawns in the field experiment was small and we mostly captured juveniles early on in the season, which coincided with most of the cool air temperature trials (Figs. B.1, B.2). The influence of air temperature was mediated by the length of air exposure, emphasizing the importance of capture and handling methods to maximize post-release survival.

Capture and handling methods drive large variation in post-release survival for all fisheries, including those for marine invertebrates. Previous research investigating post-release survival for invertebrate fisheries focuses on invertebrate trawl fisheries and while there is variability in the exact methods and survival estimates, survival estimates tend to be lower for trawl-caught invertebrates than trap-caught. In a paper investigating the survival of mantis shrimp, Lorenzon et al. documented 100% survival of individuals caught by trap in October compared to 0% survival for those caught by trawl at the same time of year (2013). Other trawl-based survival estimates are more optimistic including ~50% survival of mantis shrimp exposed on deck for 10 minutes after a 30-minute trawl (Hill and Wassenberg 1990) and 37-51% survival of Norway lobster subjected to different sorting methods (Mérillet et al. 2018). Within trap-based fisheries, there is evidence that slower hauling speeds contribute to higher survival rates (Basti et al. 2010).

A field experiment provides a more realistic setting to evaluate post-release survival than in the lab; however, there were still several factors we were unable to account for including mechanical damage from handling and from descending in traps, post-release mortality due to predation, and longer term sublethal effects. The relatively higher survival of smaller prawns might be explained by lower susceptibility to injury from handling and from mechanical damage in the traps post-treatment during descent and ascent at the end of the trial. Larger prawns would be subject to higher drag during the hauling process and might have been more likely to get pushed against the sides of traps. Alternatively, despite a lower surface area to volume ratio, larger prawns might have higher absolute metabolic demands that could lead to higher post-release mortality. Further investigation is necessary to understand size-based trends in post-release mortality and the size-related results from this experiment should be interpreted cautiously.

To evaluate post-release survival of prawns without needing to recapture released prawns (and the additional complexity of recapture rates) we 'released' prawns in traps with the openings closed and thus did not account for additional mortality due to predation. Post-release mortality due to predation is difficult to measure and likely varies depending on predator abundance, descent speed of released individuals, and impairment of predator escape behaviour. There is evidence that air exposure affects the response behaviour of crustaceans including their ability to evade predators at least in the short term (Brown and Caputi 1983; Vermeer 1986; Haupt et al. 2006). Past research has estimated it takes 9-10 seconds for released crustaceans to sink below 1 m (relevant for predation from birds) and found that over 80% of bait set on a vertical drop line were intact after recovery (Hill and Wassenberg 1990), but it is tenuous to generalize such experiments too far. Nonetheless, some proportion of released prawns likely succumb to predation and further research would be necessary to incorporate this component of post-release mortality. We do not expect that the factors noted above impact our estimates of *relative* survival with increasing air exposure and temperature, but the absolute survival probability might be considered as a 'best case' estimate.

Finally, it is possible that additional mortality would occur beyond the experimental period considered here. We did not track survival after 24 hours but evaluated long-term survival potential using an established relationship between reflex behaviour and long-term mortality (Stoner 2012). While uncertainty remains regarding the precise estimate of post-release survival for spot prawns captured by trap, our results suggest that potential survival could be relatively high given the right handling and environmental conditions (Fig. 3.7). Understanding the range of potential survival outcomes fills an important information gap with respect to spot prawn fisheries and the effectiveness of size-based release measures.

The post-release survival estimates generated through this study have implications for commercial and recreational spot prawn fisheries as well as scientific surveys, all of which should seek to maximize post-release survival by keeping air exposure brief and taking seasonality into account. The license conditions for the commercial spot prawn fishery specifies that traps must be sorted individually as they are hauled and non-target individuals (under-sized males and egged females) must be released immediately (DFO 2019). Compliance with these conditions minimizes mortality due to air exposure and presumably also increases the probability that released prawns return to suitable habitat from where they were captured. Compliance and enforcement of this management measure is variable (Coady Webb, *personal communication*, 2020) and our results underline its importance. The progression of the commercial season often leads to higher catches of under-sized males as the larger females are fished down which coincides with warmer air temperatures in June and July. Releasing under-sized males promptly may be critical to maintaining a healthy population that will subsequently transition and represent the following season's females. While we did not investigate the influence of salinity in our analysis (all included trials occurred in high salinity conditions), there is evidence that post-release survival declines when release occurs through low salinity layers (Harris and Ulmestrand 2004), which is consistent with our anecdotal observations. Accounting for salinity will be important for commercial fishing that occurs in the heads of fjord systems where there can be a significant low salinity layer. In contrast to the specific license conditions for the commercial fishery, there are no strict regulations for size limits or sorting practices in the recreational fishery, which has grown substantially in recent years. This study suggests that recreational fishers can maximize survival of released egged females and small males through efficient sorting and consideration of warm weather.

Considering this first foray into estimating post-release survival of trap-captured spot prawns, we highlight several potential avenues for future work. In our Discussion, we note several uncertainties and caveats to do with estimating post-release survival. Alongside further empirical work to address these uncertainties (e.g., predation mortality), we encourage future research to evaluate the potential population-level effects of discard mortality and associated implications for the current management framework. This could be achieved by incorporating discard mortality estimates into future Management Strategy Evaluations (Punt et al. 2016). Previous research suggests that the effectiveness of minimum length limits in fisheries management can be influenced by post-release survival, and that for certain levels of discard mortality reducing fishing effort is necessary to prevent overfishing (Coggins et al. 2007). Incorporating the estimates produced by this study into a more comprehensive population model would provide more specific insights into the management implications of accounting for discard mortality in the spot prawn fishery.

Filling information gaps in fisheries management frameworks with empirical estimates rather than assumptions is a challenging but important task, and there are consequences for overlooking sources of cryptic mortality (Coggins et al. 2007). Estimating post-release survival is especially difficult because it is so fishery- and species-specific, but this study provides a first pass at filling that information gap for trap-captured spot prawns. While uncertainty remains, pointing to plenty of avenues for further investigation, we can be confident that prawns prefer their time out water to be cool and minimal and that efforts to return under-sized or egged spot prawns efficiently are worthwhile.

Chapter 4.

Fishery-independent surveys suggest that spot prawn (*Pandalus platyceros*) spring spawner escapement in Pacific Canada often falls short of management targets

4.1 Introduction

Fishery-independent data is a critical component of sustainably managed fisheries (Hilborn and Walters 1992). These data underpin robust estimates of the abundance and distribution of fished species, information which cannot be reliably gleaned from catch data alone. Management informed by fishery-dependent data alone is risky because fishermen do not randomly sample the population – they strive to catch fish as efficiently as possible. It is not hard to imagine the problem posed when managers rely on catch rates as proxies for population size. Perhaps the foundational risk comes when high catch rates mask population declines, due to increasing fishing efficiency or shifting fish behaviour in response to depletion (e.g., Erisman et al. 2011; Ward et al. 2013; Walsh et al. 2018; Free et al. 2020). This phenomenon, often referred to as 'hyperstability' contributed to some of the most notable fishery collapses of the last century, including the collapse of Atlantic cod in the 1990s (Hutchings and Myers 1994). Although easy to point out clear risks in hindsight, many fisheries today are still informed solely by catch data. Independent data from, for example, standardized research surveys are expensive and time consuming to collect. Overcoming logistical and budget constraints to inform management with fisheries-independent data is particularly important for developing fisheries, which are susceptible to excess fishing effort and often lack fundamental biological information about the harvested species (Hilborn and Sibert 1988).

Commercial fisheries for marine invertebrates are on the rise globally (Anderson et al. 2011b) and locally on the Pacific coast of Canada (Perry et al. 1999). Although an integral part of Indigenous food systems and stewardship for thousands of years (Augustine and Dearden 2014; Salomon et al. 2023), commercial invertebrate fisheries as we know them in Pacific Canada developed in the early to mid-1900s and have rapidly expanded over the past 50 years (Perry et al. 1999, 2002). Since the late 20th century, the collapse of commercial Pacific salmon fisheries has been accompanied by a growth in fisheries for many invertebrate species including crab, shrimp, urchins, geoduck, and sea cucumbers among others. Today, invertebrate fisheries comprise the highest value group of fisheries on the Pacific coast, surpassing that of salmon, groundfish, and pelagic species (DFO 2023). Marine invertebrate life histories are diverse but often begin with a pelagically dispersing larval stage before individuals settle and develop as relatively sessile adults. Developing management approaches for marine invertebrates is challenging – population structure is often unknown, fundamental knowledge gaps regarding recruitment and mortality persist, and fishery expansion often outpaces the production of scientific information (Anderson et al. 2008). Recent collapses in major invertebrate fisheries such as Gulf of Maine shrimp (Richards and Hunter 2021) and Bering Sea snow crab (Szulwalski et al. 2023) emphasize the importance of confronting these challenges head on.

In British Columbia (BC), the last 30 years saw the rise of a trap fishery for spot prawns (*Pandalus platyceros*), a fishery characterized by both a unique life history and a unique management framework. Spot prawns are sequential protandrous hermaphrodites, beginning life and reproducing as males before transitioning to and completing their lives as reproductive females (Butler 1964). Males fertilize females directly, and females brood eggs from the early fall through to the start of spring when larvae hatch and enter a ~2-3 month pelagic dispersal phase. Life span estimates vary throughout their geographic range, but in British Columbia spot prawns are assumed to live four years – the first ~3 years as male, and the final year as female. Females are assumed to die after releasing their eggs in the spring. The commercial trap fishery in BC began at a small scale in the early 1900s but didn't start to expand until the 1970s, prompting the Canadian Department of Fisheries and Oceans (DFO) to develop the foundation of what is now the Spawner Index management framework (Boutillier and Bond 2000). Since the 1980s, the commercial spot prawn fishery in BC has been managed as a 'derby' style fishery. To avoid overlapping with the spring period when egged females (fertilized during the previous reproductive year) release hatching larvae, the fishery typically opens no earlier than May. There are no fixed quotas and the exact length of the fishery each year varies depending on how quickly the female population is fished down to fixed escapement targets set by DFO (Fisheries and Oceans Canada 2025). In the early decades of the fishery, the commercial season spanned most of the year, but since 2001 when a single daily haul rule was implemented, the fishery length has dropped from 79 days to as low as 27 days in 2025 (Fisheries and Oceans Canada 2025). Today, multiple levers are used to manage the commercial fishery including minimum length limits, minimum mesh sizes, single daily haul rules, trap limits, and restricted fishing hours. In this study, we focus on the foundation of the management framework – the Spawner Index fixed escapement tool – which determines when managers close spatial management units to fishing.

Core to the spot prawn fishery management framework is ensuring that enough reproductive females escape the summer fishery and survive to release eggs the following spring. The fishery is managed based on an index of the reproductive female population – the 'Spawner Index' (SI) or the average number of spawners-per-trap. We will generally refer to 'spawners' rather than females throughout this chapter, because depending on the time of year, 'spawners' encompasses females and 'transitionals' – individuals transitioning from male to female. During the commercial fishery, at-sea fishery observers board fishing boats and collect trap-level stage structure data (i.e., individuals-per-stage-per-trap) from commercial catch. These data inform in-season estimates of the SI for a given spatial management unit. The scale of management is based on Pacific Fishery Management Areas (PFMAs), originally delineated to manage Pacific salmon. PFMAs are further divided into Subareas which vary in their exact size but typically represent a portion of an inlet, sound, or channel. Managers close subareas when the SI nears or falls below management targets (Fig. 4.1) and closures are announced twice weekly. As more subareas close, fishing effort is concentrated into the remaining open fishing grounds, and eventually a coastwide closure notice is issued.

The SI framework relies entirely on fishery-dependent data and in-season decision making; however, the management targets themselves are set relative to a target escapement of spawning spot prawns the following spring (late March) when they release their eggs. In other words, managers aim to close the fishery in the summer such that sufficiently many spawners survive the fishery and, accounting for post-fishery mortality, there will be sufficiently many females on the grounds to release eggs the following spring. The original spring spawner target was 1 spawner-per-trap at the end of March, defined based on research surveys conducted in Knight

Inlet and Kingcome Inlet in the 1980s (Boutillier 1987). Minimum monthly index targets for the rest of the year were back-calculated based on the assumption that the annual mortality rate for spot prawns was 1.5^{-yr}. The origin for this mortality estimate is unclear (Kyle Krumsick, *personal communication*, 2025). The Spawner Index targets have been adjusted over time with buffers to account for mortality uncertainty, changing trap types, etc. Today, all regions of the coast are managed to a March SI target of 1.9 spawners-per-trap or higher (Figure 4.1).

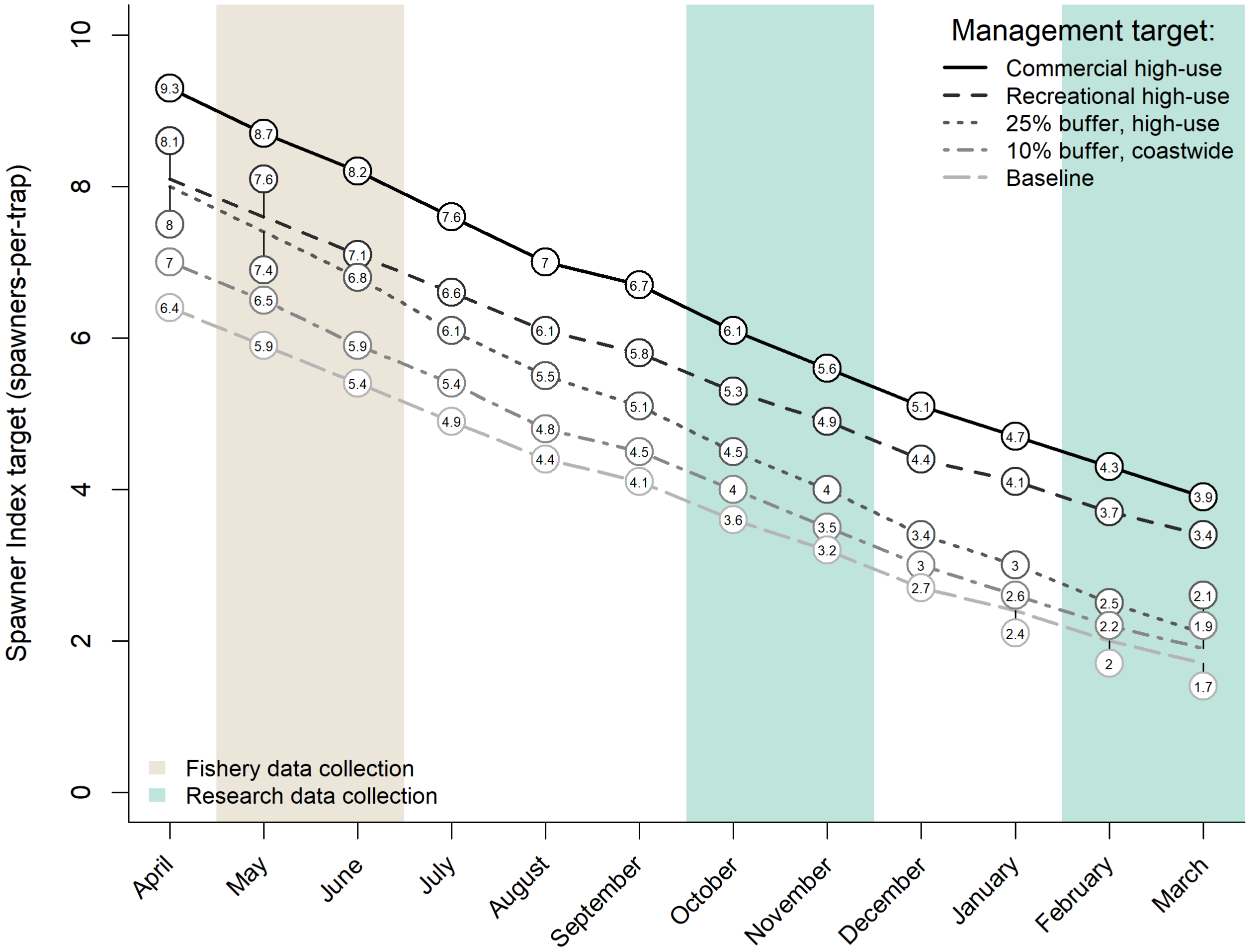

Figure 4.1 Monthly targets as defined by the Spawner Index management framework. Each line depicts a set of monthly SI targets defined in DFO's current management framework. Subareas are managed to different sets of targets depending on the recreational and commercial fishing pressure they experience. The "baseline" set of targets are based on the original targets defined in 1987, multiplied by 1.7 to account for a shift in gear type in 1988. Today, all subareas are managed to the "10% buffer" targets or higher.

There has been no empirical evaluation of the realized spring Spawner Index relative to management targets or relative to the observed Spawner Index at fishery close. As the length of the fishery declines (Fisheries and Oceans Canada 2025) and evidence for high fishery efficiency emerges (Rossi et al. 2023), addressing this gap is a necessary step to evaluate the assumptions of the current management framework. The current management framework makes several assumptions that have not been tested. Among others, managing to the same set of targets regardless of region or year reflects an assumption that post-fishery mortality – combined mortality due to natural processes and non-commercial fishing – is constant across the coast and over time. Current management further assumes that a fishery-dependent catch index (spawners-per-trap) is a robust proxy for population size and as such should decline linearly as the population declines. Finally, the management framework as practiced (i.e., without empirically evaluating spring spawner escapement) implicitly presumes that evaluating the Spawner Index at the end of the fishery (~June-July) is a sufficient indicator for whether spring Spawner Index targets are being met the following March. The Spawner Index is presumed to decline month-to-month according to some exponential mortality rate but the most recent published estimates of post-fishery mortality rates are 25 years old (Boutillier and Bond 2000). Fortunately, for some regions on the coast, there are current fishery-independent data with which we can begin to tackle these uncertainties.

During parts of the year, at-sea fishery observers and scientific researchers collected Spawner Index data from the commercial fishery and research surveys respectively. Normally fishery observer data span May through June or July, coinciding with the commercial fishery opening. Government scientists and managers use these data, in-season, to generate estimates of the Spawner Index (average number of spawners-per-trap) at a PFMA Subarea level and these estimates are evaluated relative to SI targets to inform closure decisions. Government, academic, and Indigenous-led research teams also conduct scientific surveys that vary in their exact timing but generally occur during the fall, spring, and on occasion, immediately following the commercial fishery in July. The inception of spot prawn research surveys originates at DFO with the inception of the Spawner Index management framework. During its development in the 1970s and 1980s, exploratory surveys were conducted in Howe Sound, Knight Inlet, and Kingcome Inlet (Boutillier 1987; Boutillier and Bond 2000). Originally, DFO intended to maintain research surveys in several focal areas across the coast, but budget limitations led to just one longstanding DFO-led research survey in Howe Sound (DFO Area 28) spanning from the 1980s through to the present. In the 1990s, the Kitasoo Xai'xais Stewardship Authority initiated a spot prawn research survey in their territories on the Central Coast (DFO Area 6 and 7), following the same methods and with guidance from DFO (Ken Cripps, *personal communication*, 2022). The KXSA survey ran from 1993-1996 and recently restarted, with the current survey dataset spanning 2021-2024. An additional research survey was initiated in collaboration with the Musgamagw Dzawada̱'enux̱w Fisheries Group in their territories in the Broughton Archipelago (DFO Area 12), which ran from 2022-2024. Fishery data and research data differ primarily in their sampling design. Observer data are collected off commercial boats by sampling fishery catch whereas research data are collected by setting strings of traps at fixed station sampling locations. Despite these differences, the method for collecting stage structure data (hereafter referred to as 'indexing') is consistent between data sources.

In this study, we set out to generate empirical estimates of the Spawner Index at the end of March relative to the Spawner Index at the closure of the previous year's fishery season. We generated these estimates by drawing on fishery-dependent and fishery-independent Spawner Index data from three regions on the coast: (1) Howe Sound (DFO Area 28), (2) the Broughton Archipelago and mainland inlets (DFO Area 12), and the mid Central Coast (DFO Areas 6 and 7) (Fig. 4.2). These are three regions for which post-fishery research surveys have been conducted for some period (3 to 24 years) using consistent methodology. We construct an exponential decay model that captures the core elements of the within-year Spawner Index dynamics and estimate in-season and post-season mortality rates that allow us to generate Spawner Index predictions at key time points within the year. We fit separate models for each region and account for the fact that the data come from fishery-dependent and -independent sampling processes. We assess evidence for temporal and spatial variation in Spawner Index dynamics and evaluate the uncertainty associated with different data sources. Our assessment of spring spawner escapement using fishery-independent data suggests that the spring Spawner Index often falls short of current management targets and the post-fishery mortality rate varies regionally. This investigation comes at a timely moment, as DFO is in the process of defining Limit Reference Points under the Fisheries Act and evaluating the underlying management framework is critical to inform future science and management efforts for a rapidly changing fishery.

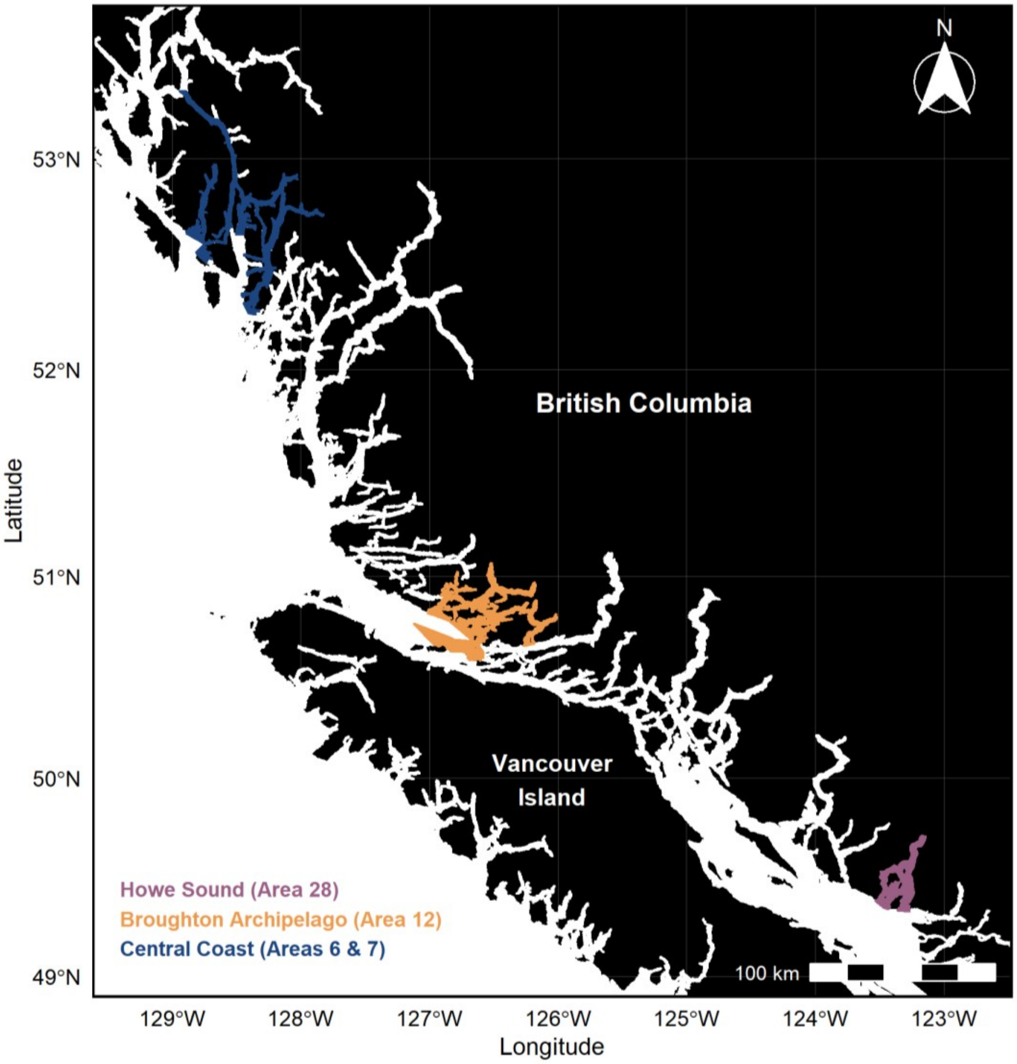

Figure 4.2 Map of British Columbia highlighting focal regions included in Spawner Index analysis.

4.2 Methods

We estimated within-year Spawner Index dynamics for three regions in British Columbia. For each region we fit a statistical model capable of generating SI predictions at given time points within the year relevant to the management framework and the ecology of the species. We used this statistical framework to ask (1) how within-year SI dynamics vary temporally, (2) whether SI dynamics vary between regions, and (3) how estimated SIs compare to relevant management targets. Because the data for different parts of the year come from different data sources, we also estimated separate variance parameters for the fishery-dependent and fishery-independent data sources which correspond to the "in-season" and "post-fishery" periods respectively.

For each region, we fit an annual exponential decay model to Spawner Index data (spawners-per-trap counts) from two data sources: (1) fishery-dependent data collected by at-sea fishery observers during the commercial fishery and (2) fishery-independent data collected during scientific surveys conducted outside of the commercial fishery period. There are specific nuances to calculating the SI depending on the time of year (see *Statistical analysis*), but generally it is a catch index of the individuals in the population who will reproduce as females each year.

We note that spot prawn years do not directly align with calendar years. In this study, we will generally refer to "spawner years", which we define as spanning from May of a given calendar year through April of the next. Beginning the spawner year in May is slightly different from the DFO management framework which defines April as the first month of the spawner year (Fig. 4.1). We defined May as the start of the spawner year primarily for implementation reasons because (1) the first Spawner Index observations from the commercial fishery always occur in May and (2) in the Broughton, it allowed us to include data from a spring survey conducted in April 2022 as a measure of spring spawner escapement from the 2021 fishery.

Consistent with current assumptions (Fisheries and Oceans Canada 2025) we assume that spot prawns survive for one year as reproductive females. In May, the number of spawners in the population is approximately at its peak as mature males transition to females through the spring months. The number of spawners declines, with natural and fishery-related mortality, throughout the year until berried females release hatching eggs the following spring (and presumably die shortly thereafter). Below, we outline the data sources used in our analysis, the data cleaning and assembly conducted, and details of the model structure and fitting procedure.

4.2.1 Data sources

In our analysis, we include fishery observer data (for all regions) and research survey data (from Howe Sound/DFO Area 28) sourced from the Invertebrate Data Section at DFO. Additionally, we draw on research survey data collected by the University of Alberta in collaboration with the

Musgamagw Dzawada̱’enux̱w Fisheries Group (MDFG) in their territories in the Broughton Archipelago/DFO Area 12 and on research survey data collected by the Kitasoo Xai’xais Stewardship Authority (KXSA) in their territories on the Central Coast/DFO Areas 6 and 7 (Fig. 4.2).

Fishery-dependent observer data

Spawner Index data collected by at-sea observers during the commercial spot prawn fishery are the foundation for the management framework. The at-sea observer sampling program is operated by a contracted service provider, J.O. Thomas, which coordinates data collection and processing in-season. Ultimately, the data are stored by DFO and available publicly and through data requests via the Invertebrate Data Section. We obtained updated fishery-dependent Spawner Index from DFO on March 13, 2025.

The fishery-dependent index data consist of trap-level counts of individuals-per-stage collected from strings of traps set and hauled by commercial fishermen. Fishery observers were deployed across the coast within the first few days of the commercial fishery opening and they collected data throughout the season. Data collection was coordinated to achieve broad spatial coverage across multiple vessels.

An observer sampling event involves boarding a commercial vessel and counting the contents of 12+ traps from a ~50-trap string as it is hauled and processed by the fishermen. Typically, observers sampled every third trap, though the sampling interval can be as wide as every fourth trap. As the string is hauled, fishermen emptied the entire contents of every third trap and the fishery observer indexed the catch, examining the second swimming leg of each prawn to determine its sex. During the commercial fishery season, catch typically included males, transitionals, and females (with less frequently captured juveniles, egged females, and spent females). The reproductive appendages on the second swimming leg reveal the sex of the individual. Observers recorded the number of individuals per-stage per-trap, including undersized or egged prawns that were released from the fishery. They also recorded the trap type and bait used by the fisherman.

Fishery-independent research data

DFO and other groups collected fishery-independent SI data during research surveys conducted at points in the year outside of the commercial fishery season (Table 4.1). These research surveys are not conducted coastwide, and as such we restricted our analysis to regions for which research data are available: Howe Sound (DFO Area 28), the Broughton Archipelago (Area 12), and the Central Coast (Areas 6 and 7). We constrained our analysis to 2001 onwards when the single daily haul rule was implemented. Prior to 2001, there *are* fishery and research data (for Howe Sound and the Central Coast); however, the observer program was much patchier, and the single daily haul rule had not yet been implemented in the commercial fishery, making it difficult to compare traps as units of effort before and after 2001. We compiled research survey data from Howe Sound (2001-2024), the Broughton Archipelago (2022-2024), and the Central Coast (2021-2024). The non-DFO led research surveys followed the same sampling protocol used in Howe Sound and the general methods are consistent between surveys, with a few slight differences. The lead author of this study has participated in all three surveys herself to ensure that survey methods are consistent and to document and account for any methodological differences. Below, we describe the general survey design and sampling methodology, and we refer the reader to Appendix C for region-specific details.

Research surveys typically occurred twice per year, with one survey in the fall (circa October-November) and one survey in the spring (circa February-March). In a few instances, KXSA also conducted research surveys immediately after the commercial fishery in July. The exact survey timing shifted slightly year-to-year but generally took 7-14 days and involved sampling ~30-50 sites. At each site, the research vessel set a string of 10-20 prawn traps (76 cm tapered stainless steel traps with 1.9 cm mesh) which were spaced approximately 22-24 meters apart on a groundline. Anchors were placed at either end of the ground line from which float lines rose to the surface with marker buoys on either end of the string. Traps were usually baited with approximately 2/3 cup of standard prawn bait pellets, although the bait type shifted halfway through the Howe Sound survey (see *Data cleaning* section below).

Perhaps the most important but hardest to standardize aspect of the survey is the process of where and how traps are set. Spot prawns typically inhabit rocky shelf type habitat, the depth and location of which varies depending on the bathymetry of a given sampling location. Ideally, a research survey aims to randomly sample the population to produce the most robust estimate of population status. In the case of spot prawns, solely sampling at locations frequented by commercial fishermen might produce a positively biased index of abundance. On the other hand, completely randomly sampling with respect to bathymetry or only sampling at a single fixed depth regardless of the bathymetry of a given location could lead to the opposite problem. The methods for site selection and string setting protocol are not thoroughly documented (though see Appendix C for further details) but generally, sites were selected in feasible prawn habitat along the contour lines of shelves at approximately 55-110 meters depth. The sampling design most closely resembled a fixed station design, with strings set at generally the same set of locations each survey (with slight variation in exact coordinates). After setting, strings soaked overnight, for ~24 hours, and were hauled and processed the following day.

Across surveys, sampling teams collect stage structure, length, and weight data from the contents of the research traps. In this study, we only draw on stage structure data and focus our methods description accordingly. Biologists count the contents of each trap and index individuals to stage, as in the commercial fishery by examining the reproductive appendages on the second swimming leg. During the fall survey, the most common stages present are males and egged females. During the spring survey, all stages are present including juveniles, males, transitionals, females, egged females, and spent females. The raw trap-level counts of individuals-per-stage are then summarized as trap-level or string-level Spawner Indices (the exact formula for which depends on time of year, Table 4.2). Trap-level counts are also assigned ‘use codes’, indicating whether or not the trap count should be considered usable data for Spawner Index calculations. For example, a trap might be deemed unusable because of a dislodged bait cup or hole in the trap mesh. A use code of zero indicates that the trap is useable whereas a non-zero use code indicates that the trap count should not be included in SI calculations (the specific number indicates why).

Table 4.1 Fishery-dependent and fishery-independent sources of Spawner Index data used in our analysis.

Note that the time span is listed in terms of calendar year and thus is slightly offset from the range of spawner years encompassed by our analysis.

Data type	Region	Time span	Source	Sites per survey	Notes
Commercial fishery observer Spawner Index data	All regions	2001-2024	DFO Invertebrate Data Section		
Howe Sound research survey Spawner Index data	DFO PFMA 28 Subareas 1, 2, 3, 4, and 5	2001-2024	DFO Invertebrate Data Section	~40-50	Data aren't associated with specific site names but ~40-50 fixed locations are sampled per survey
Broughton research survey Spawner Index data	DFO PFMA 12 Subareas 6, 35, 36, 37, 38, 39, 40, 41, 43, 44, 45, 46, 47, and 48	2022-2024	Musgamagw Dzawada̱'enux̱w Fisheries Group and University of Alberta	29-36	
Central Coast research survey Spawner Index data	DFO PFMA 6 (Subareas 18, 19, 25, and 24) and PFMA 7 (Subareas 6, 7, 9, 10, 11, 29).	2021-2024	Kitasoo Xai'xais Stewardship Authority	30-36	

Table 4.2 Spawner Index formulation based on time of year.

The Spawner Index is a catch index of the individuals in the population that will reproduce as females each year. Depending on the time of year, the Spawner Index is calculated as the sum of a different set of stages to accurately reflect the status of the spawner population at different time points within the year. Adapted from (Fisheries and Oceans Canada 2025).

Time of year	Spawner Index (count-per-trap)
January – April	egged + spent
May – July	transitionals + females
August – September	transitionals + females + egged
October – November	females + egged
December	egged

4.2.2 Statistical analysis

Filtering and cleaning data and calculating Spawner Index

To ensure that the research data used in our analysis was collected and processed as consistently as possible between regions, we applied a consistent set of data quality criteria to filter the research data and calculated the Spawner Index from scratch from the filtered dataset.
We assembled fishery and research data for Howe Sound, the Broughton Archipelago, and the Central Coast and applied a set of filtering criteria to arrive at a final dataset consisting of comparable Spawner Index counts. We investigated apparent outliers with extremely high counts (i.e., >100 spawners-per-trap), with odd dates, or with extremely long or short soak times. Where reasonable, we made corrections to what were clearly typos and where appropriate, we excluded outliers. With input from government biologists, we systematically filtered trap-level counts based on use codes, soak times, trap types, and bait codes. We excluded data from traps with non-zero use codes, traps with soak times shorter than 16 hours or greater than 30 hours, and non-standard trap types (Boutillier 1988).

Research survey data from the Broughton Archipelago and the Central Coast were collected using exclusively pellet bait; however, the bait type used in the commercial fishery and for the Howe Sound research survey varied. Bait type was most variable for data collected in Howe Sound. The DFO-led research survey originally used tuna bait but shifted to pellet bait in the early 2010s (with several years during which both baits were used) (Figs. C.1, C.2). Pellets have been the predominant bait type used in the commercial fishery but reported bait types include herring, sardines, and gurdy bait (fish scraps), among others (Fig. C.3). In Howe Sound, we retained data from pellet-type and fish-type baits (there were a few records of geoduck and starfish being used as bait, which we filtered out), and we include a bait effect in our model (details below). For the Broughton and Central Coast, the vast majority of the fishery bait types were reported as pellets (Figs. C.4, C.5) and all of the research data, so we filtered the datasets to only retain observations from traps baited with pellets.

Using the filtered dataset, we calculated the Spawner Index for each trap as the number of 'spawners'-per-trap. The Spawner Index reflects an index of the prawns who will breed as females in a given spawner year, but the exact stages that go into the calculation differ depending on the time of year. We use the delineations adopted by DFO to be consistent (Table 4.2). From January through April, the Spawner Index is the sum of the egged and spent females in each trap, as these are the individuals who are about to or already have released the eggs they have been brooding through the fall and winter. The start of May marks the start of the new "Spawner Year" and from May through July, the Spawner Index is the sum of the transitionals and females in each trap, as those are the individuals who will be fertilized and brood eggs through the upcoming fall. This is the group and the season most heavily impacted by fishing pressure. There are very few data collected during August and September but in principle, the Spawner Index is calculated as the sum of the transitionals, females, and egged females in each trap as breeding season begins many are egg-bearing. In October and November, the Spawner Index is calculated as the sum of the females and egged females. In December, the Spawner Index is the sum of the egged females.

Model structure

To estimate the rate of decline of the Spawner Index during and after the commercial fishery and generate Spawner Index predictions at set time points within the year, we fit an exponential decay model with separate in-season and post-season mortality rate parameters. For each region, we model the spawner dynamics as independent annual dynamics – the dynamics of a given spawner year do not influence the next. At the start of the "spawner year" (May 1), the spawner population is approximately at its highest and we model its decline throughout the year (from fishing and other sources of mortality) as an exponential decay process. Because spawning females are assumed to die shortly after releasing their eggs in the spring, the spawners of one year have no direct demographic connection to the spawners of the following year. Below, we outline the details of the modelling framework.

For each year, y, the expected Spawner Index, λ, for any given day, t, is a count which declines according to an exponential decay deterministic process model. During the fishery season, the Spawner Index, $\lambda(t)$, is defined as $\lambda(t) = N_{0,y} \exp(-Z_y \cdot t) \exp(\alpha_s)$ and during the post-fishery season the Spawner Index is defined as,

$$\underbrace{\lambda_y(t)}_{\substack{\text{expected}\\ \text{SI on day}\\ t\text{ of year }y}} = \underbrace{N_{0,y}}_{\substack{\text{initial}\\ \text{SI at start}\\ \text{of year }y}} \exp\left(-\left(\overbrace{Z_y}^{\substack{\text{daily}\\ \text{in-season}\\ \text{mortality}\\ \text{rate}}} \underbrace{t_{1,y}}_{\substack{\text{fishery}\\ \text{length in}\\ \text{year }y\\ \text{(days)}}} + \overbrace{M_y}^{\substack{\text{daily}\\ \text{post-season}\\ \text{mortality}\\ \text{rate}}} \underbrace{\left(t - t_{1,y}\right)}_{\substack{\text{days after}\\ \text{fishery end}}}\right)\right) \underbrace{\exp(\alpha_s)}_{\substack{\text{string-level}\\ \text{random effect}}}, \tag{1}$$

where, $N_{0,y}$ is the Spawner Index at the start of each year y, an estimated parameter. Also estimated annually, Z_y and M_y are 'in-season' and 'post-season' mortality rates. We define them this way to make clear that they are not estimates of fishery and natural mortality rates. For example, Z_y represents the mortality rate during a period of the year when fishery mortality is likely the dominant source of mortality, but it also encompasses mortality due to natural processes such as predation during that period. Similarly, M_y represents natural mortality but also any non-commercial fishery mortality that we know occurs during the post-season but lack sufficient data to incorporate in our analysis.

To account for possible shared variation between traps on the same string (due to ecological and sampling factors, see Discussion), we included a log-normally distributed random effect for string such that each string effect, α_s, was drawn from a Normal distribution with mean zero and variance σ_f. The f subscript indicates that we estimated two variance parameters, one for the fishery data (in-season) and one for the research data (post-season) to account for potential differences between datasets. For the Howe Sound model, we also estimated a multiplicative bait effect, exp (β_b), where the base case ($\beta = 0$) corresponded to counts from traps baited with tuna and non-zero values were estimated for each subsequent bait type to facilitate estimating correction factors that we could use to generate model predictions on the scale of different bait types. We chose tuna as our base case because it is the original bait type that was used to generate the initial management targets (Rutherford et al. 2004).

The predicted Spawner Index counts followed a zero-inflated negative binomial observation model:

$$C_i \sim \mathrm{ZINB}\big(\lambda_y(\mathrm{t}), \phi_f, \pi_f\big)\,, \tag{2}$$

where C_i, the predicted count for trap i, was drawn from a distribution with mean $\lambda(t)$, dispersion parameter ϕ_f, and zero-inflation parameter π_f. We estimated separate dispersion and zero-inflation parameters for the different data sources. We chose a negative binomial distribution to account for overdispersion in the count data (the variance was substantially higher than the mean for all regions). We included a zero-inflated component to account for the high frequency of zeroes by estimating the probability of structural zeroes in the data, which is common in trap data. The probability mass function is,

$$P(C_i = 0) = \big(1 - \pi_f\big) + \pi_f \cdot \mathrm{NB}\big(0 \big| \lambda_y(t), \phi_f\big), \text{for } c = 0 \tag{3}$$
$$P(C_i = c) = \pi_f \cdot \mathrm{NB}\big(c \big| \lambda_y(t), \phi_f\big), \text{for } c > 0,$$

where $\mathrm{NB}(c|\lambda(t), \phi_f)$ is the negative binomial probability mass function with mean $\lambda(t)$ and dispersion parameter ϕ_f.

Table 4.3 Parameters estimated for each region and prior distributions.

Parameter	Description	Prior	Notes
$N_{0,y}$	Initial Spawner Index on the day of the first observation of year y	$\mathrm{Lognormal}(\ln(20)\,, 1)$	
Z_y	Daily mortality rate during the fishery season	$\mathrm{Lognormal}(\ln(0.07)\,, 1.4)$	
M_y	Daily mortality rate during the post-fishery season	$\mathrm{Lognormal}(\ln(0.005)\,, 0.75)$	
σ_f	Variance of the string effect distribution from data source f (fishery or research)	$\mathrm{Half\ Normal}(0, 2)$	
ϕ_f	Dispersion parameter for the Negative Binomial observation model	$\mathrm{Gamma}(1, 0.1)$	Must be greater than 1.
π_f	Zero-inflation parameter	$\mathrm{Beta}(1, 1)$	
β_b	Bait effect estimated for bait type b	$\mathrm{Normal}(0, 2)$	Only included in Howe Sound model.

Model fitting and evaluation

We fit independent models for each of the three regions using a Bayesian estimation framework and specified loosely informative priors, defining prior distributions such that the coefficient of variation was greater than one (i.e., standard deviation greater than the mean) in all cases (Table 4.3). We specified priors for Z_y and M_y based on estimates from (Rossi et al. 2023) and (Boutillier 1987; Boutillier and Bond 2000) respectively. We fit all models with variations on the prior distributions to ensure our results were not contingent on the priors. We fit each model using a Markov Chain Monte Carlo procedure implemented in Stan (Stan Development Team 2025) in Version 4.5.1 of R (R Core Team 2025). We ran four chains, a 1,500-sample warm-up, and 2,000 samples per chain (thinning every second sample for a total of 1,000 retained samples per chain) (McElreath 2020). We assessed convergence by visually assessing trace plots for all parameters and calculating the diagnostic statistics, r-hat and Effective Sample Size (ESS), for each model.

Generating model predictions

We generated model predictions of the median Spawner Index at given time points in the year by drawing posterior samples of the parameter values and, for each draw, generating an expected Spawner Index count. We also generated model predictions that incorporated uncertainty due to string-level variation by drawing string effect samples (from the fishery or research string effect estimates, depending on the time of year) for each expected count. To compare empirical estimates to management targets on the correct scale, we generated Spawner Index model predictions corrected to account for bait type (i.e., on the 'tuna scale'). To assess how Spawner Index estimates compared to current management targets we generated regional and annual model predictions of the Spawner Index on the last day of the fishery and on March 31, the time point for which DFO's spring spawner escapement targets are defined. Consistent with the targets used in practice (Fisheries and Oceans Canada 2025), we assessed Howe Sound estimates relative to the '25% High Use' targets and we assessed estimates from the Broughton and Central Coast relative to the 'Coastwide 10% Buffer' targets (Fig. 4.1).

4.3 Results

Spawner Index estimates relative to management targets

Most of our Spawner Index estimates at the end of March fell below current escapement targets regardless of region (Figs. 4.3, 4.4). In five of 24 years in Howe Sound, the median predicted spawners-per-trap met or exceeded the management target of 2.1 spawners-per-trap in March (Fig. C.11). The spring Spawner Index estimate in the Broughton exceeded the management target (1.9 spawners-per-trap) in one of three years (Fig. C.12). The Central Coast had the lowest spring Spawner Index estimates, never exceeding 0.5 spawners-per-trap (C.13). Across the three regions, there were 19 cases when the median predicted SI at the end of March fellow below the current proposed Limit Reference Point (1.56 spawners-per-trap) delineating the benchmark between the 'Cautious' and 'Critical' zones under DFO's Precautionary Approach Policy (Fisheries and Oceans Canada 2009). There were eight cases (four years for Howe Sound, one year for the Broughton, and all three of the years for the Central Coast) when the median predicted SI at the end of March fell below 1 spawner-per-trap, the original, unbuffered target set at the inception of the management framework in the 1980s (Boutillier 1987). The predicted Spawner Index at fishery close was generally higher relative to escapement targets; there were nine years in Howe Sound (Fig. C.11) and one year in the Central Coast (Fig. C.12) where the median predicted SI at fishery close fell below escapement targets.

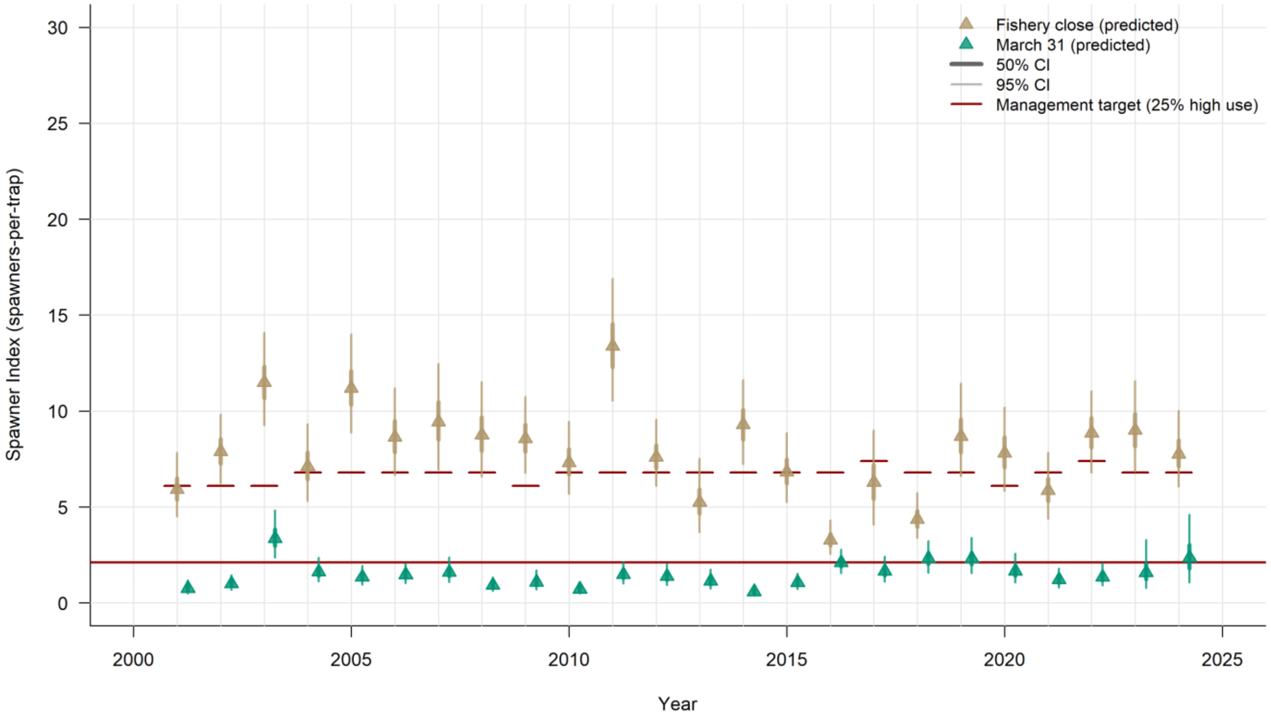

Figure 4.3 Median predicted Spawner Index at fishery close and following March for Howe Sound.

Brown triangles represent median predicted Spawner Index at the end of the summer commercial fishery (exact timing changes year-to-year). Turquoise triangles represent median predicted Spawner Index on March 31 of each year (the time point for which spring spawner escapement targets are set). Thick and thin segments reflect 50% and 95% credible intervals respectively. DFO escapement targets are indicated by red line (spring) and dashes (end of fishery). Exact fishery escapement target depends on the month in which the fishery closes, hence the interannual variation.

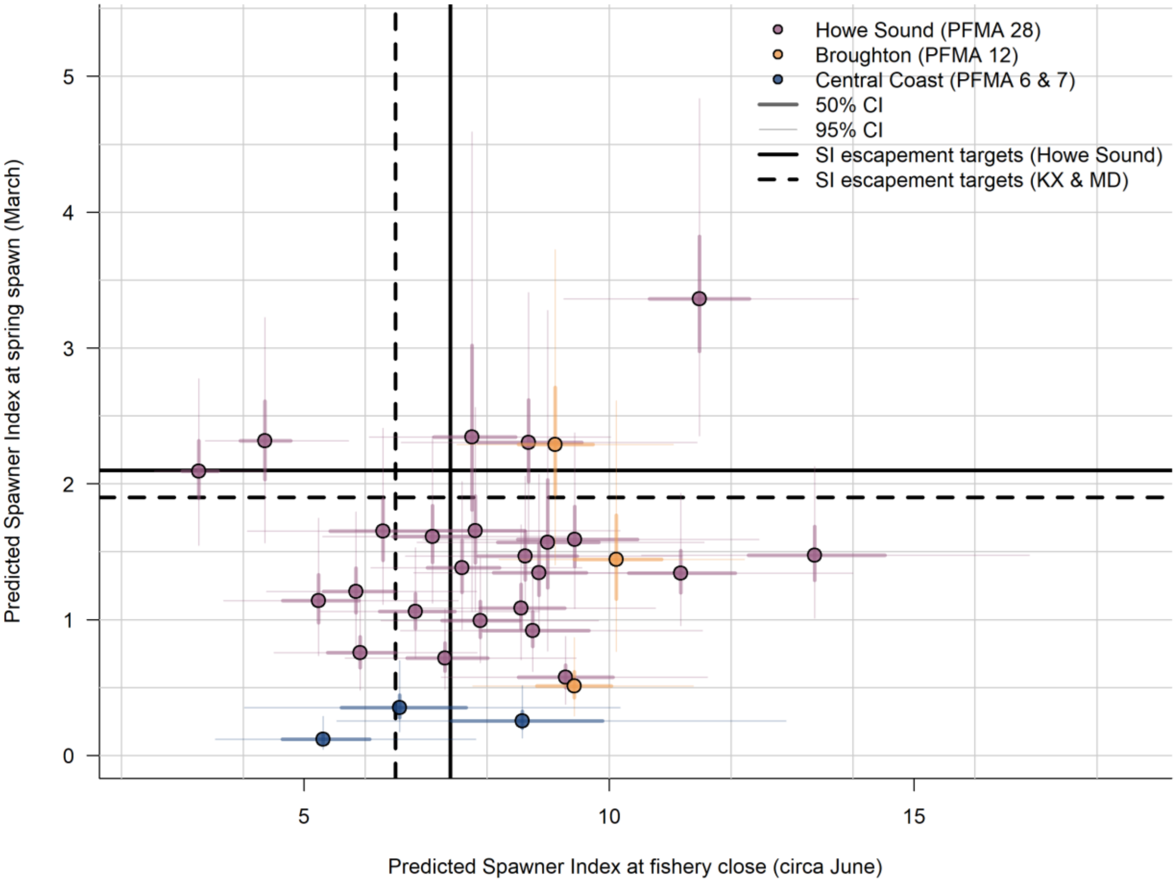

Figure 4.4 Predicted spring Spawner Index relative to predicted Spawner Index at fishery close across regions.

For each region and year, we generated model predictions of (1) the median Spawner Index (spawners-per-trap) on the last day of the fishery (the exact date varied year-to-year) and (2) the median Spawner Index on March 31, the date for which DFO's spring spawner escapement target is defined. All predictions are appropriately scaled to the tuna bait type in order to compare to management targets developed based on data collected with tuna-baited traps. Points indicate median predictions and light and dark segments represent 50% and 95% credible intervals respectively. Colour indicates region: Howe Sound (purple), Broughton (orange), or Central Coast (blue).

Trends over time in Howe Sound

The 24-year time series for Howe Sound allowed us to assess trends across years. The time period appears characterized by a shift in fishery dynamics in the early 2010s (Figs. 4.3, 4.5). Throughout the first decade of the time series, estimates of fishery mortality (both the daily rate, Z_y, and the proportional mortality over the length of the fishery season, $N_{0,y}\exp(-Z_y t_{1,y})$), were relatively stable and certain (Fig. 4.5, 4.6, 4.7). There is a slightly increasing trend in both the daily mortality rate (Fig. 4.5) and the cumulative fishery mortality (Fig. 4.6) until 2012 when the dynamics become much more variable and uncertain (Fig. 4.8). From 2012 through the early

2020s, the fishery mortality rate estimates were generally higher and the posterior distributions were wider, especially for years when the length of the fishery was quite short (e.g., 2016 and 2017). This was also the period when the Spawner Index at fishery close more frequently dipped below the management target. The cumulative mortality over the course of the fishery also varied from as low as ~20% in 2022 to as high as close to 80% in 2012 (Figure 4.6). The period of higher variability and uncertainty also coincides with a dramatic shortening in the length of the commercial fishery from >35 days (2001-2011) to as low as 13 days in 2017 (Figure 4.9).

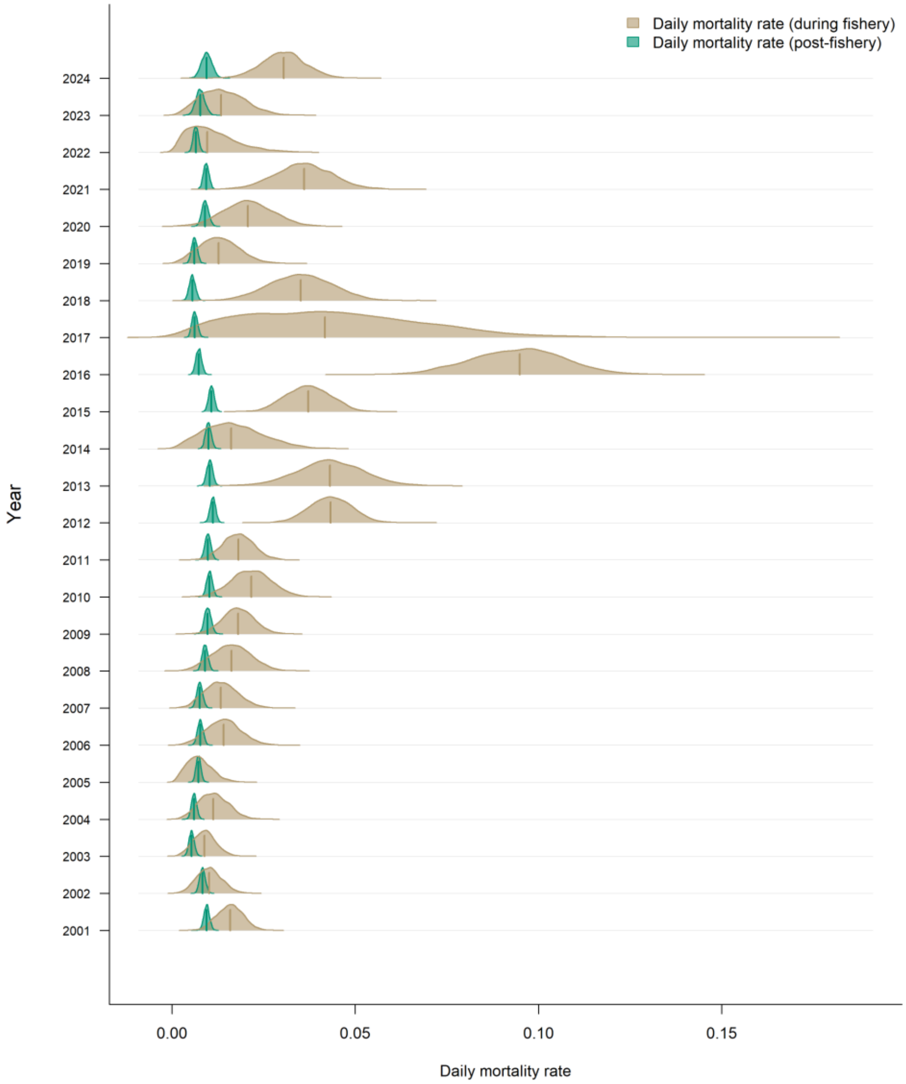

Figure 4.5 Posterior distributions of daily in-season and post-season mortality rates in Howe Sound from 2001-2024.

Solid lines indicate the median of the distribution. Posteriors are plotted as scaled distributions to be able to clearly visualize on the same plot.

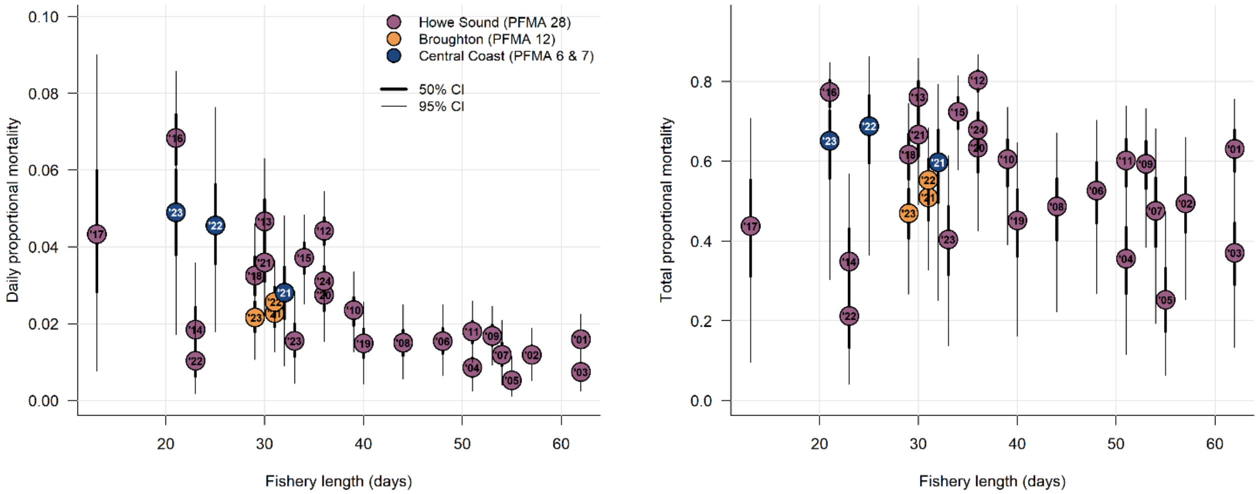

Figure 4.6 Daily proportional in-season mortality and total proportional in-season mortality relative to fishery length.

Daily proportional mortality calculated as $1 - \exp(-M_y)$ to reflect the proportion of the population estimated to die daily during the fishery. Total proportional in-season mortality calculated as $1 - \exp(-M_y \cdot t_{1,y})$ to reflect the proportion of the population estimated to die over the length of the fishery for each year, $t_{1,y}$. The annual fishery length has generally shortened over time as daily mortality has. Total proportional mortality ranges from ~20-80%.

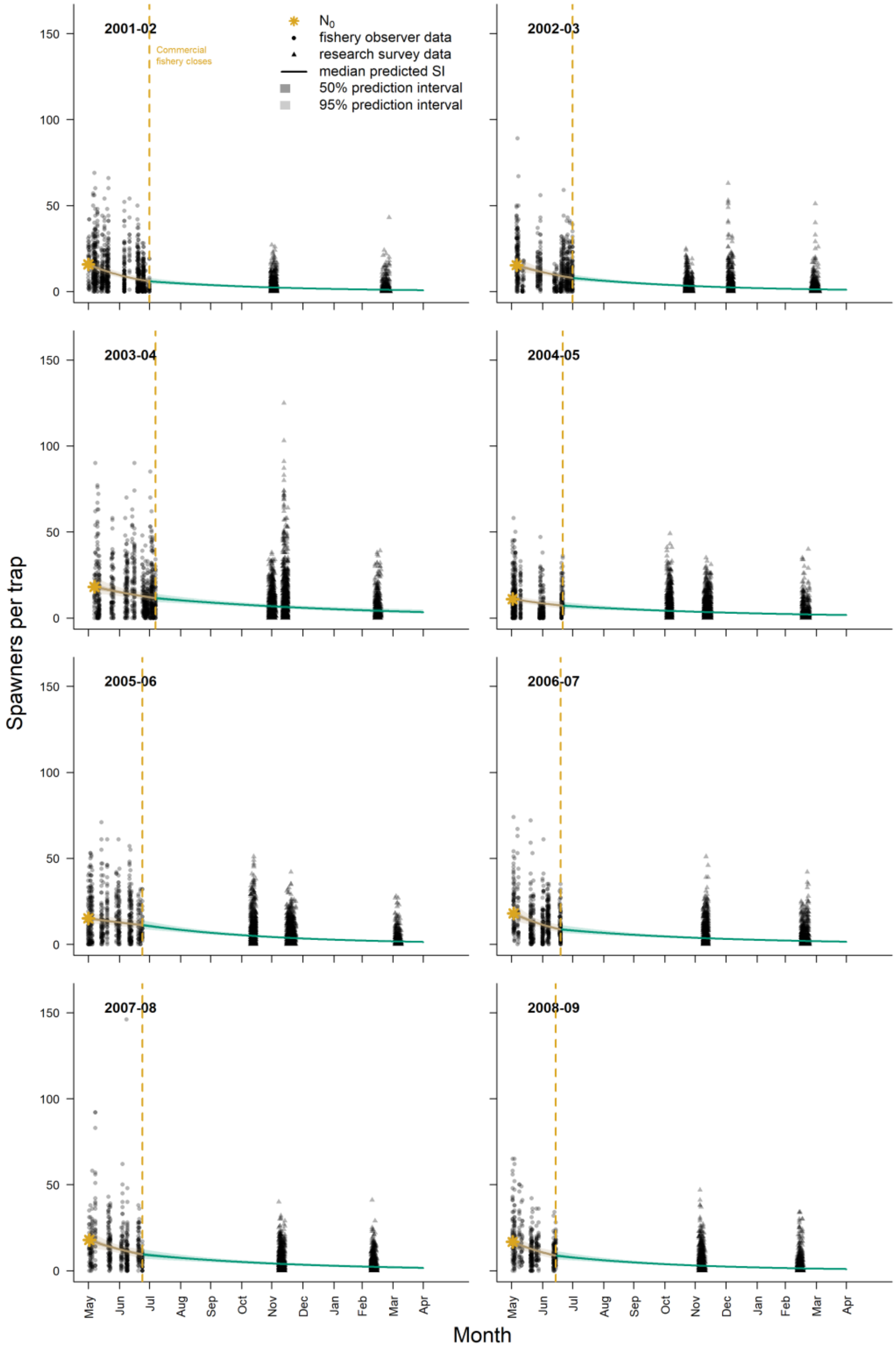

Figure 4.7 Spawner Index exponential decay model fit for Howe Sound (2001-2008).
Median model predictions plotted as solid lines with polygons visualizing 95% credible interval. Brown represents in-season period and turquoise represents model predictions for the post-season period. Dashed yellow line denotes fishery closure. Black points indicate raw trap-level Spawner Index counts (circles for fishery data, triangles for research data).

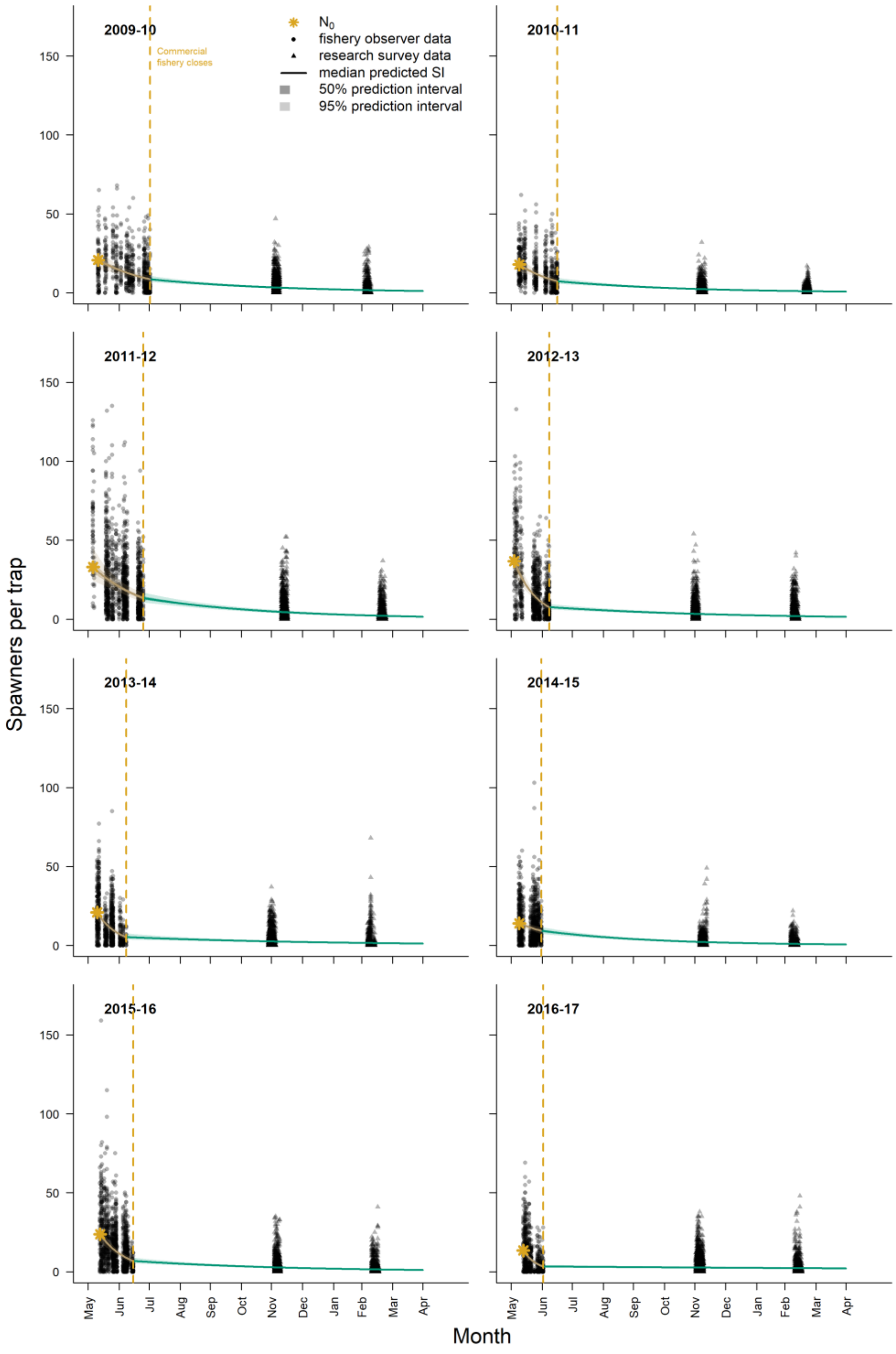

Figure 4.8 Spawner Index exponential decay model fit for Howe Sound (2009-2016).
Median model predictions plotted as solid lines with polygons visualizing 95% credible interval. Brown represents in-season period and turquoise represents model predictions for the post-season period. Dashed yellow line denotes fishery closure. Black points indicate raw trap-level Spawner Index counts (circles for fishery data, triangles for research data).

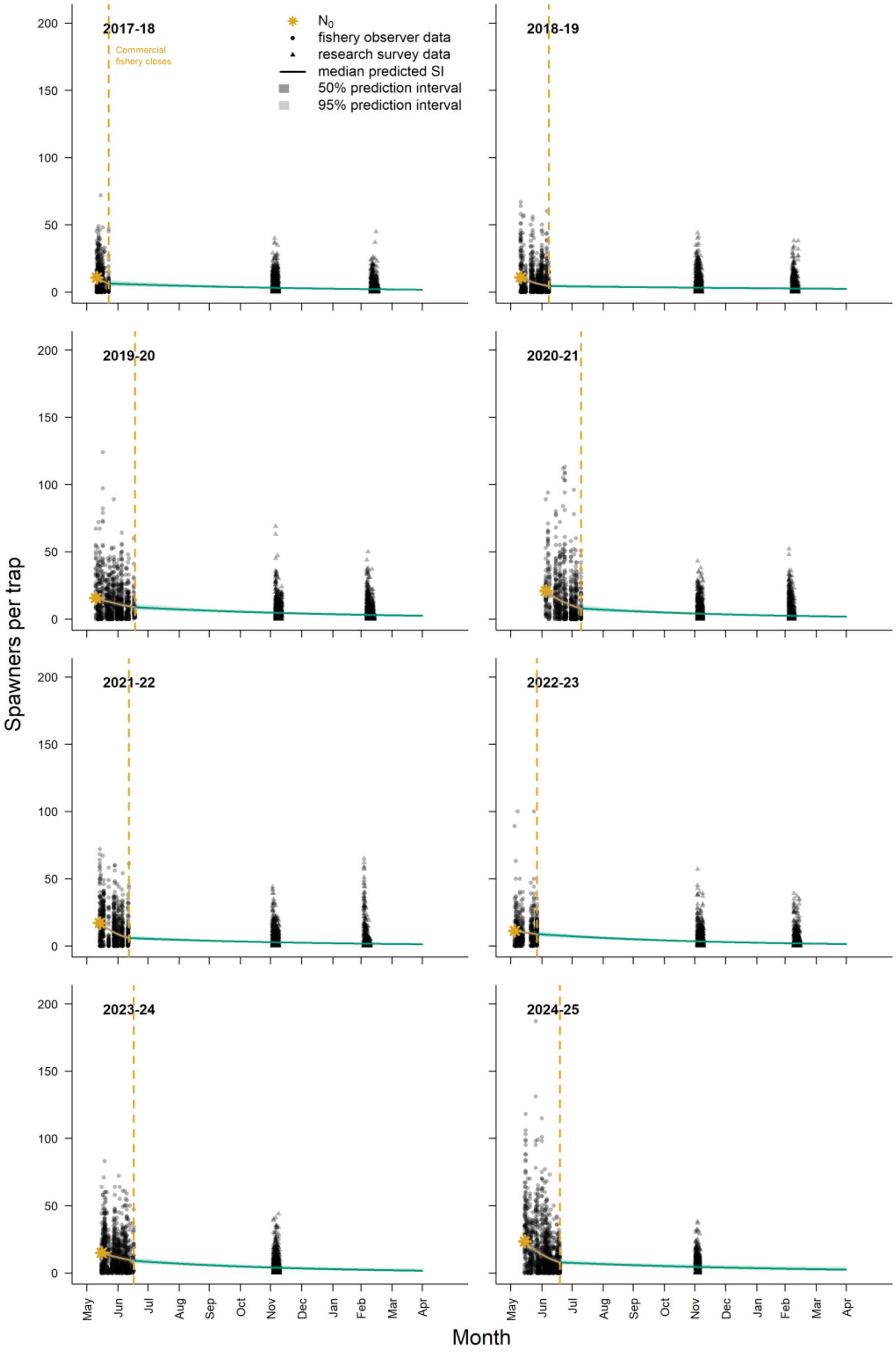

Figure 4.9 Spawner Index exponential decay model fit for Howe Sound (2017-2024). Median model predictions plotted as solid lines with polygons visualizing 95% credible interval. Brown represents in-season period and turquoise represents model predictions for the post-season period. Dashed yellow line denotes fishery closure. Black points indicate raw trap-level Spawner Index counts (circles for fishery data, triangles for research data).

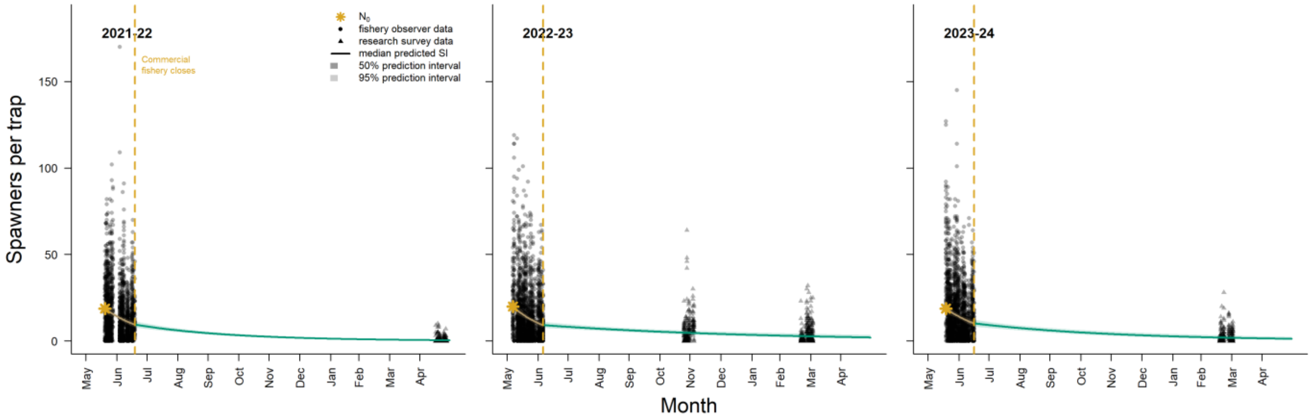

Figure 4.10 Spawner Index exponential decay model fit for the Broughton (2021-2023). Median model predictions plotted as solid lines with polygons visualizing 95% credible interval. Brown represents in-season period and turquoise represents model predictions for the post-season period. Dashed yellow line denotes fishery closure. Black points indicate raw trap-level Spawner Index counts (circles for fishery data, triangles for research data).

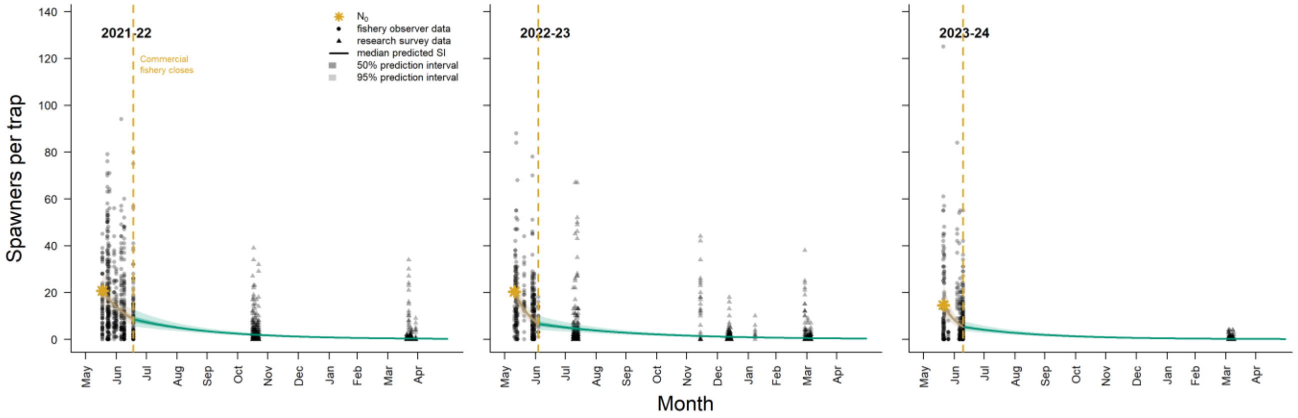

Figure 4.11 Spawner Index exponential decay model fit for Central Coast (2021-2023). Median model predictions plotted as solid lines with polygons visualizing 95% credible interval. Brown represents in-season period and turquoise represents model predictions for the post-season period. Dashed yellow line denotes fishery closure. Black points indicate raw trap-level Spawner Index counts (circles for fishery data, triangles for research data).

Regional variation in Spawner Index dynamics

The time period with available fishery-independent data for the Broughton and Central Coast regions was much shorter than for Howe Sound, but for the three spawner years with data from all regions (2021-2023, Figs. 4.9-4.11), Howe Sound and the Broughton exhibited relatively similar dynamics in terms of fishery mortality rates (Fig. C.7) and predicted spring Spawner Indices (Fig. 4.4). Results from the Central Coast stood out from the other two regions (Figs. 4.4, 4.9-4.11) We estimated consistently higher post-fishery mortality rates for the Central Coast than for either of the other two regions (Fig. 4.12). Accounting for structural zeroes in the data, the median predicted SI at the end of March fell below 0.5 spawners-per-trap in all three years and the lowest three spring SI estimates all came from the Central Coast (Fig. C.13). The daily mortality rate estimates during the fishery season in the Central Coast were similar to the other regions in 2021, but in 2022 and 2023 the fishery season mortality rates were the highest in the Central Coast (Figure C.7). Across regions, estimated proportional mortality from the fishery season ranged from ~20-80% and has stayed relatively high in recent years despite the shorter fishery length (Figure 4.6).

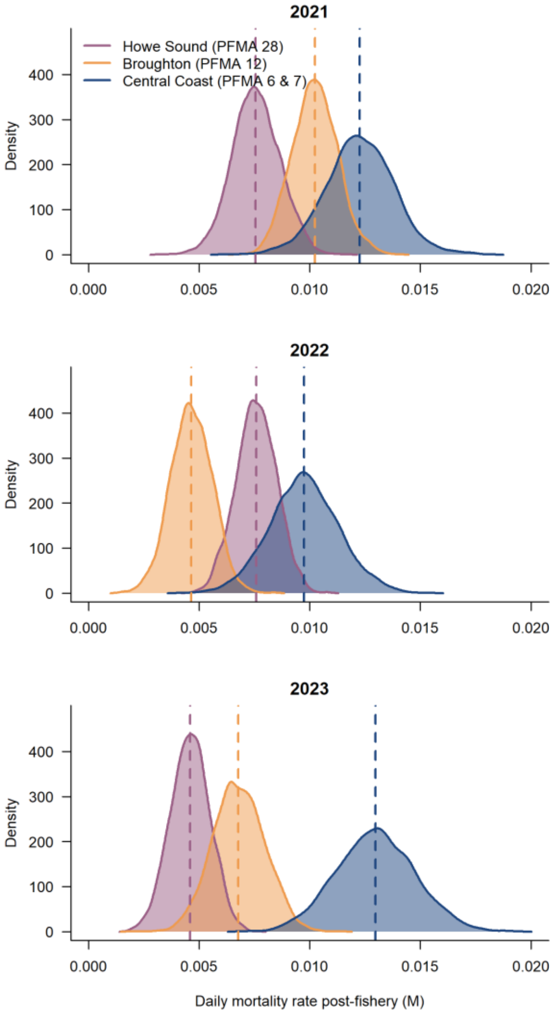

Figure 4.12 Posterior distributions of post-fishery daily mortality rate (M_y) across regions. Posterior distributions visualized for the three years with data from all three regions (2021-2023). Dashed lines indicate the median of the distributions for Howe Sound (purple), the Broughton (orange), and the Central Coast (blue).

Uncertainty and sources of variation in Spawner Index estimates

Spawner Index counts were highly variable, as captured by the wide range of estimated string effects (Figure 4.13) and high uncertainty in Spawner Index predictions incorporating uncertainty from string-level variation (Figs. C.14-C.18). The distribution of string effects also varied depending on the data source – there was generally a wider distribution of string effects for the research data than the fishery data, with a stronger negative skew (i.e., proportionally more string effects below average) (Fig 4.13). In general, there was higher uncertainty in parameters estimated from the research data for the Broughton and the Central Coast (Figs. C.8, C.9) which is not surprising given the much smaller datasets, especially for the Central Coast where even fishery observer coverage is quite low (Fig. 4.11). Our model estimated higher trap-level variation and higher zero-inflation in the Central Coast research data (Fig. C.8, C.9) than for the other two regions.

Most of our estimated bait effects had posterior distributions that overlapped one (i.e., overlapped with the mean SI of tuna-baited traps) (Fig. C.10). Sardine was the only bait type for which we estimated confidently higher Spawner Indices relative to tuna. The median effect of pellet bait on the Spawner Index was 1.07, suggesting that pellet-baited traps catch 7% more spawners than tuna-baited traps, though the 95% credible interval overlapped with one. This is lower than the current correction factor for pellet traps of 1.27 (Rutherford et al. 2004).

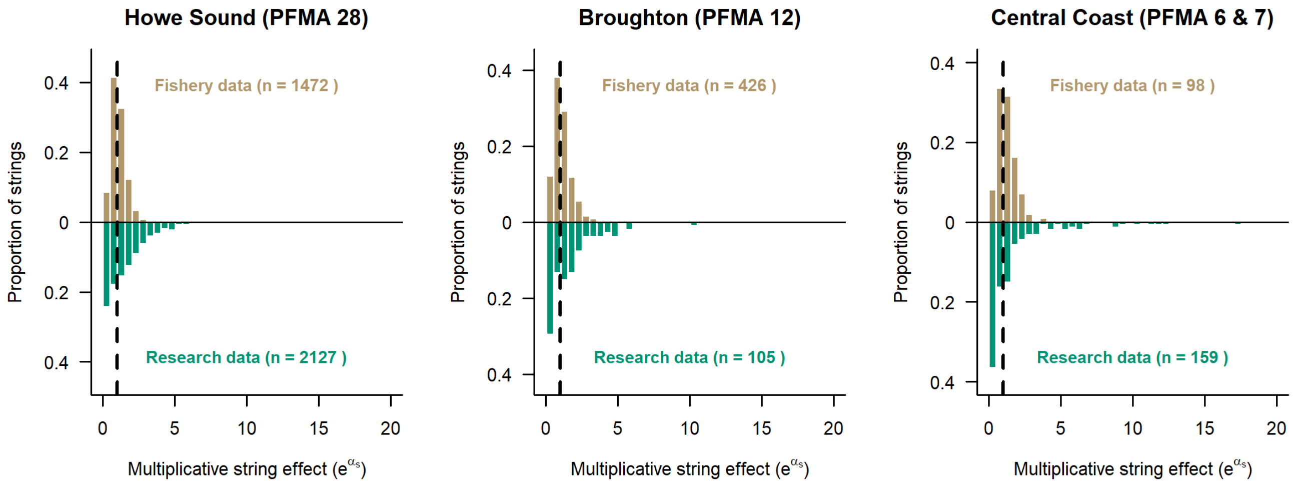

Figure 4.13 Distribution of estimated string effects for fishery and research data sources in Howe Sound.

Dashed line indicates the mean string ($\exp(\alpha_s) = \exp(0) = 1$); string effects above 1 indicate strings that caught more spawners than the average string and effect below 1 indicate strings that caught fewer spawners than average. A string effect of, for example, 10 indicates a string that caught 10 times the average string for that region and data source. In general, the distribution of research string effects was wider and more negatively skewed than that of fishery string effects.

4.4 Discussion

Our study is the first to empirically estimate in-season and post-fishery Spawner Index dynamics for the spot prawn fishery in BC. We found that while the fishery usually closed at or above current management targets, predicted spring spawner escapement often did not meet or exceed escapement targets and sometimes fell below the current Limit Reference Point defined in DFO’s fishery management plan (Fisheries and Oceans Canada 2025). Spawner Index dynamics have varied over time, with a distinct shift in Howe Sound in the early 2010s. Evidence suggests that the Central Coast may be distinct from the other two regions with generally lower spring spawner escapement. The Spawner Index data exhibited high string-level variation, the distribution of which differed between fishery-dependent and fishery-independent data sources. Our study takes a step towards grounding management of the spot prawn fishery in data-driven assessments, underlines the value of fishery-independent data, and provides information that can support refining and expanding research surveys in the future.

Spring spawner escapement relative to fishery escapement

The Spring Spawner Index often fell below management targets despite the fishery generally closing at or above current management targets, a pattern which could be explained by multiple mechanisms. First, the mortality rate of spawners post-fishery might be higher than assumed by the current management framework. The Spawner Index management framework assumes that closing the commercial fishery in the summer at some fixed escapement target corresponds to an ultimate escapement target the following spring when females release the eggs they have brooded through the winter – a relationship which depends on information about the post-fishery mortality rate. It is possible that the assumed post-fishery mortality rate underlying the current management framework (1.5^{-yr}, the origin of which is not entirely clear but dates back to the 1980s, Kyle Krumisck, *personal communication*, 2025) is an underestimate. This could be due to higher than assumed (or time varying) natural mortality due to predation, environmental conditions, etc. It could also be due to unaccounted for non-commercial fishing pressure from the recreational fishery and from First Nations rights-based fishing outside of the commercial season. It is beyond the scope of this study to disentangle potential other sources of mortality, and data from non-commercial fisheries is sparse, but the decline of salmon and other finfish fisheries may have contributed to increased interest in invertebrate fisheries over the past several decades.

It is also possible that the fishery-dependent Spawner Index data provide, to some extent, a positively biased index of the population. In this scenario, managers could be closing the fishery at a Spawner Index that appears to fall above their escapement targets, but the underlying population might be lower than is reflected by the data. This scenario is feasible because we expect that fishers target their catch rather than randomly sample the population and catch-based management is broadly understood to be vulnerable to hyperstability whereby fisheries catch rates stay high despite underlying declines in abundance (Hutchings and Myers 1994; Ward et al. 2013; Walsh et al. 2018). As a result, spring Spawner Indices would fall below management targets not necessarily because post-fishery mortality is high but rather because the population at fishery close was lower than indicated by the Spawner Index.

A combination of the two mechanisms is also possible, and there are plausible reasons that both might be at play. A recent study found evidence for high fishing efficiency in the spot prawn fishery (Rossi et al. 2023). Without fishery-independent estimates of the population during or immediately after the commercial fishery, it is difficult to disentangle the two mechanisms. Because we do not explicitly incorporate hyperstability into our analysis, the model attributes low spring Spawner Index estimates to high post-fishery mortality rates. Given our inability to disentangle the relative contribution of the two mechanisms, it may be more appropriate to think of our post-fishery mortality estimates as *apparent* post-fishery mortality rates. The post-fishery mortality rate underlying the current Spawner Index management targets is on the high end of previous empirical estimates (Boutillier and Bond 2000 estimated mortality rates of $0.42\text{-}1.46^{-yr}$), and was thought to be a precautionary estimate. Other modelling studies over the last decade usually fix natural mortality to the mean estimate from (Boutillier and Bond 2000) of 0.88^{-yr} (e.g., Smith 2014; Rossi et al. 2023). By contrast, we estimated apparent post-fishery mortality rates equivalent to $0.5\text{-}4.7^{-yr}$ with all but two of our estimates falling above the equivalent of 1.5^{-yr}. Disentangling the relative contribution of high post-fishery mortality and potentially biased catch indices is a clear avenue for future work, but our results suggest that current targets are unlikely to be as precautionary as currently considered.

High apparent post-fishery mortality on the Central Coast

The Central Coast had distinctly different Spawner Index dynamics from Howe Sound and the Broughton. In all three years for which data from all regions were available (2021-2023), the estimate for post-fishery mortality in the Central Coast was higher than the Broughton or Howe Sound (Fig. 4.12) and our estimates of spring Spawner Index on the Central Coast were the lowest three estimates, all below 0.5 spawners-per-trap. These results come with caveats – there are just three years of fishery-independent data, there are fewer survey sites on the Central Coast relative to the size of the region than there are in Howe Sound, and fishery observer coverage is lower on the Central Coast than the other two regions. On the other hand, the survey sites included in this analysis are sites that were surveyed by KXSA in the early 1990s and research staff who participated in both surveys report that many of the sites that are now ‘dead’ were highly abundant in previous decades (Ken Cripps, *personal communication*, 2025). The magnitude and consistency of the difference in Spawner Indices suggests that the pattern is unlikely just a sampling artifact and applying a precautionary approach to our interpretation suggests that even an uncertain pattern of this nature warrants concern. Fishery-independent estimates of the spring Spawner Index also seem to track changes in the fishery escapement, at least anecdotally. For example, in 2023, the fishery closed at 5.6 spawners-per-trap (lower than previous years and below the management target of 6.5 spawners-per-trap). The predicted Spawner Index the spring following the 2023 fishery was also lower than predictions for either of the other years.

Potential drivers of regional differences in mortality

Understanding potential drivers of apparent higher post-fishery mortality on Central Coast is important for effective management. It will require future work and there are several possible mechanisms to investigate. First, a castrating parasite, *Sylon* spp., occurs at much higher prevalence on the Central Coast (as high as ~50%) than it does on the South Coast (close to 0%) (Madeleine Abbott, *personal communication*, 2025). The direct mortality effects of this parasite are not well understood but related parasites are known to sterilize both males and females, feminize hosts, and alter host growth (Høeg 1995) and sterilization is thought to occur in most cases for *Sylon* infections of spot prawn (Bower and Boutillier 1990). It is possible that *Sylon* could negatively affect population productivity both through direct lethal or sublethal effects and through its effect on fertilization and reproduction. Second, it is also possible that different oceanographic conditions and/or fishing histories could contribute to the current Spawner Index dynamics on the Central Coast. The North Pacific and Subarctic Currents off Canada's west coast split around the top of Vancouver Island, which leads to different flow patterns above and below that split (Thomson 1981). It might not be too surprising that the Broughton and Howe Sound have similar Spawner Index dynamics and that it is the Central Coast region which diverges. This could be due to a variety of oceanographically influenced factors such as larval dispersal dynamics or nutrient dynamics.

It is also possible that spot prawn populations on the Central Coast respond differently to fishing pressure than populations on the South Coast. Although the Central Coast has been subject to relatively lower fishing pressure (in terms of vessels and trap days) than the South Coast in recent years, DFO PFMA 6 and 7 experienced their highest recorded fishing pressure in the mid-

1990s with the highest reported annual catch for both Areas occurring in 1996. This pattern is not reflected in PFMA 12 or 28, both of which have experienced stable or growing effort and catch since the 1990s. It is possible, albeit speculative, that currently depressed Spawner Index dynamics on the Central Coast are, in part, a legacy of this high fishing pressure in the 1990s. For a species with pelagic larval dispersal, recovery from overfishing may be determined, in part, by recruitment settlement and repopulation of overfished areas. The Central Coast is an oceanographically complex region with deep fjords and inlets and complicated current patterns (Pickard 1961). There is no research on how these environments shape the population structure of spot prawns but there are examples of locally isolated populations of other species, like Dungeness Crab, in fjord or inlet environments (Beacham et al. 2008).

Spawner Index dynamics over time in Howe Sound

Fishery dynamics in Howe Sound shifted in the early 2010s (Fig. 4.5). Estimates of in-season daily mortality rate dates were similar across the first decade of the time series but shifted in the early 2010s to higher and more variable estimates. The shift in fishery dynamics in Howe Sound may have been driven by a combination of shifting fishery technology, shifts in management decision making, higher variability in the population dynamics themselves, or some combination thereof. Starting in 2012, the estimated rate of decline in the Spawner Index during the fishery became generally higher and the length of the fishery also generally trended shorter than the previous decade. This pattern coincides with a general period of change in the development of fishing technology – bottom mapping technology increased in sophistication and there has been a general shift away from a ‘slow’ style of fishing with old-style freezer boats that process and freeze their catch onboard to ‘fast’ boats which are smaller high-powered boats that deliver their catch live to buyers and processors each day. The current management framework incentivizes efficiency because a given boat’s annual catch is not governed by quota but rather by how efficiently a boat makes use of its fixed daily effort over the course of the fishery.

There are several years when the Spawner Index at fishery close fell below management escapement targets, suggesting that for one reason or another the fishery did not close early enough relative to stated management goals. From 2016-18, despite the steep rate of decline and a closing Spawner Index below target, the estimated spring Spawner Index was close to or above target (Fig. 4.5). The commercial fishery was extremely short in 2016 and 2017 (less than 20 days) which might have led to idiosyncrasies in observer sampling and resulting estimates of in-season mortality rates. The last ~5 years have seen an uptick in both the predicted Spawner Index at fishery close and the predicted spring Spawner Index (Figs. 4.3, C.11), perhaps pointing to another shift in fishery dynamics and/or management.

String-level variation in Spawner Index

We estimated high variability in Spawner Index counts and differences in the variability between fishery and research data sources. This information can inform future fishery and research survey sampling design, and the nature of the data also lead to several important caveats in the interpretation of our results. We account for string- and trap-level variation in the Spawner Index but we do not attribute that variation to particular ecological or sampling factors, both of which likely influence Spawner Index. Strings within a region may vary in the Spawner Indices because of setting location (some subareas will have more abundant prawns than others), boat (some commercial fishermen are more skilled than others), depth, and tide cycle among other factors. The fishery and research data differed in the shape of the distribution of string effects across regions (the fishery distribution was narrower and less negatively skewed, Fig. 4.13) but the two sampling types also occur at different times of year. The narrower distribution of string effects estimated from the fishery data may indicate 'targeted' sampling (intuitive for a commercial fishery), which could be one mechanism by which you would expect hyperstability to occur. Conducting fishery-independent surveys in tandem with or immediately following the commercial fishery would be a useful step towards disentangling the drivers of the different variance patterns between data sources. There was generally higher uncertainty associated with post-fishery Spawner Index dynamics in the Broughton and Central Coast due to the relatively shorter research survey time series and higher zero-inflation in the research data from the Central Coast survey. Further work to ensure consistency between surveys and to standardize site selection would be beneficial, though we note that our post-fishery Spawner Index predictions account for the higher proportion of structural zeroes in the Central Coast data.

We acknowledge several limitations in our study. First, the inference we draw regarding regional differences is based on shorter time periods for the Broughton and Central Coast than for Howe

Sound and thus comes with higher uncertainty. It is also difficult to speculate on how representative the temporal trends in Howe Sound are of fishery and post-fishery dynamics for the rest of the coast. Second, we generate Spawner Index predictions from the global model, which likely overweights the annual dynamics when estimating spring escapement. To generate Spawner Index estimates comparable to DFO's end-of-March escapement targets, we generated Spawner Index predictions for March 31 based on the global model fit, likely overweighting the annual dynamics relative to the measurement of spawners during the spring survey. An alternative approach could be to fit a refined state-space version of the model that treats the 'true' spawner index as a latent state that updates over time. While we currently account for spatial heterogeneity by estimating string effects, we do not account for temporal stochasticity in the trajectory of the exponential decay process itself. By including temporal process error, observations from spring surveys would directly update our belief about the state of the population at the end of March and would more appropriately propagate uncertainty through time.

Management implications and future directions

Our investigation connects directly to the spot prawn fishery management framework by confronting the previously assumed relationship between the Spawner Index at fishery close and at the end of March with data. Our results suggest a discrepancy between the underlying assumptions of the management framework and empirical observations: spring spawner escapement does not relate to fishery escapement the way it is presumed. The discrepancy we find may be driven by higher-than-assumed post-fishery mortality, positively biased fishery-dependent Spawner Indices, or some combination of the two. Regardless of the mechanism, our findings suggest that relying solely on a fishery-dependent catch index to manage and assess a species subject to multiple sources of commercial and non-commercial fishery mortality as well as uncertain sources of non-fishery mortality is likely insufficient. Our study underlines the importance of fishery-independent data sources. Recent assessments of the spot prawn fishery have relied entirely on fishery-dependent data (Rossi et al. 2023; Fisheries and Oceans Canada 2025), leading to different conclusions regarding the status of the fishery and the degree to which current management is precautionary.

It is difficult to conclude from this analysis whether the current spot prawn fishery and its management approach is ‘sustainable’ with respect to population persistence. While we find that spring spawner escapement consistently falls below current management targets, it appears that this has been the case for most of the past 24 years, at least in Howe Sound. The spot prawn fishery continues to open annually in Howe Sound and so it could be argued that the fishery is ‘sustainable’ in so far as there are still spot prawns in Howe Sound. We can more confidently argue that there are clear risks associated with the current approach to assessing and managing spot prawn populations.

First, without resolving the extent to which hyperstability is at play in the spot prawn fishery, it is challenging to evaluate the reliability of fishery-dependent Spawner Indices as indicators of the spawner population and its decline during the fishery. As a result, it is risky to assume that the index at fishery close accurately reflects the state of the population at that time point, let alone as a proxy for spot prawn escapement the following spring. Second, our findings suggest clear differences in spot prawn dynamics on the Central Coast relative to the south coast regions included in our analysis. It is likely not reasonable to assume that spot prawn populations follow the same dynamics across regions, as the current management framework assumes.

Finally, it is difficult to assess the sustainability of particular Spawner Index targets without understanding where the reproductive source comes from for local spot prawn populations. We do not know on what scale and how spot prawn populations are connected. The consequences of fishing a given subarea to a given level of spawners depend on the source of juvenile recruitment. For example, a subarea might continue to produce abundant spot prawn catches even if all the spawners were harvested if recruitment comes from elsewhere. Conversely, overfishing a subarea that acts as a reproductive ‘source’ could have disproportionate consequences if the persistence of a broader spatial region hangs on reproduction from that subarea. To provide a concrete example, in the case of northern shrimp (*Pandalus borealis*) in Atlantic Canada, there is evidence that the majority of larval input to southern management areas may come from a single northern management area (Le Corre et al. 2019), highlighting the importance of identifying and carefully managing reproductive sources. Pacific Canada has a biogeographically complex coastline, and the majority of the commercial spot prawn fishing effort occurs within inshore waters. Resolving the spatial scale of population connectivity through genomic work and/or biophysical modelling (e.g., particle tracking simulations) could help managers determine the relative risk of their management decision making in different regions.

Our study examined key assumptions underlying the current spot prawn fishery management framework and produced cross-regional estimates of spring spawner escapement. Taken together, the results of this work emphasize the importance of collecting fishery-independent data *and* integrating it within assessment practices alongside fishery-dependent data sources.
We hope that this work can serve as a constructive contribution to the ongoing evaluation and refinement of spot prawn stewardship in Pacific Canada both by the Government of Canada and by First Nations governments stewarding their territorial waters. Resolving knowledge gaps, through this study and future work, is needed to support the information needs associated with complex ongoing governance processes.

Chapter 5.
General Discussion

5.1 Overview

There is no doubt that fisheries impact the populations they target. Understanding *how* fisheries influence populations is a critical question tasked to managers and scientists across the world. My thesis delves into the spot prawn trap fishery in BC to examine the interaction between the management framework and the population biology of hermaphroditic spot prawns. Specifically, I compare fishery dynamics under alternative management and survival regimes, test the effectiveness of release-based management measures, and confront the fixed escapement framework with data to estimate spring escapement of spawning spot prawns relative to current targets.

Connected insights across chapters

I began this thesis by constructing a relatively simple stage-structured population model for spot prawns in Chapter 2. The model included each of the core elements of both the spot prawn life history and of the fishery management approach in BC. I applied the theoretical model to investigate a pattern observed on the fishing grounds: that ‘grinding down’ males at the end of a long season led to fewer spawners and a shorter season the following year. I found evidence that this variable fishing pressure on males could indeed lead to oscillating fishery dynamics. A management regime excluding male harvest (but still closing at the same fixed spawner escapement target) produced a longer, more stable annual fishery with some catch trade-offs. I noticed that when spot prawn survival was low, limiting male harvest was often the difference between a fishery season that could open and one where the starting spawner population fell below the fixed escapement target. If survival was low *and* the harvest rate was high, the spawner population deterministically declined.

Implementing measures to limit male harvest in the real world might involve leaning more heavily on the current release-based measures which mandate release of undersized spot prawns. Undersized spot prawns are almost entirely male, and increasing the minimum release size could relieve pressure on the male population but post-release survival had not been estimated. This uncertainty led me to design a field experiment to estimate post-release survival in Chapter 3. I found that predicted post-release survival of spot prawns was >75% so long as release was immediate and the air temperature was cool, but that survival quickly declined with increasing time out of water or air temperature. Prawns that survived 24 hours post-release were normally vigorous, scoring high on a scale of reflex behaviour. My results suggest that release-based measures are likely somewhat effective, although my results probably represent ‘best case’ estimates given that they do not account for predation mortality or for the probability of returning to suitable habitat.

In Chapter 4, I revisit the uncertainty in natural mortality highlighted in Chapter 2 by empirically estimating spring spawner escapement relative to spawner escapement at the end of the summer fishery the year prior. To assess spatial variation in post-fishery mortality, I collected and/or collated fishery-dependent and fishery-independent Spawner Index data from three regions across the coast. I analysed fishery-independent data collected by DFO, the Kitasoo Xai’xais Stewardship Authority, and initiated a population survey myself working with the Musgamagw Dzawada̱’enux̱w Fisheries Group. Across regions, I found that spring spawner escapement often fell short of current management targets despite the fishery often (but not always) closing at or above target. I estimated consistently higher and regionally varying apparent post-fishery mortality rates than previous estimates and than the estimates currently used to derive management targets. The analysis also highlighted the difficulty of inferring population processes from fishery-dependent data alone, emphasizing the value of present and future fishery-independent data collection.

Across chapters, I developed tools and collected data to confront interactions between fishery management and population biology for spot prawns in BC. Chapters 2 and 4, interpreted together, indicate that previously research likely underestimates post-fishery mortality rates for spot prawn (Chapter 4) and that my fishery and post-fishery mortality estimates fall most closely resemble the low survival and moderate-high harvest rate scenarios examined in my theoretical analysis (Chapter 2). Together with the reliance of current management on a fishery-dependent catch index and static escapement targets, this places spot prawn in a potentially risky situation in terms of fishery and population longevity.

5.2 Shared trends across marine invertebrate fisheries

In some respects, the story of the spot prawn fishery can be viewed as one chapter in a broader story about marine invertebrate fisheries in BC generally. Similar to the Atlantic coast of Canada, declines in finfish fisheries over the last several decades were accompanied by growth in marine invertebrate landings (Perry et al. 1999; Pauly et al. 2001). Today, shellfish fisheries are the highest value group of fisheries in Pacific Canada (DFO 2023). The growth in invertebrate fisheries has stayed somewhat under the radar and has not been matched by equivalent growth in science to support their management.

Effort and efficiency have increased in marine invertebrate fisheries in recent decades. Commercial harvesters have refined their ability to find their target. Measures intended to limit effort often result in increasing efficiency per unit effort (e.g., trap). Non-commercial harvest by recreational fishers and First Nations exercising their right to harvest has led to potentially higher mortality than still assumed by management frameworks originally developed in the 1970s and 1980s. Beyond spot prawn, evidence suggests that phenomena such as hyperstability and serial depletion are at play in other invertebrate fisheries including sea cucumber (Watkins 2024), sea urchin (Perry et al. 2002), geoduck (Khan 2006), and Dungeness crab (Frid et al. 2016; Ban et al. 2017). Such issues can be addressed, with fishery-independent data and proactive science and management initiatives.

There is also an emerging policy pattern of defining marine invertebrates as single coastwide stocks under the Fisheries Act. In 2019, amendments to Canada’s Fisheries Act introduced Fish Stock Provisions (FSP) which establish legally binding obligations on DFO to (1) manage major fish stocks at levels necessary to promote sustainability and, (2) develop and implement rebuilding plans for major fish stocks that decline below their Limit Reference Point (LRP). The Limit Reference Point is defined as “the stock level below which productivity is sufficiently impaired to cause serious harm to the stock” (Fisheries and Oceans Canada 2009). These provisions only apply to stocks prescribed under the Fisheries Act, a process which is currently under way. To prescribe stocks under the Fisheries Act, DFO must first determine the spatial scale of individual stocks. For example, for Pacific salmon, a stock might be a population of sockeye that return to a given lake. As part of the process for prescribing major stocks and defining LRPs, DFO has assessed multiple marine invertebrates, including Dungeness crab (Fisheries and Oceans Canada 2023a), spot prawn (Fisheries and Oceans Canada 2025), and geoduck (Fisheries and Oceans Canada 2023b) as single coastwide stocks. The scientific evidence for these conclusions is mixed. In some cases, such as geoduck, there is evidence for multiple genetically isolated populations (Miller et al. 2006), countering the single coastwide stock conclusion. In other cases, such as Dungeness crab, there is some evidence for genetic isolation in inlets and fjords but also very limited information on the population structure writ large (e.g., no genetic samples from any fjords or inlets on the north and central coast of BC) (Beacham et al. 2008). Why is it important to scrutinize these conclusions? Invertebrate fisheries are typically managed at a spatial resolution finer than coastwide. If the scale of the management unit is smaller than the spatial scale of the 'true' population structure, then management may be robust to uncertainties or unsupported assumptions regarding population structure. If, however, multiple isolated populations exist within a spatial management unit, setting LRPs at a coastwide scale may undermine the goal of the Fish Stock Provisions to protect fished species and the people who depend upon them. The consequences of scientific conclusions like stock structure vary depending on the user group. For commercial fishermen who could feasibly fish anywhere on the coast (spot prawn) or within a large area (Dungeness crab), local declines may just mean moving on to another region, though there could be larger impacts if metapopulation persistence is impacted. For First Nations governments and communities and the interests of their local territories, the collapse of a locally isolated population in an inlet or fjord is not offset by good productivity at a coastwide scale. How we consider scale in scientific processes has direct consequences for local communities and titleholders and the tension between broad- and local-scale priorities in fisheries is well documented (Weinstein 2007; Frid et al. 2016, 2023; Ban et al. 2017; Silver et al. 2022; Salomon et al. 2023).

5.3 Action in the face of uncertainty

It is arguable that the state of the science supporting management of the spot prawn fishery is decades behind. Invertebrate stock assessment at DFO face limited resources and capacity to undertake the necessary scientific activities to proactively and precautionarily steward the quickly changing fishery. Since 2001, only two peer-reviewed journal articles have been published on the spot prawn fishery in BC (Favaro et al. 2010, 2014), though see a Master's thesis (Smith 2014) and pre-print (Rossi et al. 2023) examining aspects of spot prawn stock assessment.

This thesis contributes to addressing specific uncertainties in the spot prawn fishery. I examined the consequences of male harvest, estimated post-release survival, estimated spatial and temporal variation in post-fishery mortality, and generated the first, to my knowledge, empirical estimates of spring spawner escapement. Important questions remain, too many to list, but I will highlight a couple key uncertainties that stand out to me. Moving forward, it will be critical to investigate the evidence and mechanisms for hyperstability in the fishery. As I allude to above, resolving population structure including potential source-sink dynamics will be critical to ensuring that fishery management is truly precautionary. Finally, given my finding of higher than assumed estimates of post-fishery mortality, it could be important to revisit our understanding of spot prawn mating biology. There is evidence for broadcast spawning marine invertebrates that fishing can 'thin' population densities enough to affect fertilization probability, even when absolute populations remain high (Lundquist and Botsford 2011). It is not hard to imagine that such phenomena could be possible for spot prawn too. In the absence of perfect information and presence of scientific capacity limitations, there are still options to buffer management to known risks.

Strategies to buffer known risks

Addressing scientific knowledge gaps is one critical piece to navigating the current fisheries governance context for spot prawn. But addressing gaps like those highlighted above often takes decades. In the presence of uncertainty, we can learn from the past and from our understanding of marine invertebrate life histories to buffer risk now. Some of these strategies are already in place.

The spot prawn fishery management framework currently buffers against risk largely through limits on effort: commercial license limitations, trap limits and restricted trap types, limited fishing hours, and single daily haul rules (Fisheries and Oceans Canada 2025). Multiple types of marine reserves, current and incoming, also may buffer against risk if protected areas act as effective reproductive refugia for spot prawn (Gale et al. 2018). Further options could be explored to buffer risk. For example, alongside permanent spatial closures, rotating area-based closures could be a strategy to mitigate the risk of local extirpations (Caddy and Seijo 1998). Additionally, adjusting current SI targets to better account for non-commercial harvest after the summer fishery could be considered.

5.4 Directions for future research

It is an important time to be asking questions about spot prawns and other harvested marine invertebrates in Pacific Canada. Each question I attempted to answer in this thesis begot many more, a few of which I will highlight here as possible avenues for future investigation.

Future theoretical directions

There are many lines of theoretical inquiry that could be explored through further work with the theoretical model developed in Chapter 2. I did not scratch the surface of addressing the possibility of fisheries-induced changes in the timing of sex change, for which there is some evidence in related species (Charnov 1979; Charnov and Groth 2019) and which would be very interesting to think about for spot prawn. Another direction could be to dig into the theoretical consequences of parasites for spot prawn population dynamics. Given that parasites like *Sylon* spp. sterilize their hosts, it would be worthwhile to revisit the mating function in our population model to explicitly incorporate parasite effects on the fertilization rate. While males are generally thought to not be a limiting reproductive factor for protandrous hermaphrodites, sterilization at sufficiently high rates might lead to an ecologically relevant Allee effect which could have consequences for fisheries management. Given the lack of empirical information on the spatial structure of spot prawn populations, theoretical models might also be a useful tool to examine the consequences of alternative assumptions regarding source-sink dynamics under different fishing scenarios.

Improving the state of fisheries-independent data

Developing additional sources of fishery-independent data is an important direction for the stewardship of spot prawns and their fishery in BC. The findings from Chapter 4 demonstrate that relying on fishery-dependent data alone is insufficient to confidently assess and manage the fishery. There is an opportunity now to re-evaluate the management framework and the data needed to inform fisheries management and governance processes for spot prawn. Expanding fishery-independent data collection moving forward would be well-served by a well-designed and publicly available protocol for designing and conducting spot prawn population surveys. The analysis in Chapter 4 was made possible by the fact that the survey methods, not without their shortcomings, were consistent across regions. The research survey in Howe Sound was initiated in the 1980s and there are aspects worth revisiting given growing interest from First Nations governments and stewardship organizations in developing their own spot prawn research programs. For example, it may be worth evaluating the option of shifting to some version of a stratified random sampling design if one objective is to refine the ability to infer population trends from catch index data. The model outputs from Chapter 4 could be used to refine aspects of the sampling design such as the relative benefit of sampling with fewer strings with more traps versus more strings with fewer traps.

Additionally, conducting fishery-independent surveys overlapping with the commercial fishery or occurring immediately post-fishery close could help disentangle the hyperstability issue. One underappreciated change over the past ~10-15 years has been the shift from ‘slow’ to ‘fast’ boats. ‘Slow’ boats are freezer boats that store their catch in holds and have limited ability to spread their gear across wider spatial scales because they can’t move very quickly. Recently, more prawn fishers have shifted to operating ‘fast’ boats, small high-powered fishing vessels that deliver their catch live to port daily. These boats travel at high speeds (>20 knots) and as a result can spread their gear across large regions and more easily shift their gear around when catches decline. They are also more common in the south coast regions than in the north coast where ports to deliver to daily are much harder to access. Fishery-independent surveys immediately post-fishery from multiple regions with varying densities of ‘fast’ boats could facilitate a space-for-time analysis testing the hypothesis that fast boats have increased the efficiency of the fishery.

Resolving the spatial scale of population structure in a biogeographically complex coast

A burning question left relatively unaddressed by this thesis is the question of how spot prawn populations are structured through space in BC. The recent designation of many marine invertebrate species in BC as single coastwide stocks rests on the conclusion that BC is a reproductive mixing bowl, or at least enough of a mixing bowl to constitute a single population. There is very sparse information to support or refute this conclusion, especially in the case of spot prawns, and it is not an easy question to answer. Understanding population connectivity through larval dispersal requires an understanding of both oceanographic dynamics and larval behaviour. The coastline of BC is biogeographically complex, studded with island archipelagos and many long fjords and inlets. These complex waters are also where many First Nations communities live and fish and scientific assumptions about how marine invertebrate populations are (or aren't) connected have implications for the people who have depended on them for a long time and still do today. To address this uncertainty in the future, the fishery observer program could be leveraged to collect tissue samples from across the coast to facilitate genomic work to assess the extent of (on evolutionary time scales) population mixing. It might also be possible to explore the theoretical consequences of complex fjord environments on larvally dispersing marine invertebrates by incorporating some kind of dendritic structure to a metapopulation model. Further work to resolve the spatial structure of spot prawn populations in BC would be ecologically interesting and quite relevant to their stewardship amidst a dynamic commercial fishery, changing climate, and the ongoing introduction of marine reserves in BC.

5.5 Significance

At a time when marine invertebrate fisheries face increasing pressure and complex governance, this thesis provides timely empirical evidence that current management assumptions for spot prawn warrant revisiting. The regional estimates of spawner dynamics and post-fishery mortality suggest that coastwide management benchmarks may not be appropriate and underscore risks of relying solely on fishery-dependent data to manage species subject to multiple sources of mortality including an increasingly efficient fishery. More broadly, this work contributes to the growing recognition that hermaphroditic life histories require explicit consideration in fisheries management. The finding that male harvest dynamics can destabilize fisheries has implications beyond spot prawn, extending to other protandrous invertebrates managed through effort or escapement controls. By generating the first empirical estimates of regional variation in post-fishery spawner survival for spot prawn in BC, this thesis highlights the value of fishery-independent data for informing adaptive management as governance frameworks evolve to accommodate multiple rightsholders and users. I also hope it shines a light on and leads to further interest in a beautiful and mysterious creature, which merits more of our attention as a source of food and intrigue.

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Appendix A.

Supporting information for Chapter 2

A.1 Supplementary methods for simulation study

We start with an aside on the mating function, included in the original population model but simplified in the version of the model simulated for this study. We then lay out the full details of the seasonal population model with the fishery sub-model, as it is implemented in simulations in R, and we expand on details of the model parameterization and data sources.

The mating function

The mating function, which specifies the probability of fertilization, is defined according to the law of mass action. This reflects the assumption that the rate of fertilization is directly proportional to the density of males and females in the population. We define the terms of the model below in terms of the stage classes during the Fall season. The probability of fertilization is defined as,

$$p_b\left(n_2^F(t)\right) = 1 - e^{-\sigma n_2^F(t)\tau}, \tag{A1}$$

where σ denotes the pair-forming rate (the rate at which males and females encounter one another) and τ denotes the length of the breeding season (set to 1). The mating model was adapted from one used for polar bears (Molnár et al. 2014) and is derived as follows:

$$\frac{dn_3}{dt} = -\sigma n_2 n_3, \tag{A2.1}$$

$$\frac{dn_4}{dt} = \sigma n_2 n_3. \tag{A2.2}$$

Here, $\frac{dn_3}{dt}$ describes the rate of decline of unfertilized females in the population as they become fertilized by males (at a rate directly proportional to the males and females in the population) and $\frac{dn_4}{dt}$ describes the rate of increase of fertilized females in the population. The goal of the mating model is to obtain a probability of fertilization based on the proportion of egged females at the end of the mating period, $p_b\left(n_2^F(t)\right)$. Given some initial female population, n_3^F, at the start of the

Fall season, the solution for the number of fertilized females at τ, the end of the mating period (and start of the Winter season) is,

$$n_4^W(t) = n_2^F(t)(1 - e^{-\sigma n_2^F(t)T}), \tag{A3}$$

which gives a mating function (Fig. A.1). The steepness of the mating curve is governed by the pair-forming rate, σ, which can be varied.

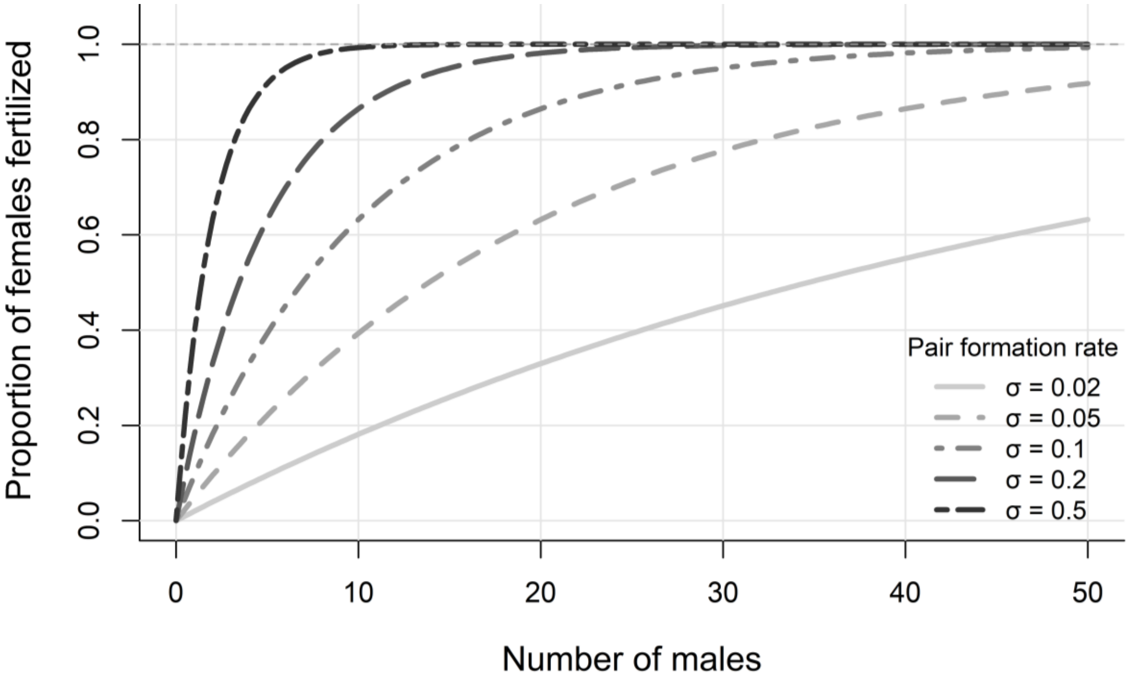

Figure A.1 Proportion of females fertilized as a function of the number of males across a range of pair formation rates.

A.1.2 Seasonal model – simulation procedure

Below, we describe the detailed season-by-season breakdown of the spot prawn population model as it is simulated in R for this study.

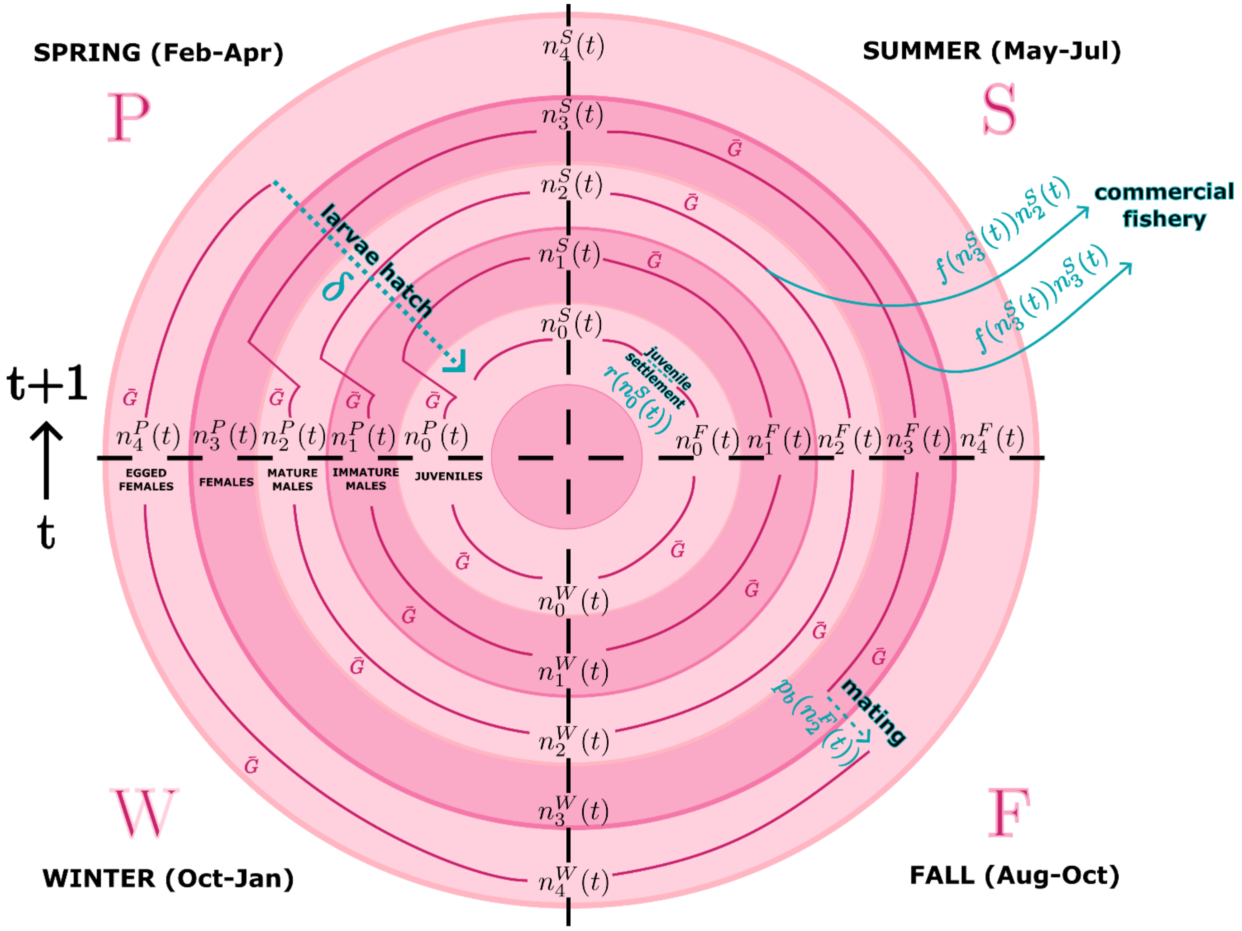

Figure A.2 Detailed schematic figure of the seasonal population model for spot prawns including commercial fishery harvest.
Individuals begin life at the centre of the figure and spiral out as they transition through life stages. Key events are highlighted in blue.

Spring

A given simulation is initiated at the start of the Spring season by setting each stage to the number of individuals corresponding to the stable stage distribution of the unfished population. The population at the start of the Summer season is defined as,

$$n_0^S(t) = \delta \bar{G} n_4^P(t), \tag{A4.1}$$

$$n_1^S(t) = \bar{G} n_0^P(t), \tag{A4.2}$$

$$n_2^S(t) = \bar{G} n_1^P(t), \tag{A4.3}$$

$$n_3^S(t) = \bar{G} n_2^P(t), \tag{A4.4}$$

$$n_4^S(t) = 0\,. \tag{A4.5}$$

During the Spring season above, egged females release their eggs (with fecundity δ eggs-per-female) which survive with survival probability G (Eq A4.1). Juveniles transition to and survive as immature males (Eq A4.2), immature males transition to mature males (Eq A4.3), and mature males transition to females (Eq A4.4). After releasing their offspring, egged females are assumed to die (Eq A4.5).

As mentioned in the main text, in principle survival could vary between stages and between seasons (e.g., G_1^P would describe survival of immature males during the Spring season) and the model is coded to allow for this flexibility. However, there is limited information available to inform such nuanced parameterization and so for the purpose of this study we assume constant survival (other than juvenile survival during the pelagic dispersal phase, α) with respect to stage and season (although we consider three alternative survival 'scenarios'). For ease of interpretation, we do not include the seasonal or stage related notation for the survival parameters here.

Summer

During the Summer season, density-dependent settlement of juveniles occurs and the commercial fishery takes place. The population at the start of the Fall season is defined as,

$$n_0^F(t) = \underbrace{r\left(n_0^S(t)\right)}_{\textbf{recruitment}} = \frac{\alpha n_0^S(t)}{1 + \beta n_0^S(t)}, \tag{A5.1}$$

$$n_1^F(t) = \bar{G} n_1^S(t), \tag{A5.2}$$

$$n_2^F(t) = \bar{G}\, \underbrace{f\left(n_3^S(t)\right)}_{\substack{\textbf{fishery} \\ \textbf{mortality}}} n_2^S(t) = \bar{G} e^{-h \cdot w\left(n_3^S(t)\right)} n_2^S(t), \tag{A5.3}$$

$$n_3^F(t) = \bar{G}\, \underbrace{f\left(n_3^S(t)\right)}_{\substack{\textbf{fishery} \\ \textbf{mortality}}} n_3^S(t) = \bar{G} e^{-h \cdot w\left(n_3^S(t)\right)} n_3^S(t), \tag{A5.4}$$

$$n_4^F(t) = 0. \tag{A5.5}$$

We conducted both deterministic and stochastic simulations. For the version of the simulations that included environmental stochasticity, we simulated recruitment as occurring with lognormal annual variability. Larvally dispersing juveniles at the start of the Summer season settle and experience density-dependent recruitment competition with some environmental stochasticity,

$$r\left(n_0^S(t)\right) = \frac{\alpha n_0^S(t)}{1 + \beta n_0^S(t)} e^{\epsilon}, \tag{A6.1}$$

$$\epsilon \sim \mathrm{N}\left(-\frac{1}{2}\sigma^2, \sigma^2\right). \tag{A6.2}$$

Mortality from the commercial fishery is applied as $f\left(n_3^S(t)\right)$, where fishery mortality depends on the annual length of the commercial fishery which in turn is determined based on $n_3^S(t)$, the size of the female population at the start of the Summer season. The procedure for modelling commercial harvest of mature males and females in the Summer season of a given year is as follows:

1. We assume that the two stages susceptible to fishing are the mature males ($n_2^S(t)$) and the females ($n_3^S(t)$) and we manage the fishery based on a fixed escapement target, n_3^{target}, for the females, as is the case for the spot prawn fishery in British Columbia. The escapement target is fixed and does not vary interannually.
2. First, we evaluate whether the incoming spawner population, $n_3^S(t)$, is sufficiently large to open the fishery. If the incoming spawner population falls below the escapement target, the fishery does not open. Note that this assumes that management has perfect information about the state of the population before and during the fishery (see main text Discussion).
3. If the incoming spawner population exceeds the escapement target, the fishery opens. We use the Baranov catch equation to calculate the weekly harvest rate (for a given simulation) and the length of the fishery (for each year within the simulation).

   We assume that females and males are fished at the same weekly harvest rate, h, and set the harvest rate based on a theoretical annual harvest for which we have empirical estimates to draw on for reasonable estimates (40-80% annual exploitation rate, Rossi et al. 2023). Given the annual harvest proportion and a typical fishery length (eight weeks), we rearrange the Baranov catch equation to solve for a weekly harvest rate that reflects the appropriate annual harvest for an eight-week long fishery:

$$C = \frac{h}{g+h}\left(1 - e^{-(g+h)\cdot 8}\right) n_3^S(t), \tag{A7.1}$$

$$\frac{C}{n_3^S(t)} = \frac{h}{g+h}\left(1 - e^{-(g+h)\cdot 8}\right). \tag{A7.2}$$

Here, $\frac{C}{n_3^S(t)}$ is the total female catch divided by the total initial female population which can also be thought of as the annual harvest proportion. Weekly non-fishery related survival is defined as g and is parameterized to align with seasonal survival. If we define annual harvest, $F = \frac{C}{n_3^S(t)}$, we can solve for h, the weekly harvest rate, in terms of F and g:

$$h = \frac{F \cdot g}{1 - e^{-(g+h)\cdot 8} - F}. \tag{A8}$$

Because it shows up on both sides of the equation, we solve for h numerically using the bisection method and use the solution as the weekly harvest rate for both mature males and females.

4. Given harvest rate, h, we simulate fishing according to:

$$n_2^F(t) = Ge^{-\left(h\cdot w\left(n_3^S(t)\right)\right)} n_2^S(t), \tag{A9.1}$$

$$n_2^F(t) = Ge^{-\left(h\cdot w\left(n_3^S(t)\right)\right)} n_3^S(t). \tag{A9.2}$$

To simulate fishery closure at the fixed escapement target for the females, we must calculate the number of weeks the fishery can stay open without overshooting the escapement target. We know the starting population, $n_3(t)$, weekly mortality rate (g), and the weekly harvest rate (h), so we can solve for $w\left(n_3^S(t)\right)$, the number of weeks the fishery stays open as a function of the starting female population:

$$w\left(n_3^S(t)\right) = -\frac{\ln\left(\frac{n_3^{\text{target}}}{n_3^S(t)}\right)}{g+h}. \tag{A10}$$

The length of the fishery is allowed to vary year-to-year, but the rate of harvest *within* the fishery, h, is assumed to be constant within a given simulation.

5. We simulate harvest of mature males and females for the given number of weeks and calculate the end population size for each stage. We calculate the annual fishery catch, $C\left(n_i^S(t)\right)$, using the Baranov catch equation and use estimates for stage-specific weights to convert fishery catch into stage-specific yield (landed biomass), $B\left(n_i^S(t)\right)$:

$$C\left(n_2^S(t)\right) = \frac{h}{g+h}\left(1 - e^{-\left(g\cdot 12 + h\cdot w\left(n_3^S(t)\right)\right)}\right) n_2^S(t), \tag{A11.1}$$

$$C\left(n_3^S(t)\right) = \frac{h}{g+h}\left(1 - e^{-\left(g\cdot 12 + h\cdot w\left(n_3^S(t)\right)\right)}\right) n_3^S(t), \tag{A11.2}$$

$$B\left(n_2^S(t)\right) = b_2 C\left(n_2^S(t)\right), \tag{A11.3}$$

$$B\left(n_3^S(t)\right) = b_3 C\left(n_3^S(t)\right). \tag{A11.4}$$

   Here, b_2 and b_3 are estimates of individual weight (g-per-individual) for mature males and females respectively (see below for details of parameterization).

6. If the length of the fishery is less than 12 weeks (the total length of the summer season), we apply the weekly natural mortality rate (g) to both mature males and females for the remaining weeks of the season to calculate the output numbers-per-stage at the end of the summer season. Given the bounds on the length of the Summer season, if the fishery length is greater than 12 weeks (e.g., due to low weekly harvest rate or high starting female population), the fishery is implemented as 12 weeks long and female escapement is higher than the escapement target (see main text for discussion of this aspect of the study).

Fall

During the Fall season, breeding occurs and females transition into the egged stage. In principle, we allow for the possibility of mate limitation through a mating function, but for this study we assume that fertilization is 100%. As such, there are no remaining individuals in the female stage class. Juveniles, immature males, and mature males survive through to the Winter season:

$$n_0^W(t) = \bar{G} n_0^F(t), \tag{A12.1}$$

$$n_1^W(t) = \bar{G} n_1^F(t), \tag{A12.2}$$

$$n_2^W(t) = \bar{G} n_2^F(t), \tag{A12.3}$$

$$n_3^W(t) = 0, \tag{A12.4}$$

$$n_4(t) = \bar{G}\, \underbrace{p_b\big(n_2^F(t)\big)}_{\textbf{fertilization probability}}\, n_3^F(t). \tag{A12.5}$$

Winter

There are no major biological or fishery events during the Winter season (though in principle one could incorporate other non-commercial sources of fishery mortality here), and individuals survive through to the end of year t and subsequently are the initial values for the start of the Spring season of year $t + 1$:

$$n_0^S(t+1) = \bar{G} n_0^W(t), \tag{A12.1}$$

$$n_1^S(t+1) = \bar{G} n_1^W(t), \tag{A12.2}$$

$$n_2^S(t+1) = \bar{G} n_2^W(t), \tag{A12.3}$$

$$n_3^S(t+1) = 0, \tag{A12.4}$$

$$n_4^S(t+1) = \bar{G} n_4^W(t). \tag{A12.5}$$

A.1.3 Seasonal model – parameterization

We parameterized the model primarily by drawing on previously published estimates and from unpublished research data collected by DFO. All parameters are defined before the simulation is initiated except for the length of the commercial fishery (in weeks) which is calculated for each year, t, within the simulation, as a function of the size of the female population at the start of the Summer season. Below, we expand on the main text methods to provide some additional details on our approach to defining parameters.

Survival estimates and conversions

We considered three survival scenarios, each derived from estimates of annual natural mortality reported in (Boutillier and Bond 2000). We used the average estimate to define an ‘average’ survival scenario. We defined our ‘low’ and ‘high’ survival scenarios as the minimum and maximum reported natural mortality rates respectively. We converted from natural mortality, M, to survival, G, according to,

$$G = e^{-Mt}, \tag{A13}$$

where M represents the natural mortality across some time period t (in this case, one year). So for example, for the average annual mortality estimate of 0.88^{-yr}, we calculate G as:

$$G = e^{-0.88} = 0.415. \tag{A14}$$

To rolldown from annual survival to seasonal survival ($\bar{G}$), we first convert the natural mortality rate from annual to seasonal ($\overline{M}$) and then convert from the natural mortality rate to survival. For example,

$$\overline{M} = \frac{M}{4} = \frac{0.88}{4} = 0.22, \tag{A15.1}$$

$$\bar{G} = e^{-0.22} = 0.8033. \tag{A15.2}$$

To roll down from annual natural mortality rate to weekly natural mortality rate, as was necessary to model the fishery dynamics (see details above), we calculated the weekly rate, g, as, for example,

$$g = \frac{G}{52} = \frac{0.88}{52} = 0.01692. \tag{A16}$$

Table A.1 Natural mortality parameter estimates.
Estimates for annual natural mortality rates (from Boutillier and Bond 2000) and associated conversions to annual survival, seasonal survival, and weekly natural mortality rates. Seasonal survival denotes estimated survival for 12-week period.

Survival scenario	Annual natural mortality rate $(^{-yr})$	Annual survival	Seasonal survival	Weekly natural mortality rate $(^{-week})$
Low	1.46	0.232	0.694	0.02808
Average	0.88	0.415	0.803	0.01692
High	0.42	0.657	0.900	0.00808

Annual harvest rates

We drew on previous estimates of annual harvest estimates to parameterize the weekly harvest rate in our simulations (Rossi et al. 2023). We picked three annual harvest scenarios representing ‘low’ (40% harvest), ‘moderate’ (60% harvest), and ‘high’ (80% harvest). We converted from annual harvest (where ‘annual’ refers to the harvest of a given annual fishery season, assumed to be ~8 weeks) as described above in the description of the simulation methods.

Fecundity

We drew on unpublished research data from DFO to parameterize δ, fecundity in terms of eggs-per-female. We defined $\delta = 2{,}700$ eggs-per-female, the mean estimate from the data.

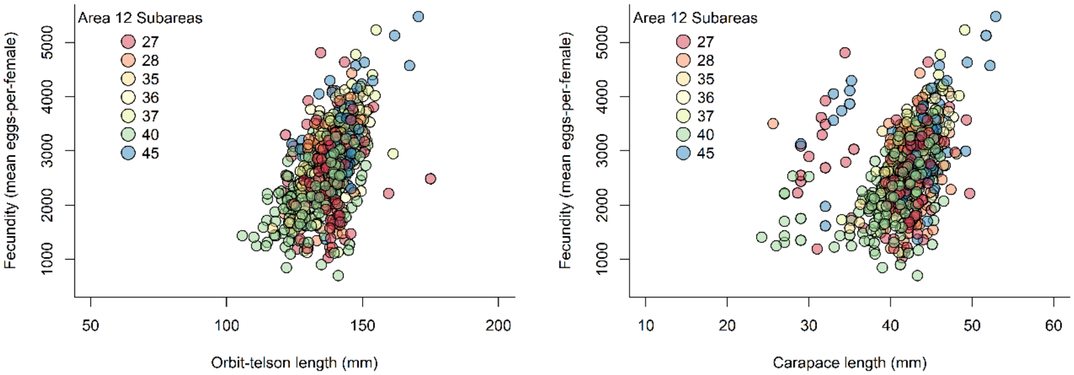

Figure A.3 Fecundity (eggs-per-female) relative to prawn length (total or carapace).
Data are from three years of research surveys (1981-83) in DFO Pacific Fishery Management Area 12 (Broughton Archipelago, Knight Inlet, and Mainland Inlets). Mean eggs-per-female are extrapolations based on egg count subsamples.

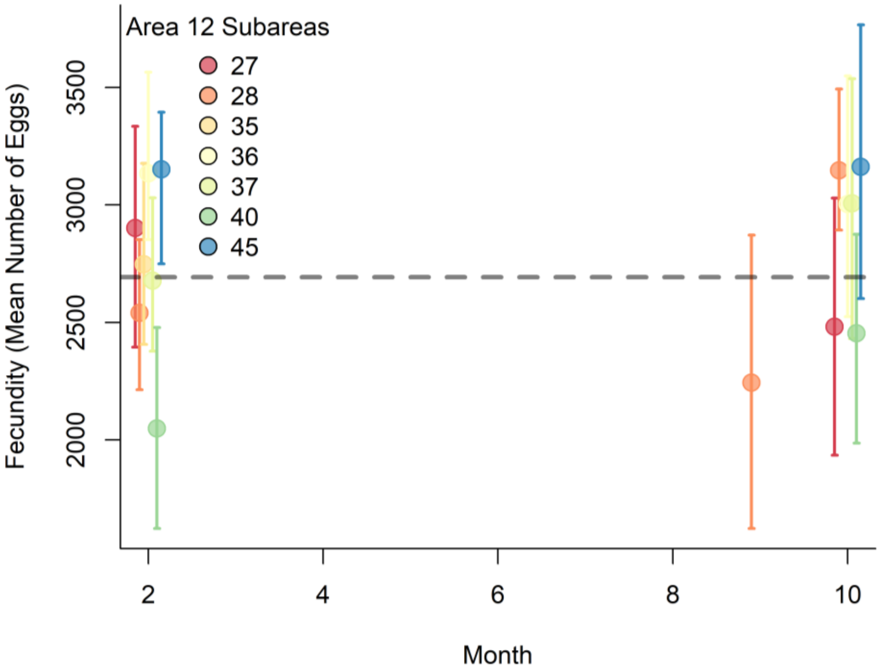

Figure A.4 Mean fecundity by month of year and Subarea.
Dashed line denotes the overall mean estimate which we use as our fecundity parameter in the model simulations.

Stage-specific weight to convert fishery catch from individuals to biomass

To convert annual fishery catch from individuals to biomass, we drew on unpublished individual-level weight-at-stage data collected in Howe Sound (DFO Area 28) by DFO. Because these research surveys are conducted in the Fall and Spring seasons, there is no direct estimate for weight-at-stage for males and females during the Summer season. Instead, we used the average weights for males (sex code=1) and transitionals (sec code=2) during the Spring survey, as those are the stages that are about to be harvested during the Summer season.

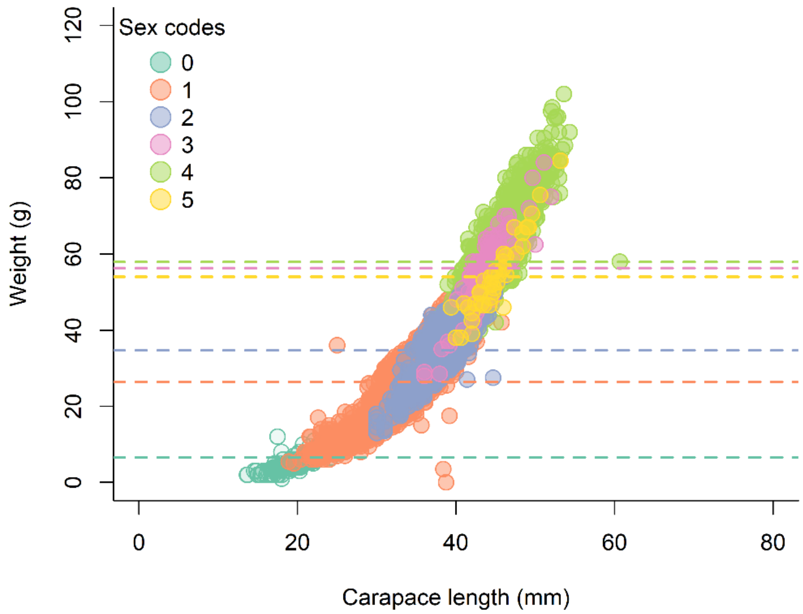

Figure A.5 Individual weight (grams) relative to carapace length (mm) across life stages. Juvenile=0; Male=1, Transitional=2, Female=3, Egged female=4, Spent female=5. These data are sourced from DFO research surveys conducted in Howe Sound in the fall (October-November) and spring (February-March). Stages 0, 1, and 4 are captured during fall surveys. All stages are captured during spring surveys, though stages 1, 2, and 4 are most common. Dashed lines denote stage-specific mean weights. We use the mean weight for stage 1 (males, 26 g) and mean weight for stage 2 (transitionals, 35 g) to estimate landed biomass in our simulations for males and females respectively.

Recruitment function and stochasticity

The recruitment parameters, α and β were the only parameters for which we did not have empirical estimates (or data) to draw on. In the absence of existing estimates, we defined the parameters to reflect relatively high larval mortality ($\alpha = 0.3$, in the range of estimates from White et al. 2014) and moderate compensatory density dependence ($\beta = 0.0000013$, equivalent to ~1 surviving settler per ~25-150 m^2 for management subareas ranging from 5-30 km^2). We considered the deterministic case as well as simulations with environmental stochasticity reflecting low, moderate, and high recruitment variability.

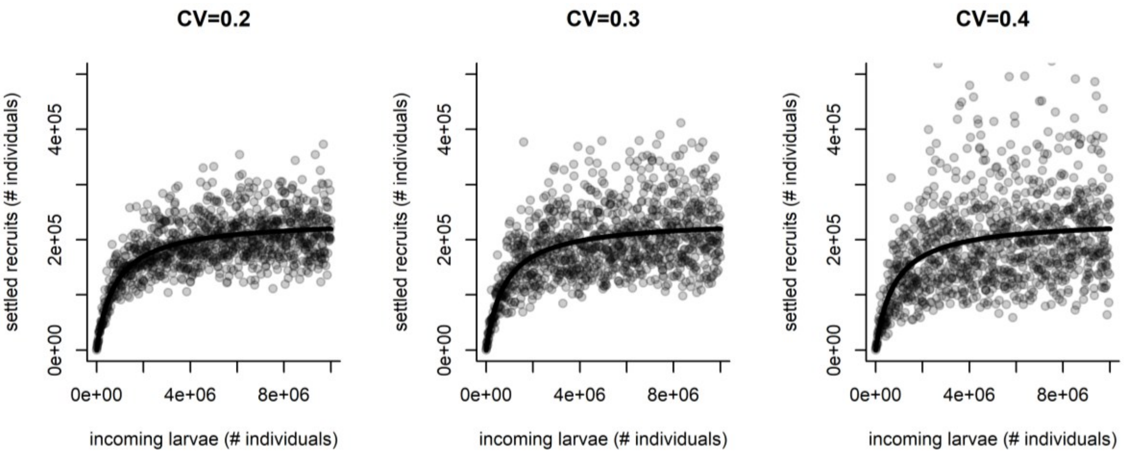

Figure A.6 Beverton-Holt recruitment function used in simulations.
Deterministic function (solid line) with recruitment predictions for three different variance scenarios (coefficient of variation set to 0.2, 0.3, or 0.4).

A.2 Supplementary results figures

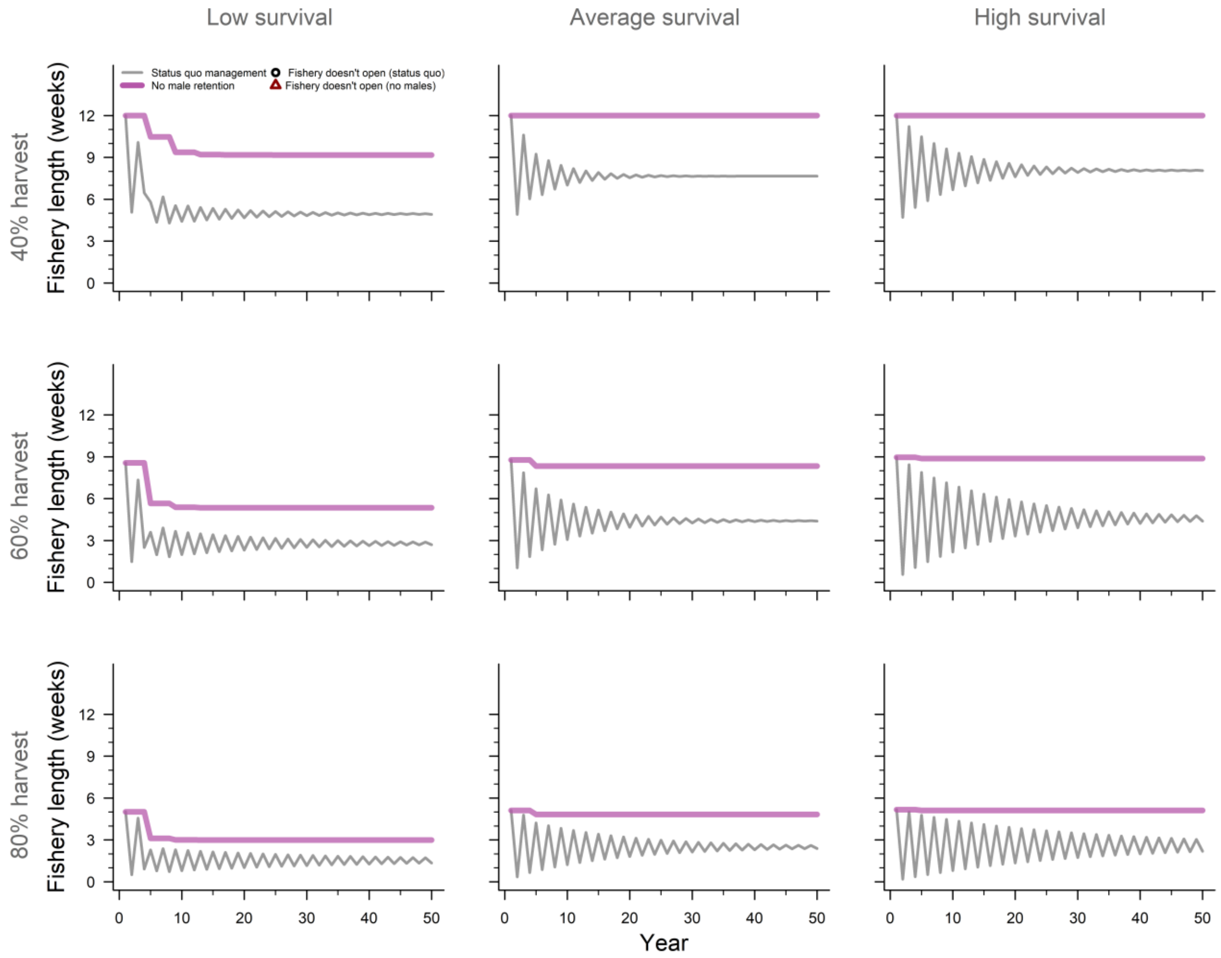

Figure A.7 Deterministic dynamics of annual fishery length across survival and harvest scenarios.
Grey line depicts oscillating dynamics of the fishery length under status quo management (male and female harvest). Pink line depicts fishery length dynamics under the no-male-harvest scenario. In the absence of male harvest, the fishery length stabilises.

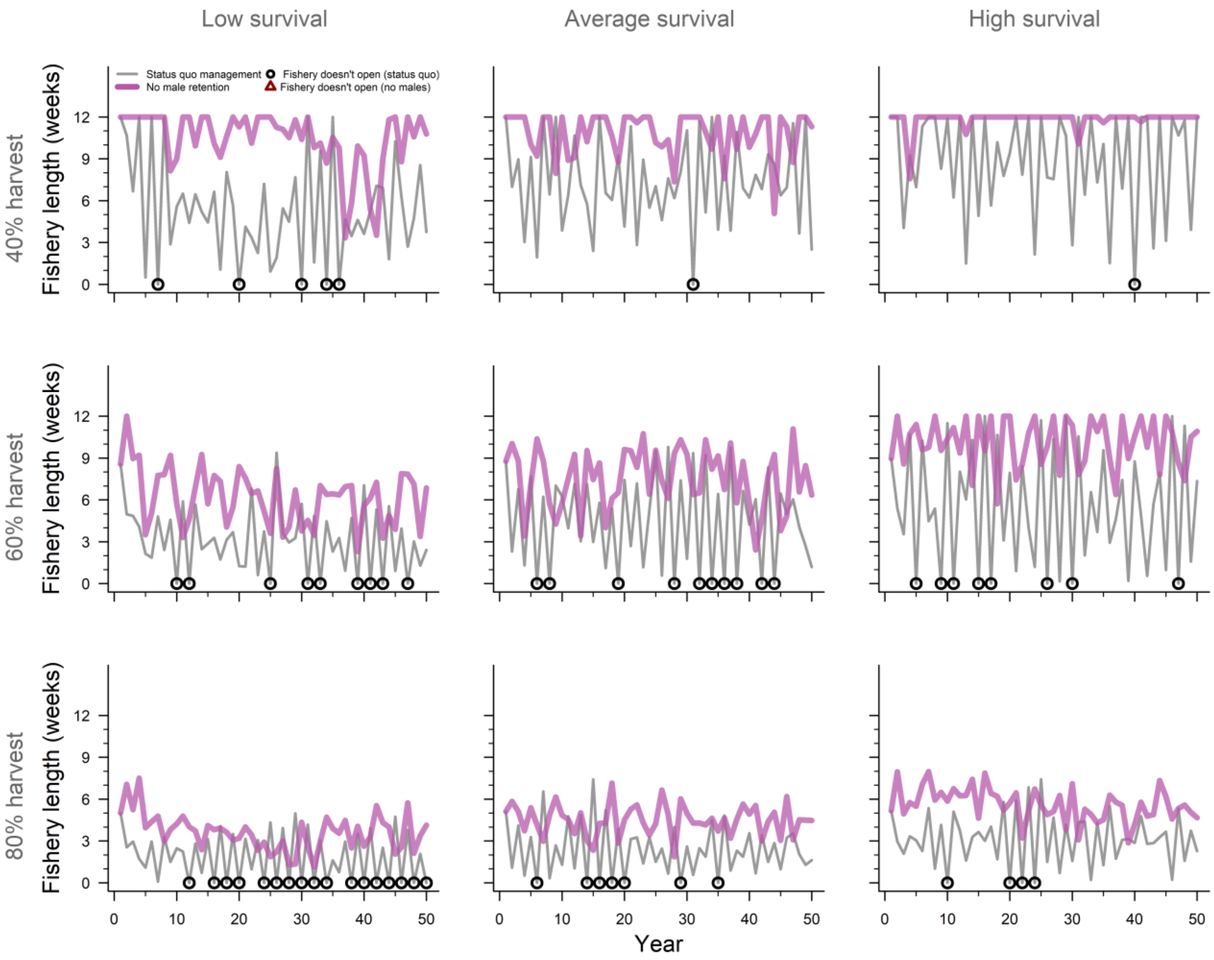

Figure A.8 Stochastic dynamics of annual fishery length across survival and harvest scenarios for recruitment CV = 0.3.

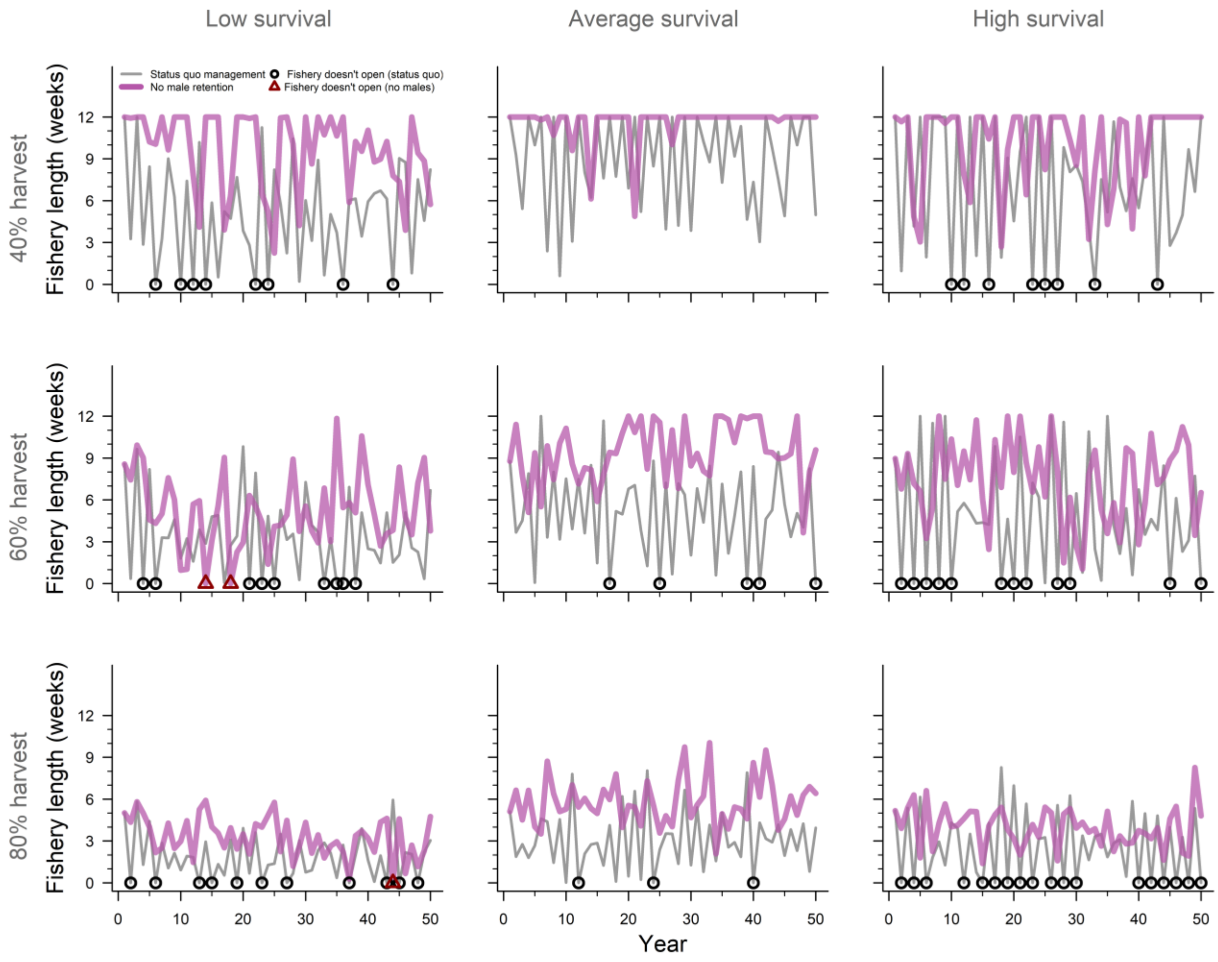

Figure A.9 Stochastic dynamics of annual fishery length across survival and harvest scenarios for recruitment CV = 0.4.

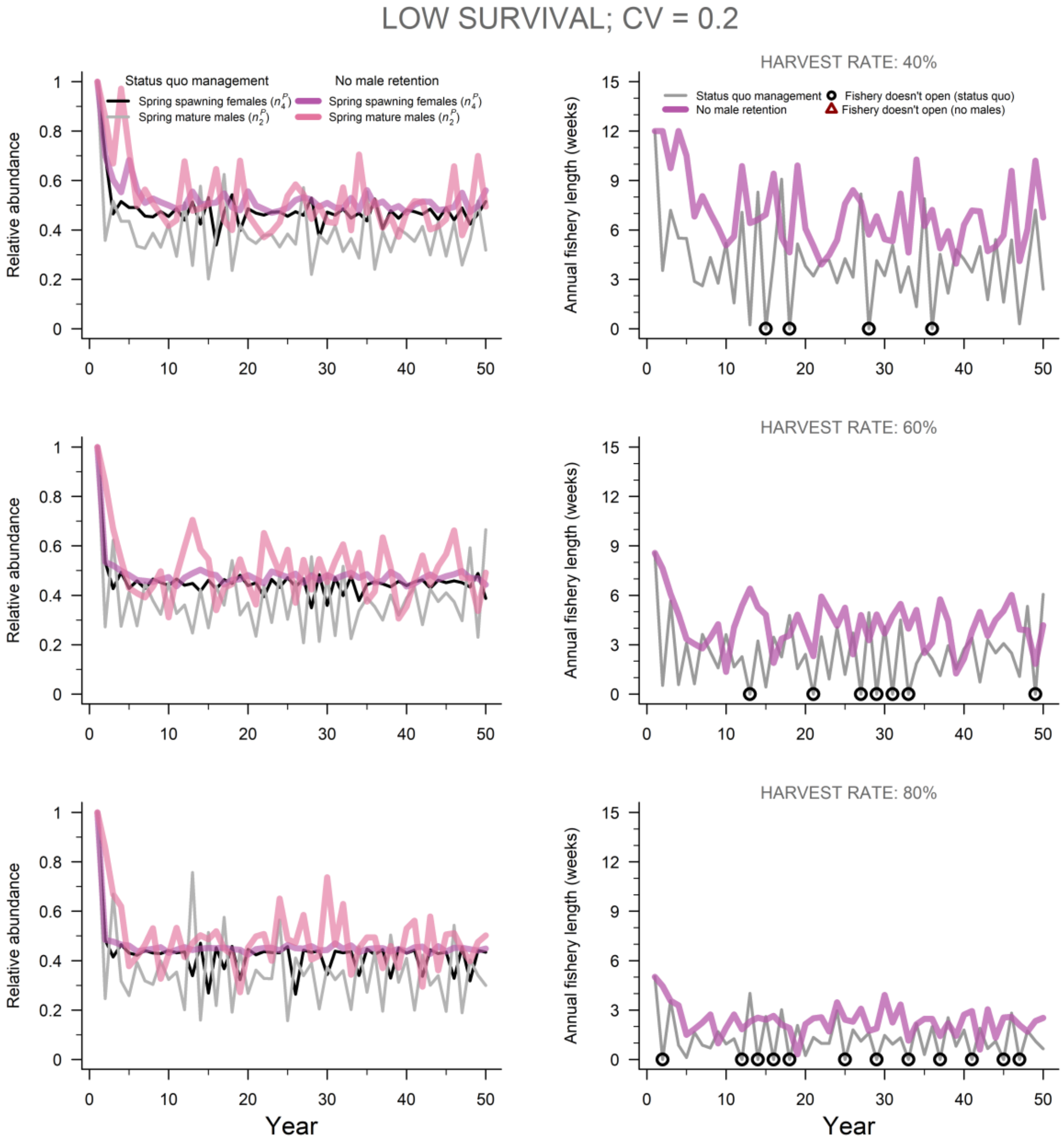

Figure A.10 Fishery length and population dynamics for low survival across all harvest scenarios for recruitment CV=0.2.

Population dynamics (left column) are plotted as stage-specific abundance relative to their stable stage abundance in the absence of fishing (the initial condition). Black circles indicate years in the status quo simulation for which the female population at the start of the summer fishing season was below the fixed escapement target.

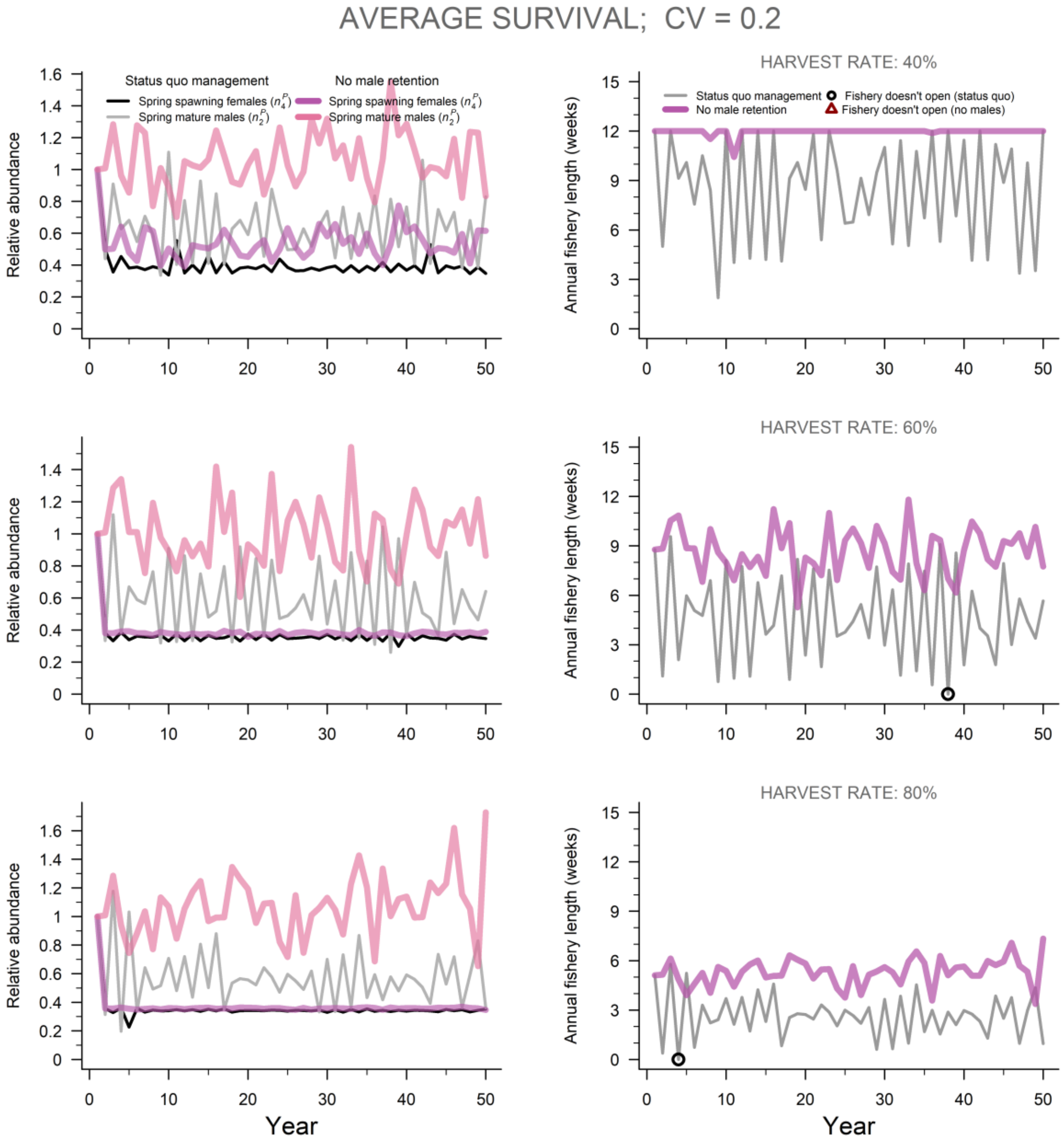

Figure A.11 Fishery length and population dynamics for average survival across all harvest scenarios for recruitment CV=0.2.

Population dynamics (left column) are plotted as stage-specific abundance relative to their stable stage abundance in the absence of fishing (the initial condition). Black circles indicate years in the status quo simulation for which the female population at the start of the summer fishing season was below the fixed escapement target.

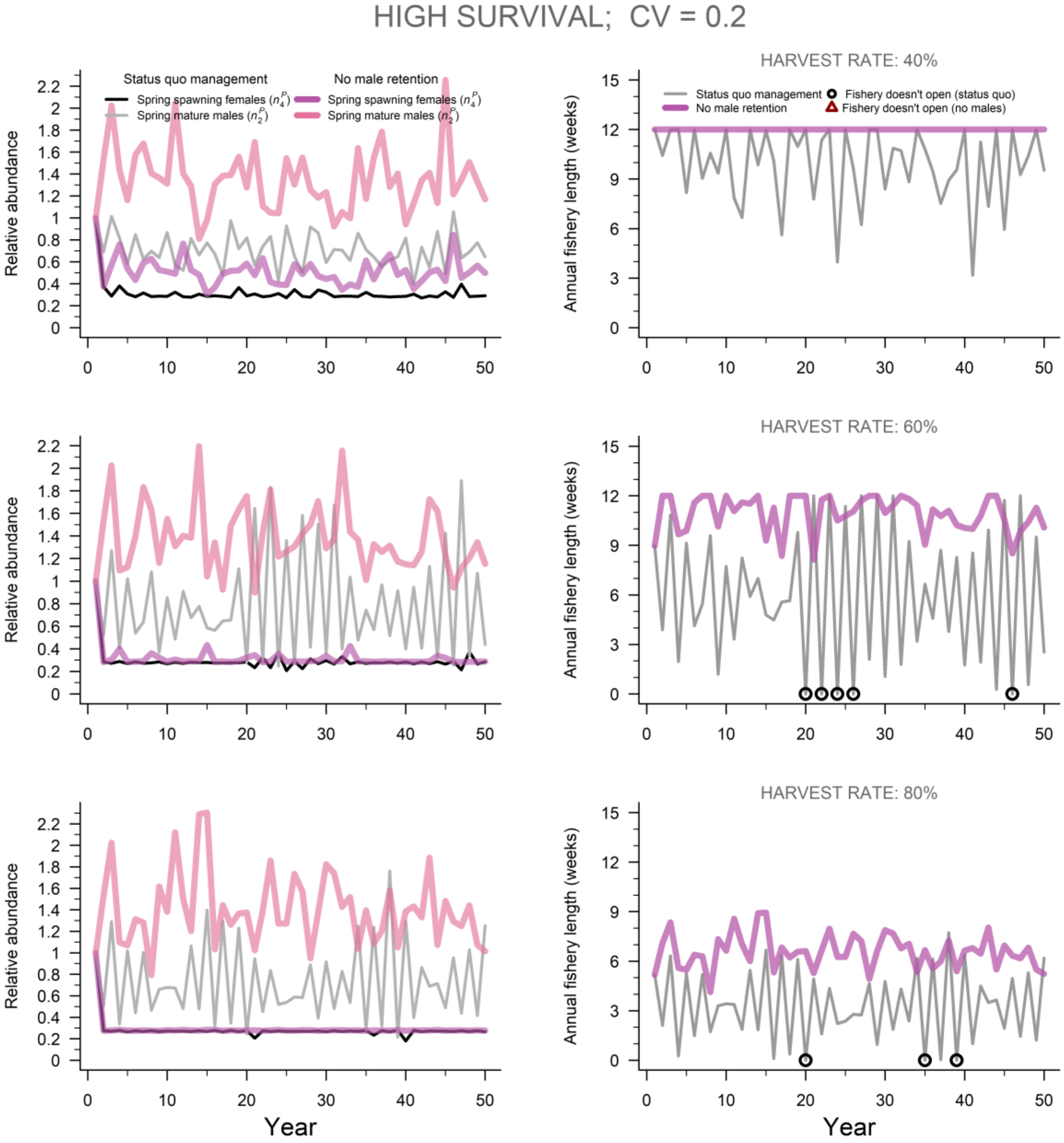

Figure A.12 Fishery length and population dynamics for low survival across all harvest scenarios for recruitment CV=0.2.

Population dynamics (left column) are plotted as stage-specific abundance relative to their stable stage abundance in the absence of fishing (the initial condition). Black circles indicate years in the status quo simulation for which the female population at the start of the summer fishing season was below the fixed escapement target.

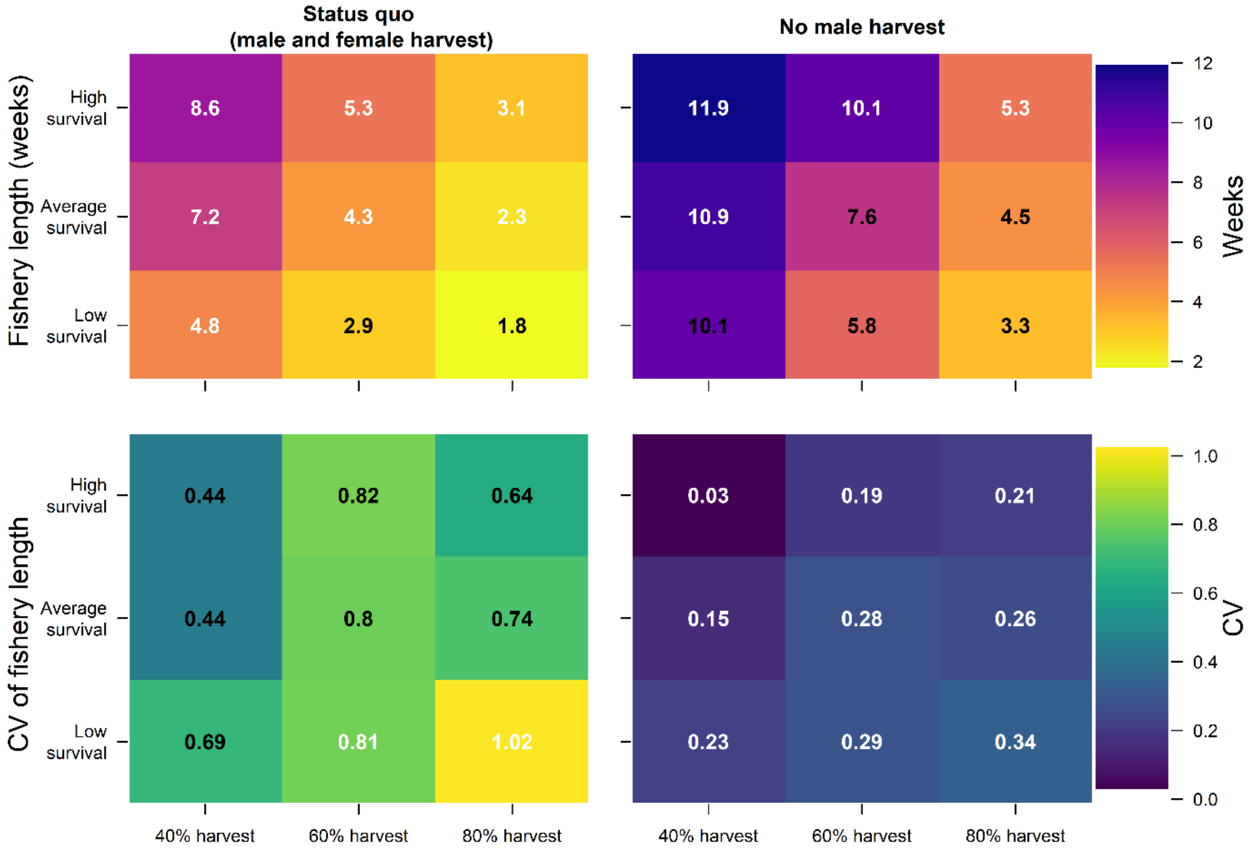

Figure A.13 Heatmap visualising average fishery length and CV in the fishery length across scenarios for recruitment CV=0.3.

Top row visualises differences in average fishery length between the status quo (left) and no-male harvest scenarios (right). Bottom row visualises differences in the variability in fishery length between the two management scenarios.

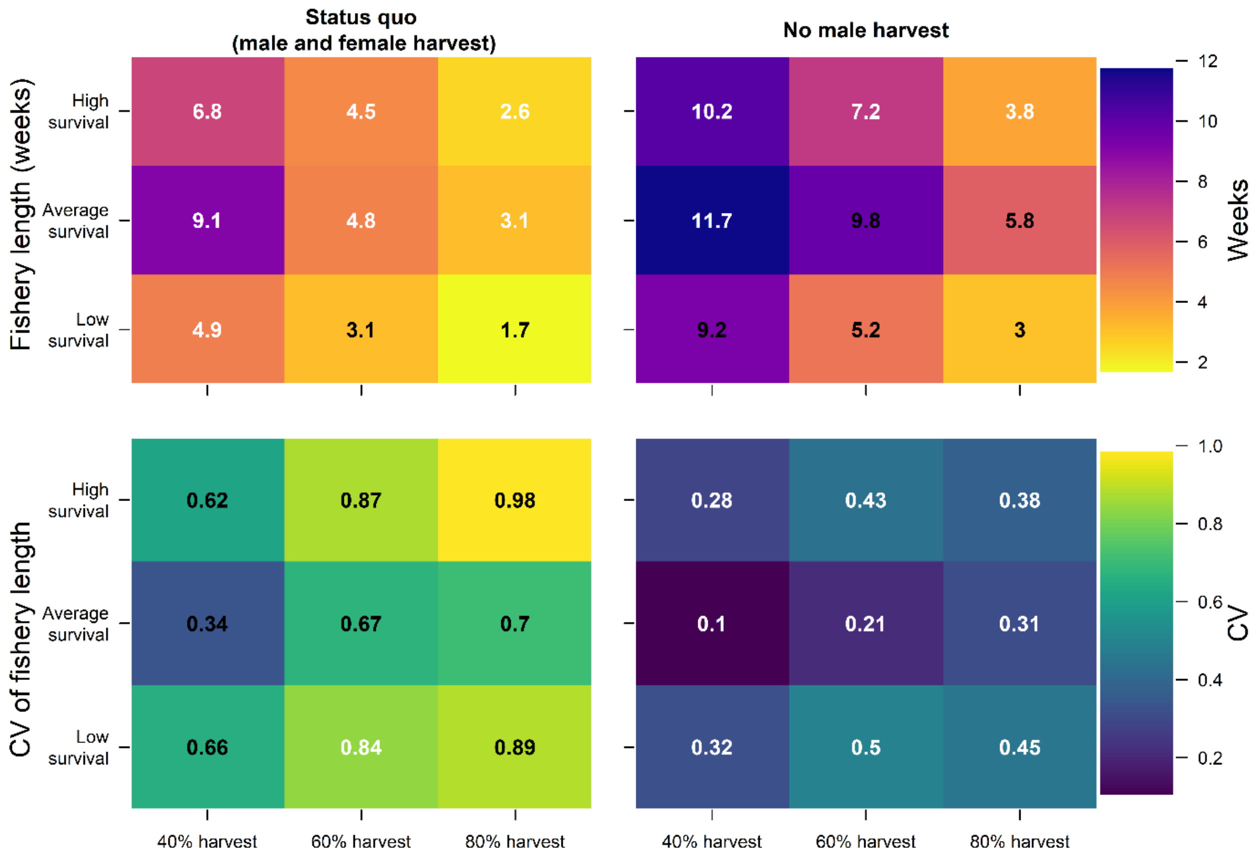

Figure A.14 Heatmap visualising average fishery length and CV in the fishery length across scenarios for recruitment CV=0.4.
Top row visualises differences in average fishery length between the status quo (left) and no-male harvest scenarios (right). Bottom row visualises differences in the variability in fishery length between the two management scenarios.

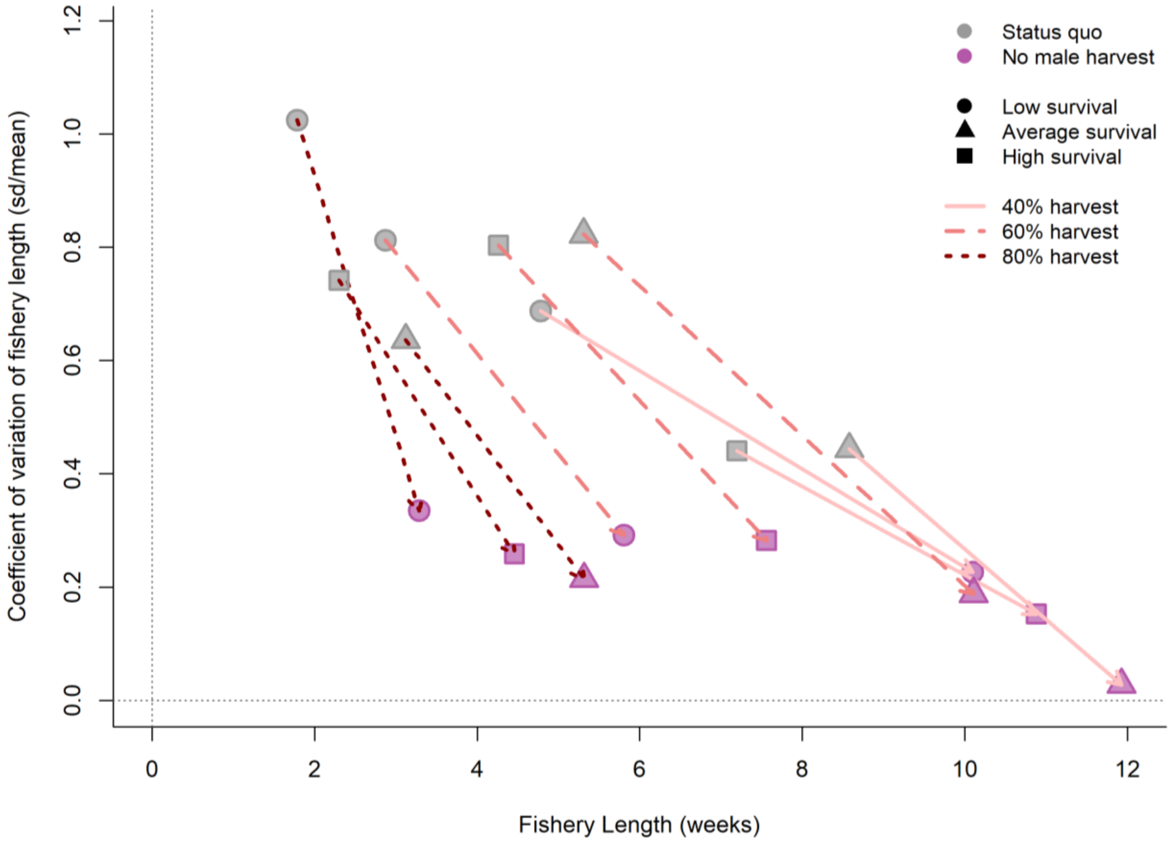

Figure A.15 Fishery length vs. fishery length variation across harvest and survival scenarios for recruitment CV=0.3.

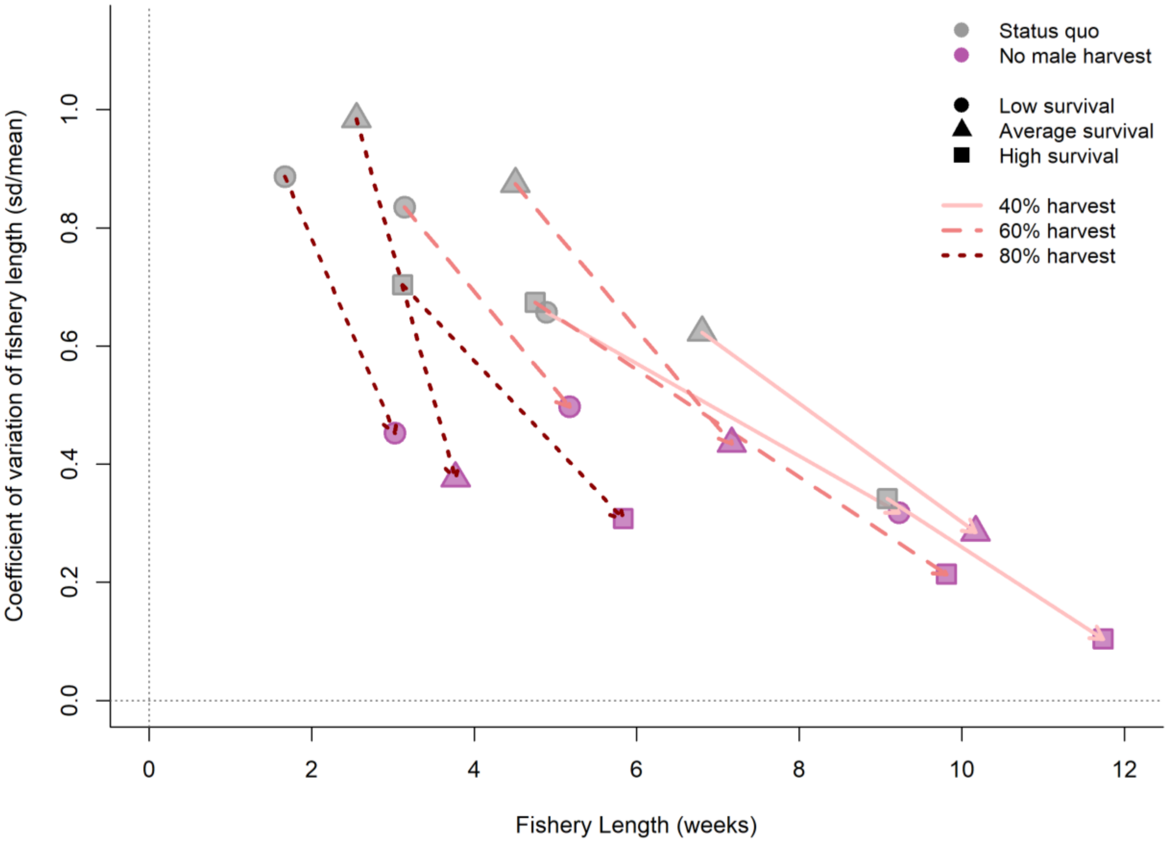

Figure A.16 Fishery length vs. fishery length variation across harvest and survival scenarios for recruitment CV=0.4.

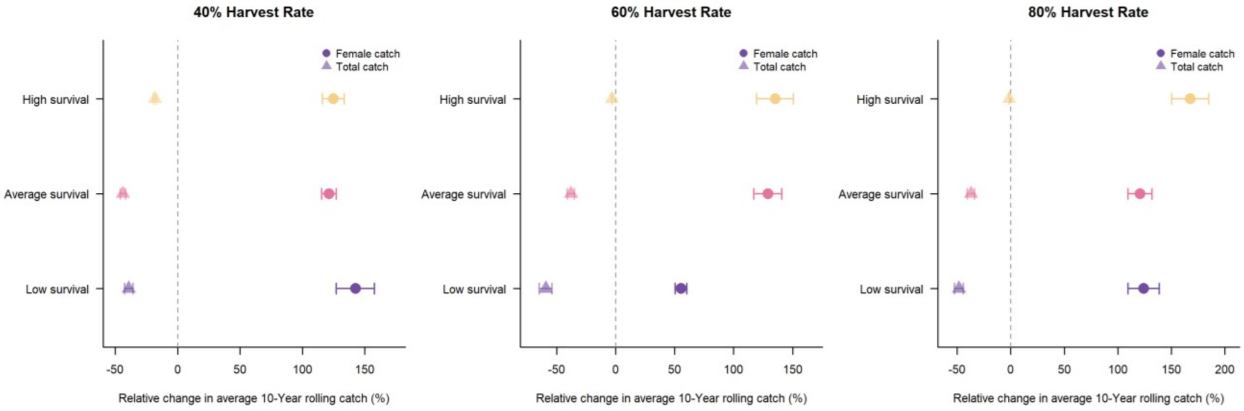

Figure A.17 Trade-offs in average 10-year rolling catch for no-male-harvest relative to status quo management across survival and harvest scenarios for recruitment CV=0.3.

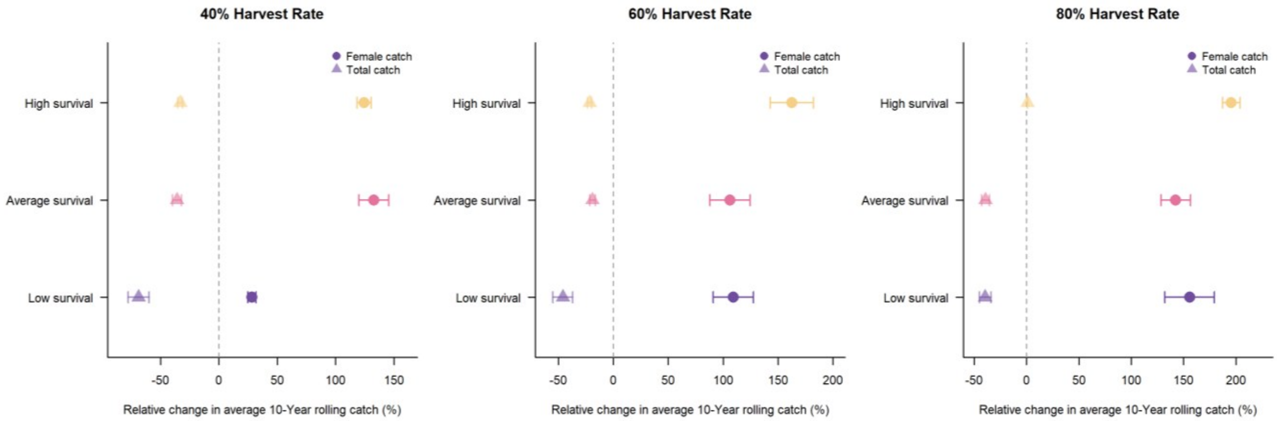

Figure A.18 Trade-offs in average 10-year rolling catch for no-male-harvest relative to status quo management across survival and harvest scenarios for recruitment CV=0.4.

Appendix B.

Supporting information for Chapter 3

B.1 Supporting tables

Table B.1 Table of ten reflex behaviours used to evaluate condition for each surviving prawn at the end of the trial.

Table contents directly replicated from Stoner et al. 2012 and each behaviour scored as a 1 (positive response) or 0 (lost response). The cumulative score of the ten behaviours (0-10) was found to be predictive of the long-term survival of spot prawns in a lab experiment described in the paper.

Reflex	Test	Positive response	Lost response
Abdomen turgor	Lift the prawn by the carapace, dorsum up	Abdomen is extended to horizontal position, or a tail flip occurs	Abdomen hangs limply and without motion
Abdomen extension	While holding the prawn as above, manually depress the abdomen	Abdomen shows resistance and extends outward or a tail flip occurs	Abdomen shows no resistance to being flexed and does not re-extend
Leg motion	Manually stimulate the pereiopods	Pereiopods move spontaneously when the prawn is lifted or upon stimulation	Pereiopods are motionless upon stimulation
Leg retraction	Draw the 1st or 2nd pereiopods in the anterior direction	Pereiopods retract in the posterior direction or present resistance to the motion	No resistance to manipulation occurs
Maxilliped motion	Manually stimulate the 3rd maxillipeds in the anterior direction	Maxillipeds move spontaneously when the prawn is lifted or upon stimulation	Maxillipeds are motionless upon stimulation
Maxilliped retraction	Draw the 3rd maxillipeds in the anterior direction	Maxillipeds retract in the posterior direction or present resistance to the motion	No resistance to manipulation occurs
Antenna motion	Manually stimulate the antenna	Antennae move spontaneously or upon stimulation	Antennae are motionless upon stimulation
Eye turgor	Touch the eye stalk with a blunt probe, or lift it from retracted position	Eye stalk retracts, moves, or shows normal turgor when stimulated	Eye stalk shows no motion or resistance to manipulation and hangs limply
Pleopod retraction	Extend the pleopods downward with a blunt probe	Pleopods are retracted close to the abdomen	Pleopods hang limply from the abdomen and do not retract upon stimulation
Mouth closure	Hold the prawn in ventrum-up position. If closed, open the 2nd maxillipeds with a blunt probe	Maxillipeds move spontaneously or move actively upon stimulation	Maxillipeds are motionless upon stimulation

Table B.2 Model-predicted survival probabilities (95% confidence intervals) for different combinations of air temperature, body length, and air exposure duration.

		Air exposure duration				
Temp	**Length**	**0 min**	**30 min**	**60 min**	**90 min**	**120 min**
10°C	22 mm	0.971 (0.954-0.982)	0.935 (0.901-0.958)	0.859 (0.796-0.905)	0.722 (0.620-0.806)	0.526 (0.400-0.649)
10°C	32 mm	0.947 (0.926-0.962)	0.884 (0.848-0.912)	0.765 (0.707-0.814)	0.581 (0.499-0.658)	0.371 (0.285-0.466)
10°C	40 mm	0.915 (0.882-0.940)	0.821 (0.769-0.864)	0.662 (0.589-0.728)	0.455 (0.372-0.541)	0.263 (0.192-0.349)
15°C	22 mm	0.935 (0.914-0.952)	0.822 (0.777-0.860)	0.598 (0.530-0.662)	0.323 (0.264-0.389)	0.133 (0.101-0.174)
15°C	32 mm	0.915 (0.895-0.931)	0.775 (0.740-0.807)	0.526 (0.479-0.572)	0.263 (0.225-0.304)	0.103 (0.082-0.128)
15°C	40 mm	0.895 (0.871-0.915)	0.732 (0.690-0.769)	0.467 (0.419-0.516)	0.220 (0.185-0.259)	0.083 (0.065-0.105)
20°C	22 mm	0.861 (0.798-0.906)	0.599 (0.492-0.698)	0.266 (0.187-0.364)	0.081 (0.050-0.127)	0.021 (0.012-0.037)
20°C	32 mm	0.866 (0.826-0.898)	0.610 (0.543-0.673)	0.274 (0.219-0.337)	0.084 (0.060-0.116)	0.022 (0.014-0.034)
20°C	40 mm	0.870 (0.829-0.902)	0.618 (0.549-0.682)	0.281 (0.226-0.345)	0.087 (0.062-0.119)	0.022 (0.015-0.034)
25°C	22 mm	0.726 (0.558-0.848)	0.326 (0.189-0.500)	0.081 (0.039-0.160)	0.016 (0.007-0.037)	0.003 (0.001-0.008)
25°C	32 mm	0.795 (0.700-0.866)	0.414 (0.309-0.528)	0.114 (0.073-0.175)	0.023 (0.013-0.042)	0.004 (0.002-0.009)
25°C	40 mm	0.840 (0.755-0.900)	0.490 (0.374-0.606)	0.149 (0.097-0.223)	0.031 (0.017-0.055)	0.006 (0.003-0.012)

B.2 Supporting figures

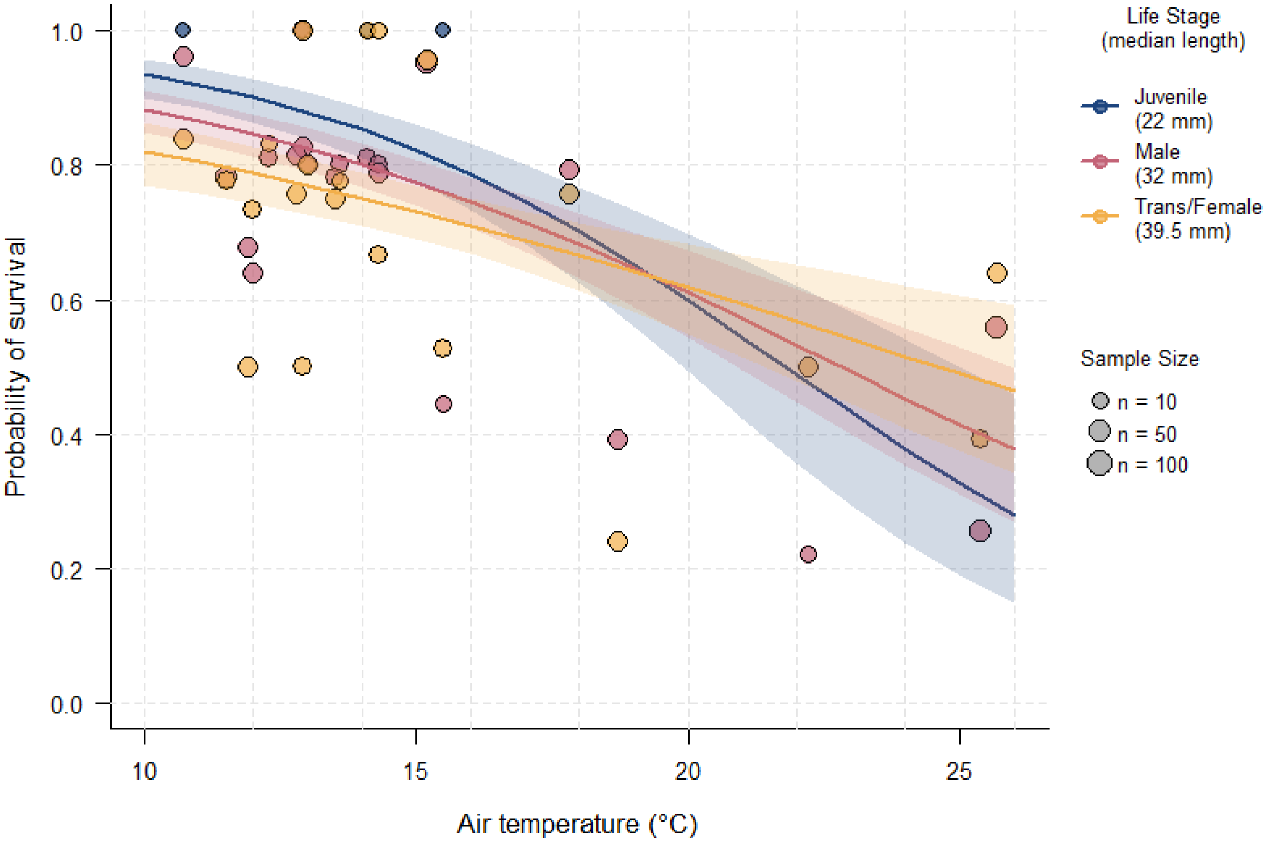

Figure B.1 Visualisation of the temperature-length interaction effect on the estimated probability of survival for prawns in the 30-minute air exposure treatment.

Curves depict model-predicted survival probability across air temperature values for three carapace lengths: 22 mm, 32 mm, and 39.5 mm. These length values correspond to the median carapace lengths for juvenile, male, and transitional/female prawns respectively. Plotted points represent the trial level mean survival proportions for prawns in the 30-minute air exposure treatment. Smaller prawns were predicted to survive with slightly higher probability at low temperatures, but the magnitude of the effect is relatively low and the relationship is contingent on relatively few data points. The slope of the curves varied for other treatments (steeper for longer air exposure treatments) but the interaction effect and its magnitude were similar.

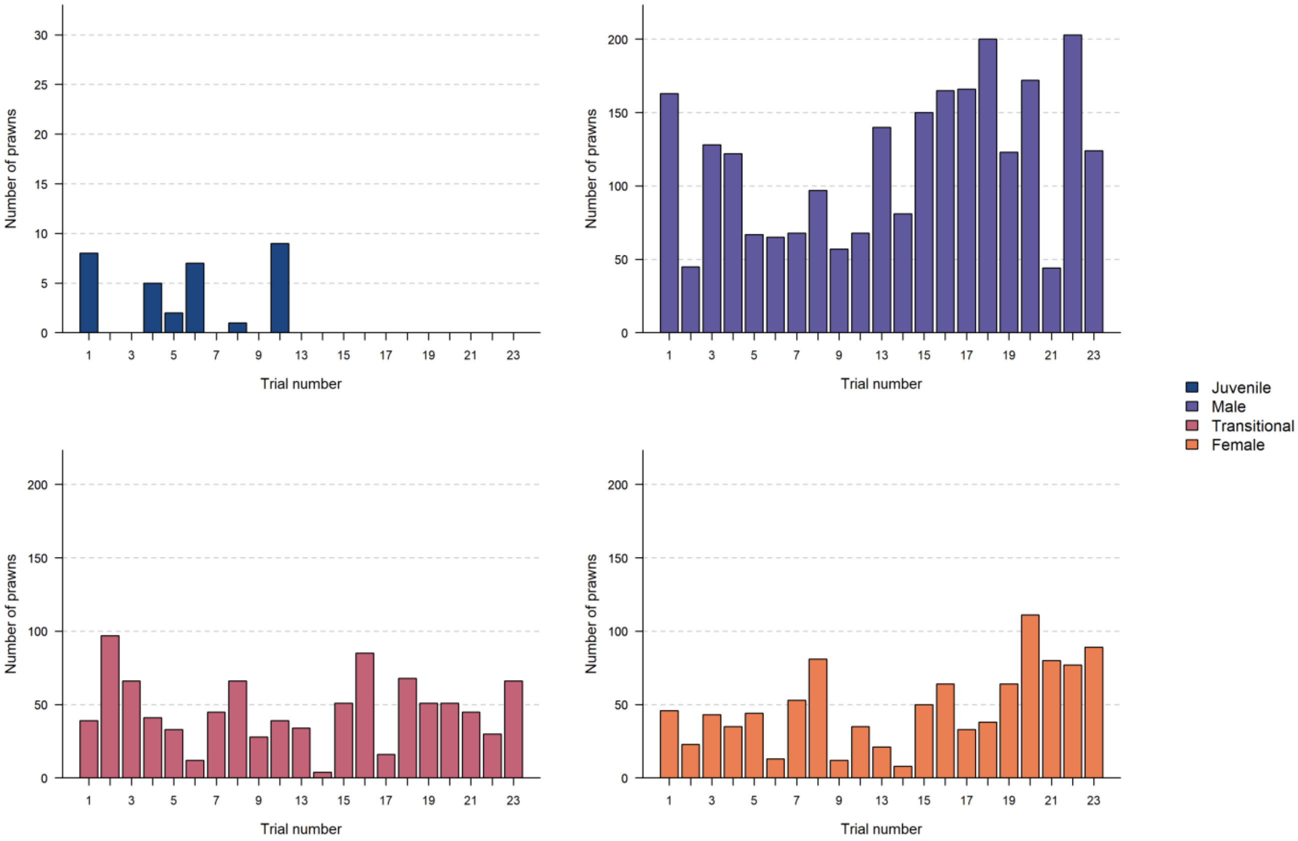

Figure B.2 Number of prawns per trial by life stage.

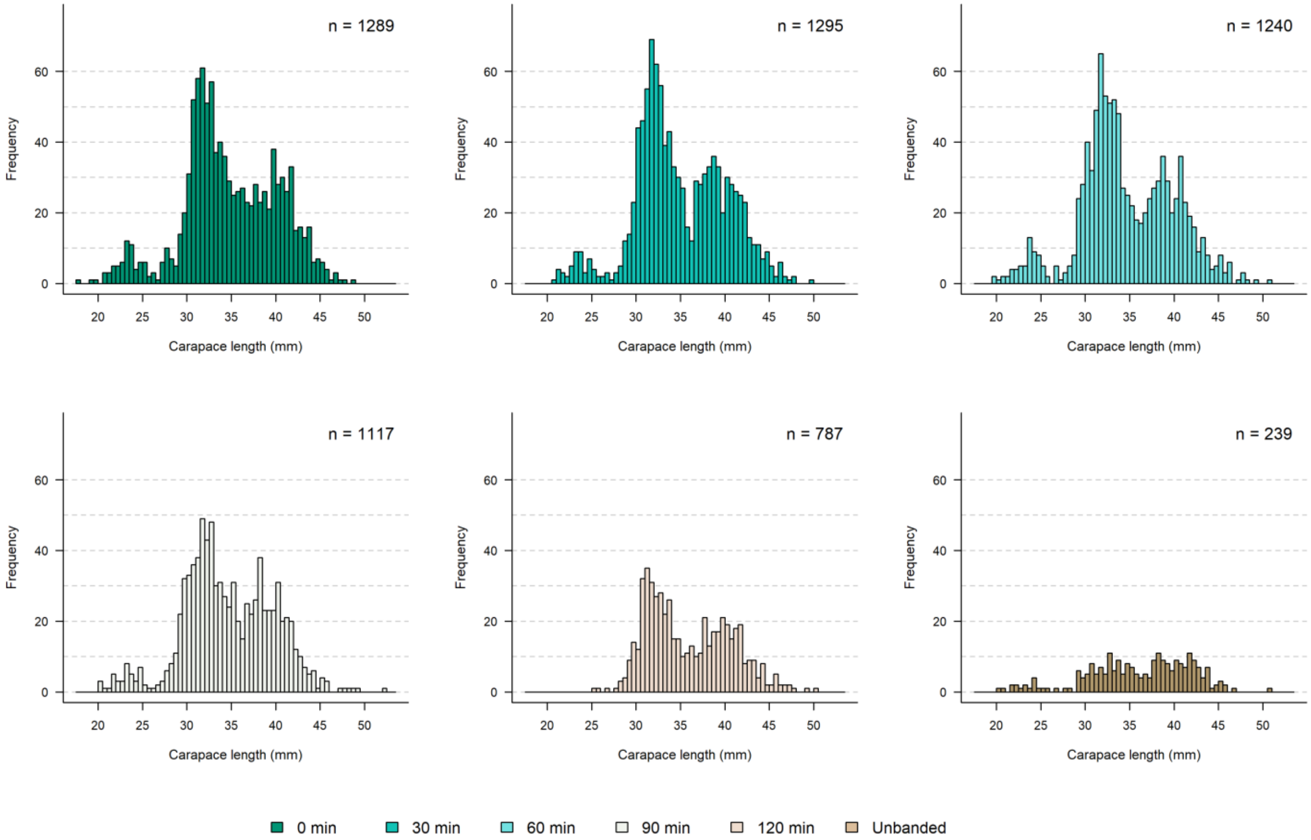

Figure B.3 Length distribution of prawns per treatment and length distribution of unbanded prawns.

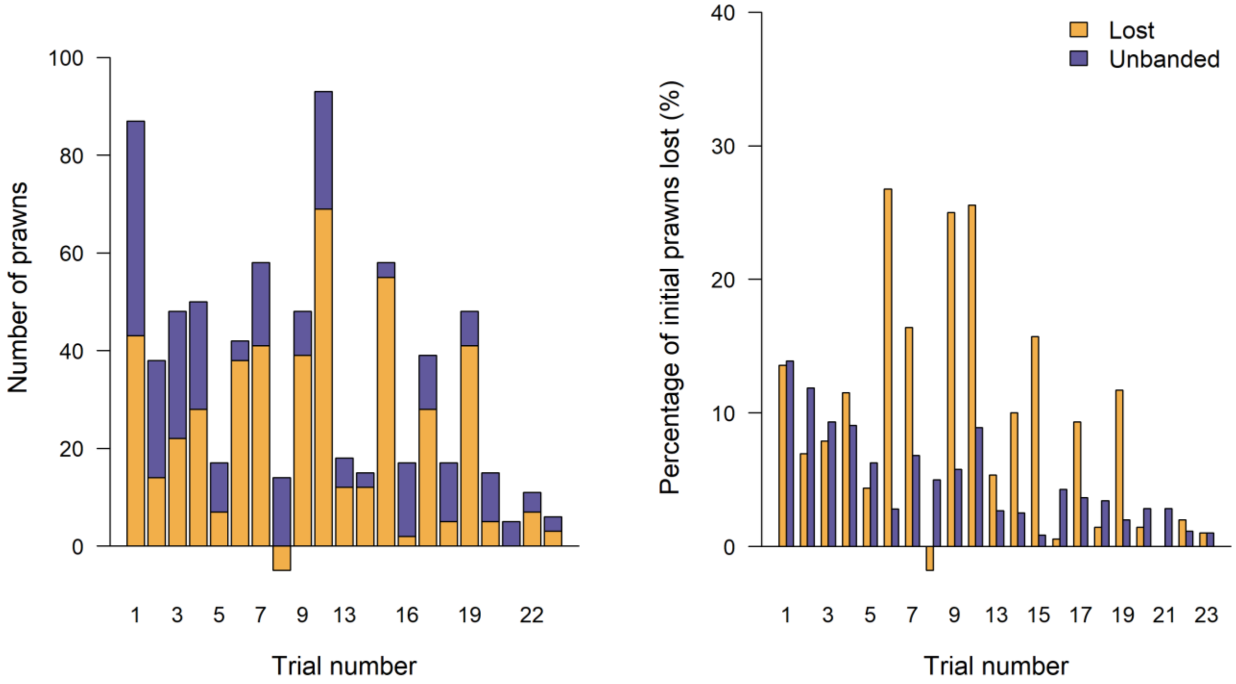

Figure B.4 Total number (left) or percentage of initial number of prawns (right) lost or recovered without a noseband at the end of each experimental trial.

The number of lost prawns is calculated as the number of prawns at the start of the trial minus the number of prawns at the end of the trial. Unbanded prawns calculated as the total number of prawns recovered without a noseband (i.e., unassignable to treatment category). Note that in trial 8, prawns were ‘gained’ likely due to miscounting at the start of the trial.

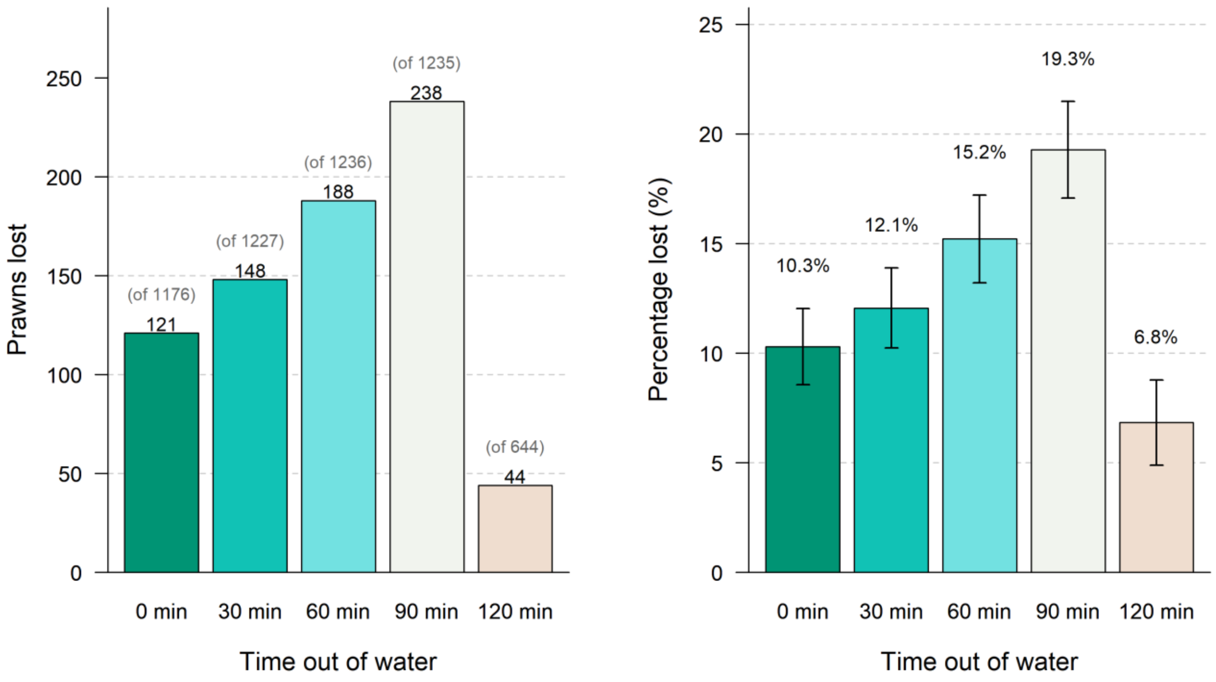

Figure B.5 Number (left) and proportion (right) of prawns lost per treatment group.
There were generally more prawns lost as air exposure increased.

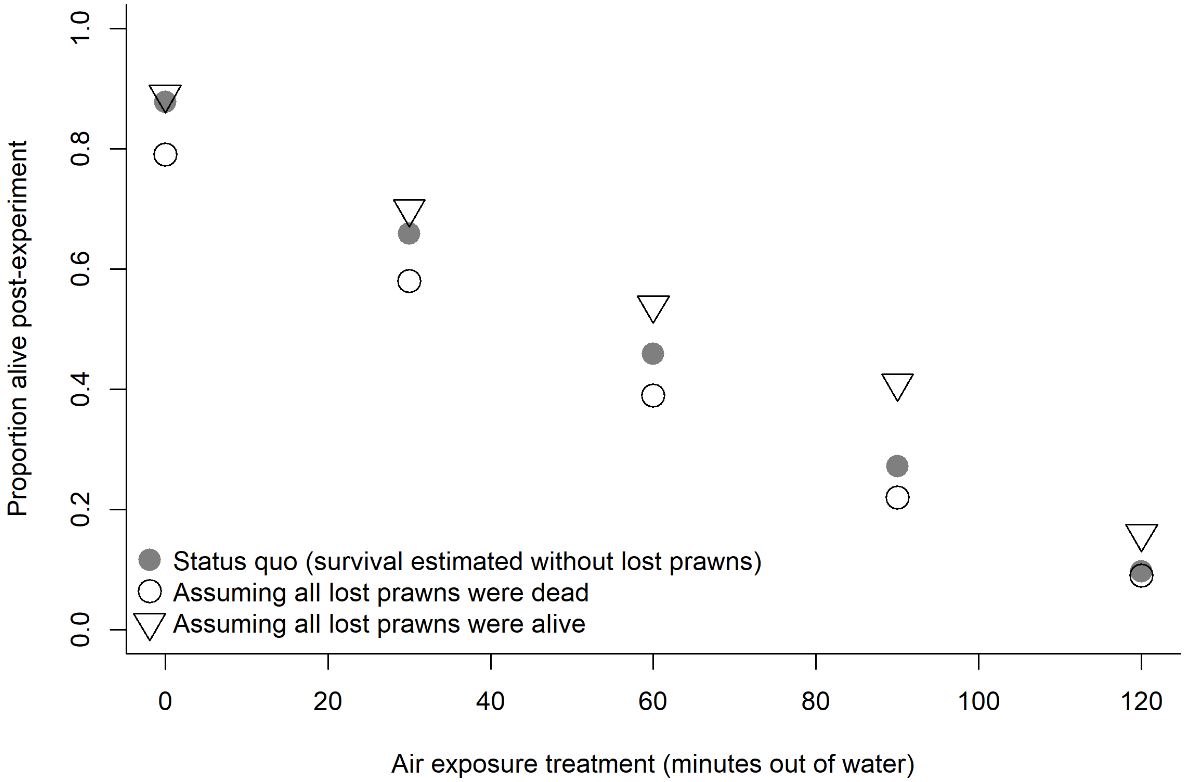

Figure B.6 Visual assessment of the consequences of biased loss of prawns across treatment groups.

Gray circles represent the calculated survival proportion, from the data, per treatment group. Open circles represent the survival estimate calculated under the assumption that all lost prawns were dead. Open triangles represent the survival estimate calculated under the assumption that all lost prawns were alive. The trend across air exposure lengths does not change, but the precise survival estimates are slightly different.

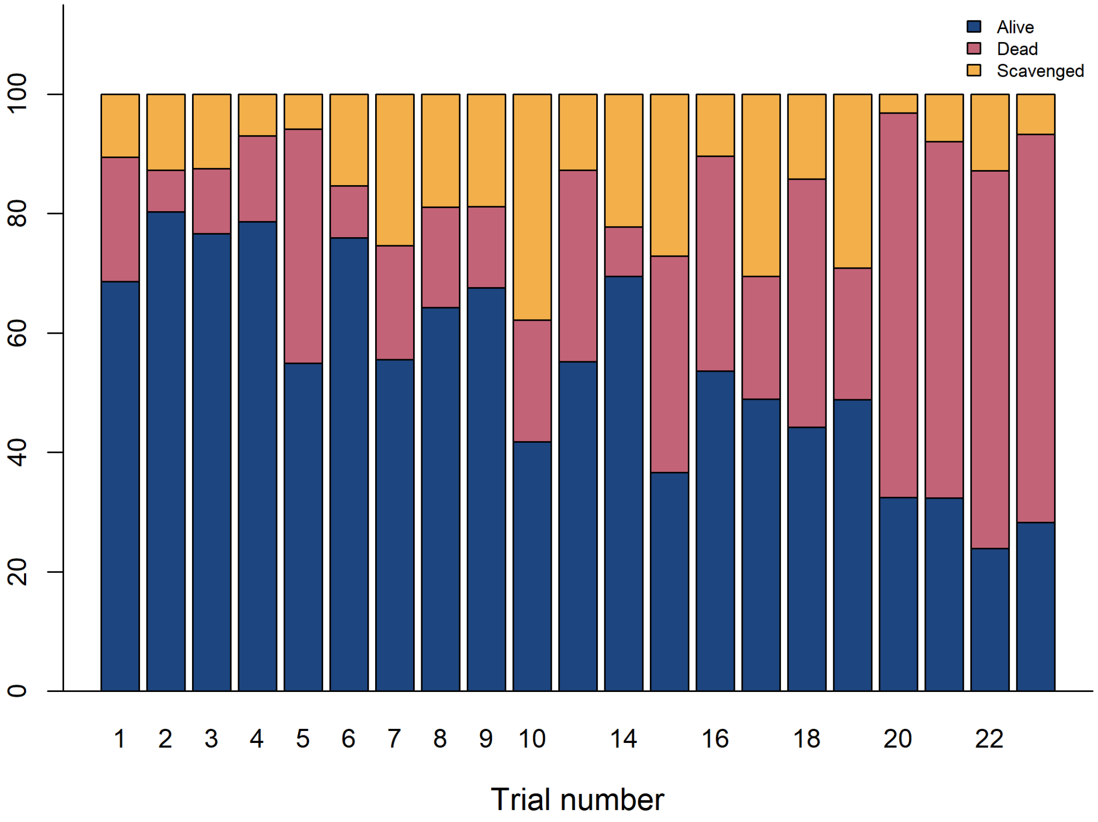

Figure B.6 Trial-level distribution of prawn condition at the end of a trial. ‘Scavenged’ indicates prawns that were dead and also missing part of their body (e.g., appendages, etc). In some cases, we were not able to assess stage or accurately measure carapace length from scavenged prawns and these were excluded from the final analysis.

Appendix C.

Supporting information for Chapter 4

In this appendix, we provide additional region-specific details for the research survey methods. The survey design for the Broughton and Central Coast surveys is based off the methods developed by DFO for their Howe Sound research survey. DFO biologists provided on-the-ground training for the Kitasoo Xai'xais research crew at the inception of their prawn survey and the lead author of this study has participated in the data collection for each survey to ensure consistency in methodology across surveys. All research surveys use the same trap type (76 cm tapered stainless steel round traps with 1.9 cm mesh) and, for the overlapping years (2021-2024), the same type of bait (~2/3 cup of fish pellets per trap). There are several survey-specific details which we outline below.

C.1 Supporting information for Howe Sound data

Research survey timing and string length

DFO normally conducts two research surveys per year in Howe Sound (DFO PFMA 28): one in the fall (October-November) and one in the spring (February-March). The exact timing of the ~7 day survey varies slightly year-to-year. The surveys are normally conducted off a large aluminum research vessel (18.8 m length) which sets strings of 20 traps at each sampling location. From 2002-2005, an additional industry-led fall survey was conducted using the same sampling gear and methods as DFO (Fig. 4.7).

Accounting for variation in bait type

Starting in 2006, DFO began to shift from tuna to pellet bait in their research survey (Fig. C.1). When using tuna, research traps were baited with a 26 g of pet food grade tuna (Rutherford et al. 2004). From 2013 onward, the research survey exclusively used commercially prepared pellet bait for prawns (~2/3 cup of pellets per trap). For the years (2006-2012) for which there are data collected using both bait types, the average Spawner Index for pellet-baited traps tends to be higher than for tuna-baited traps (Fig. C.2). The commercial fishery observer data for Howe Sound also included a range of bait types (Fig. C.3). Given the variation in bait type in both the research survey data and the fishery observer data, we included a multiplicative bait effect in the exponential decay model to account for differences in Spawner Index due to bait type.

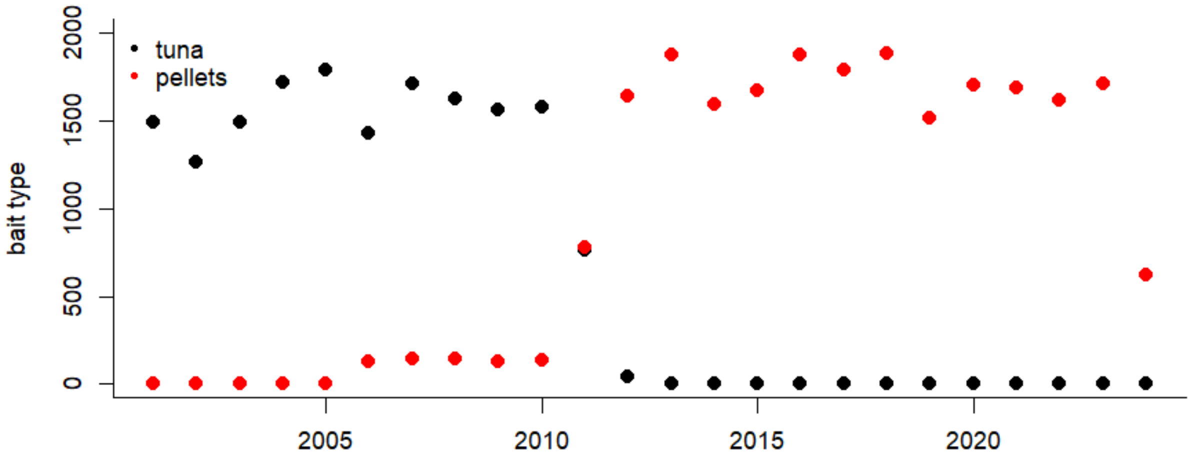

Figure C.1 Bait type over time for Howe Sound research survey.
Number of traps set with each bait type for each year in the Howe Sound survey dataset. After 2012, all traps were set with pellet bait.

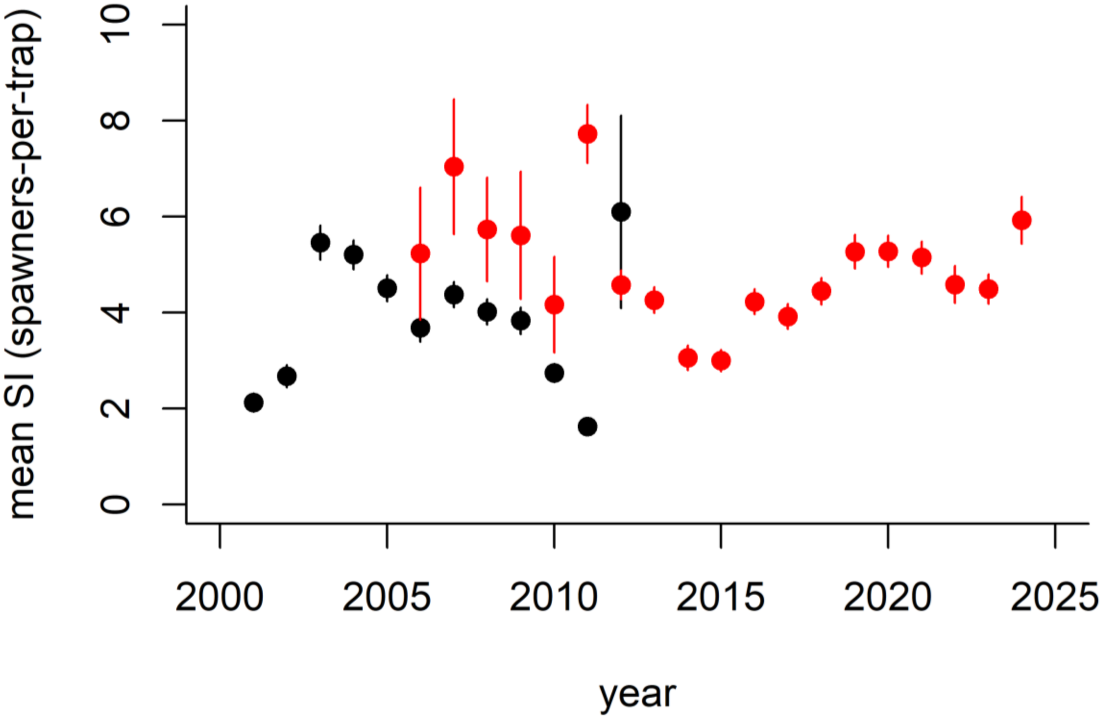

Figure C.2 Average Spawner Index by bait type for Howe Sound survey.
For years where traps were set with both bait types, Spawner Indices for pellet-baited traps (red) tends to be higher than for tuna-baited traps (black).

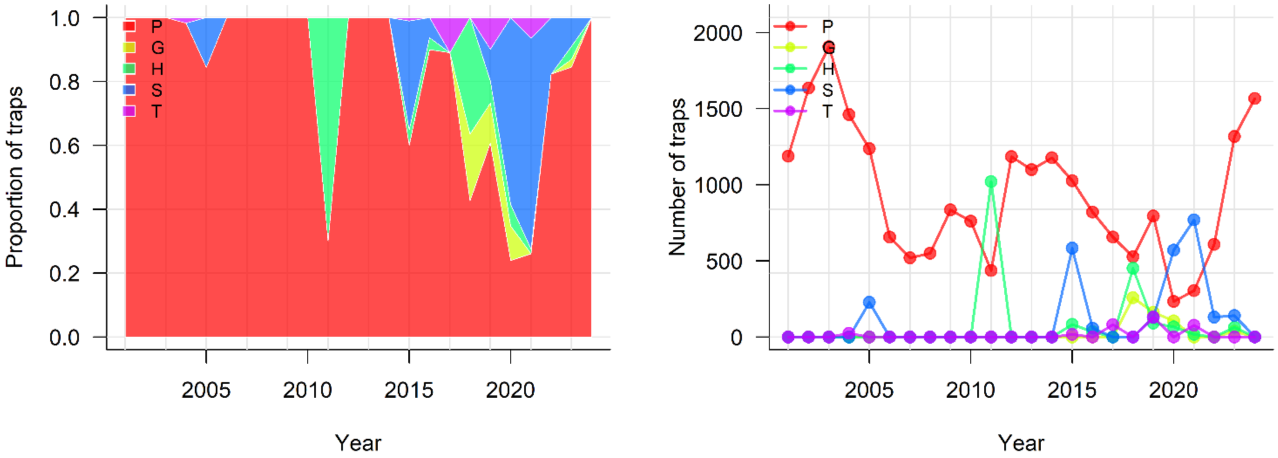

Figure C.3 Proportional (left) and absolute (right) distribution of recorded bait types in the Howe Sound commercial fishery data.

Recorded bait types include pellets (P), gurdy (G, a.k.a. mixed fish scraps), herring (H), sardine (S), and tuna (T).

C.2 Supporting information for Broughton data

From 2022-2024, researchers from the University of Alberta worked with the fishery manager and field technicians from the Musgamagw Dzwada’enuxw Fisheries Group (MDFG) to conduct four prawn research surveys in MD territories in the Broughton Archipelago (DFO PFMA 12). The surveys took place in April 2022, October-November 2022, February-March 2023, and February-March 2024. As a result, there are two spawner years in the analysis for which there are data from the spring but not the fall.

The research survey in the Broughton was collected from a 7-meter-long research motor vessel, which is much smaller than the vessel used for the DFO surveys in Howe Sound. There are several differences in the survey methods due to the difference in vessel size. First, due to limited deck space and vessel stability requirements, we set strings of 10 rather than 20 traps at each sampling location. We were also limited to sampling fewer sites per day due to longer processing time and limited deck space to hold more than three strings worth of traps. As a result, the Broughton survey typically took 12-14 days to conduct. We used pellet bait for all our surveys and thus did not have to account for bait differences in the research data. The reported bait type for the commercial fishery observer data in DFO PFMA 12 was overwhelmingly pellets with just a few observations of alternative bait types (Fig. C.4). Because there were so few traps with non-pellet bait, we filtered the commercial fishery dataset to only retain data from pellet-baited traps and did not include a bait effect in the model for the Broughton.

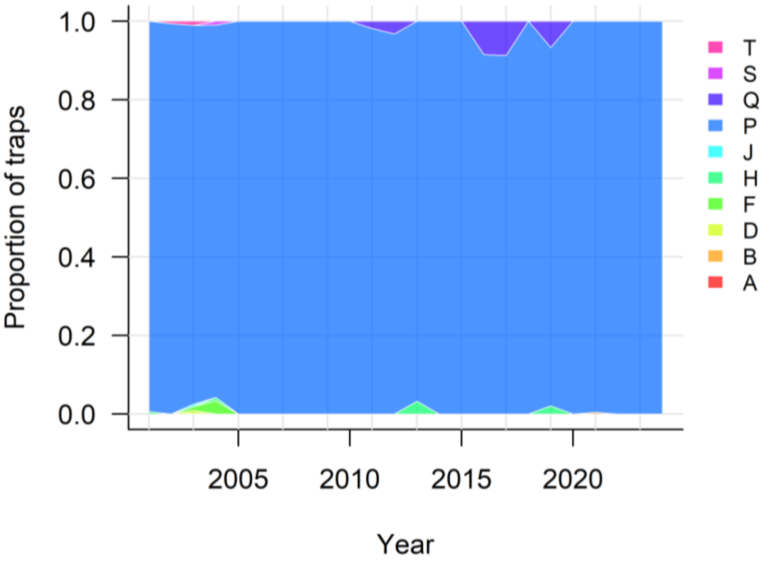

Figure C.4 Proportional distribution of bait types in the Broughton commercial fishery data.

Bait types include tuna (T), sardine (S), pellets and fish frames (Q), pellets (P), starfish (J), herring (H), fish frames (F), dogfish (D), type B pellets (B), type A pellets (A).

C.3 Supporting information for Central Coast data

From 2021-2024, the Kitasoo Xai'xais Stewardship Authority (KXSA) conducted six prawn research surveys within their territories on the Central Coast (DFO PFMA 6 and 7). The surveys were conducted in October 2021, March 2022, July 2022, November-December 2022, March 2023, and March 2024. For one of the spawner years in our analysis, 2022, there are three surveys: summer, fall, and spring. The bulk of the survey in Fall 2022 occurred in December but there were a few strings set in November and in January which we confirmed are appropriately dated and not typos in the dataset. There was no fall survey conducted in 2023 and so there is one spawner year, 2023, for which there are research data from the spring but not the fall. All the surveys were conducted using pellets for bait. As in the Broughton, KXSA conducts their prawn surveys off of smaller research vessels and sets strings of 10 traps per sampling site.

Like the Broughton, most of the reported bait used in the commercial fishery observer data for DFO PFMA 6 and 7 was pellets (Fig. C.5). For our analysis, we filtered the commercial fishery dataset to only retain data from traps set with pellet bait.

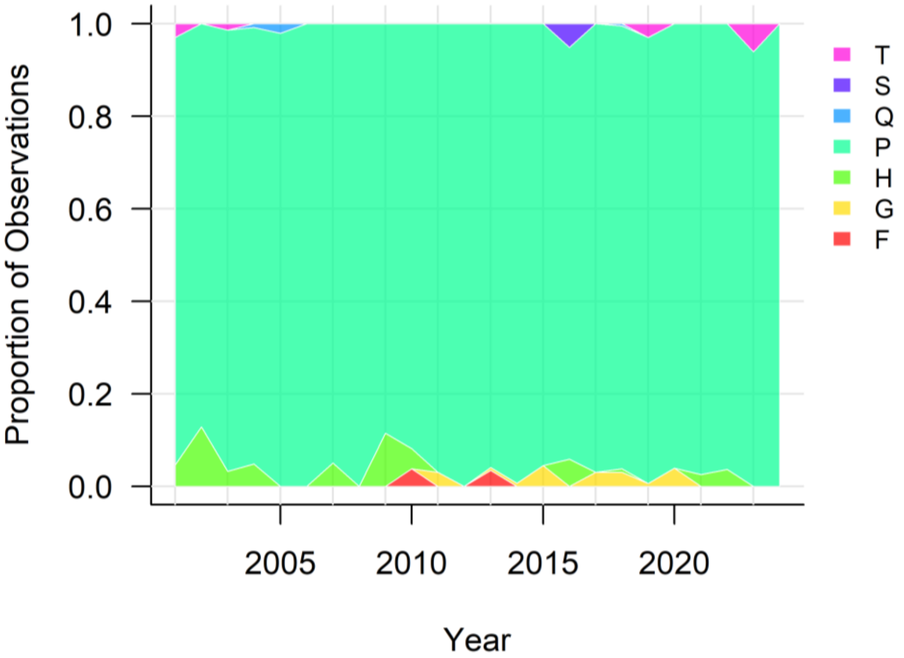

Figure C.5 Proportional distribution of bait type in the Central Coast commercial fishery data.

Reported bait types include tuna (T), sardines (S), pellets and fish frames (Q), pellets (P), herring (H), gurdy (G, mixed fish scraps), and fish frames (F).

C.4 Supporting figures for Spawner Index analysis

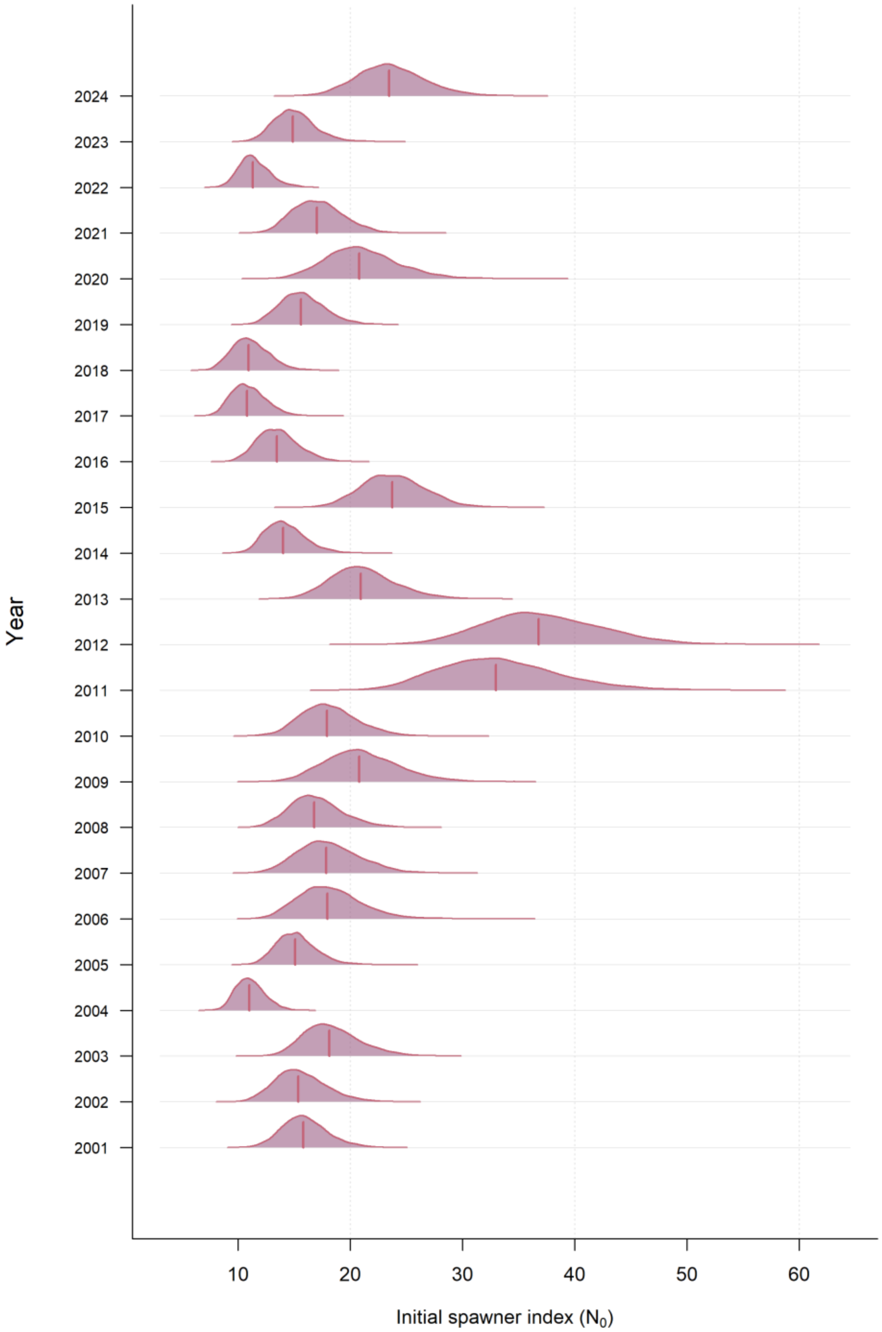

Figure C.6 Posterior distributions of annual starting Spawner Index ($N_{0,y}$) estimates for Howe Sound.

For each year, the median (pink line) estimated Spawner Index for the first day of the fishery with observations is plotted along with the full posterior distribution.

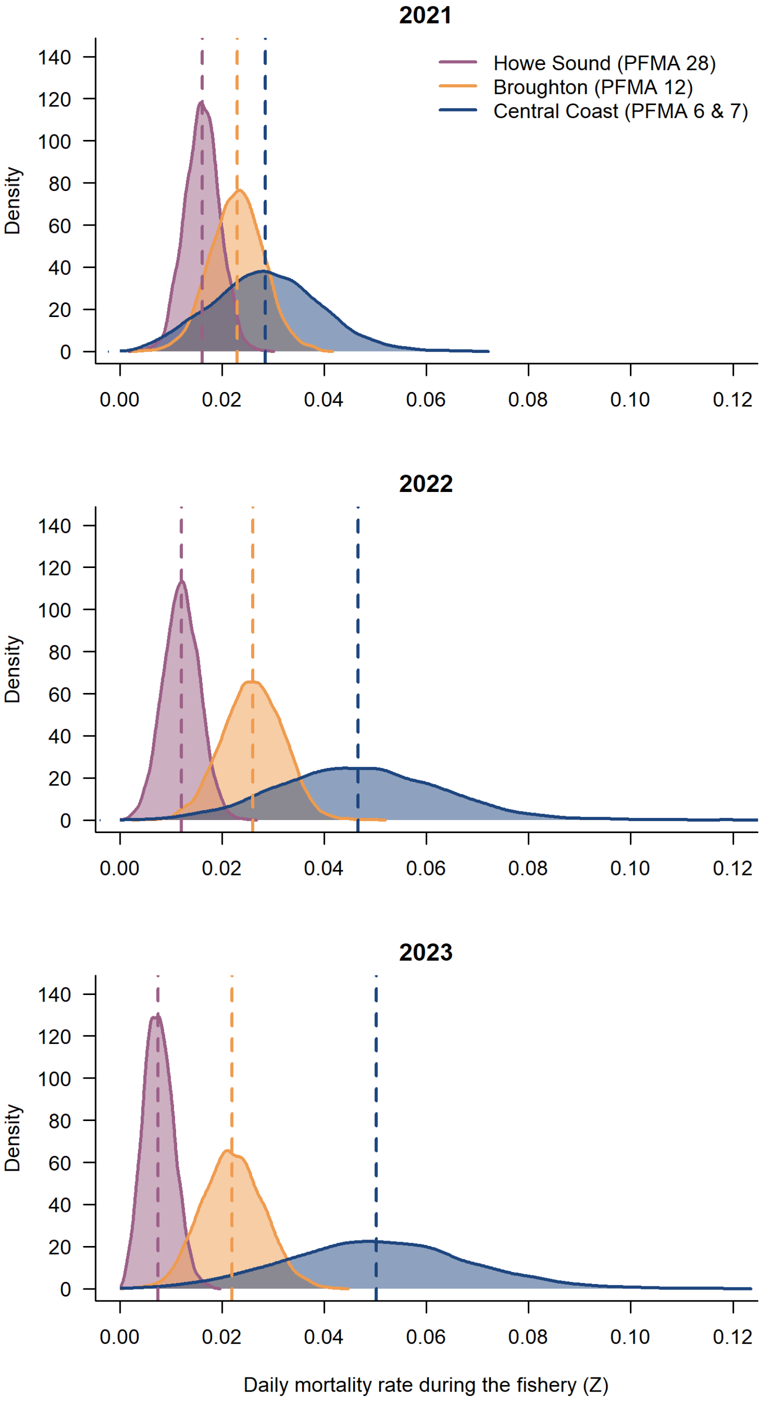

Figure C.7 Posterior distributions of the in-season daily mortality rates (Z_y) for the three years with data from all three regions (2021-2023).

Dashed lines indicate the median of the distributions for Howe Sound (purple), the Broughton (orange), and the Central Coast (blue).

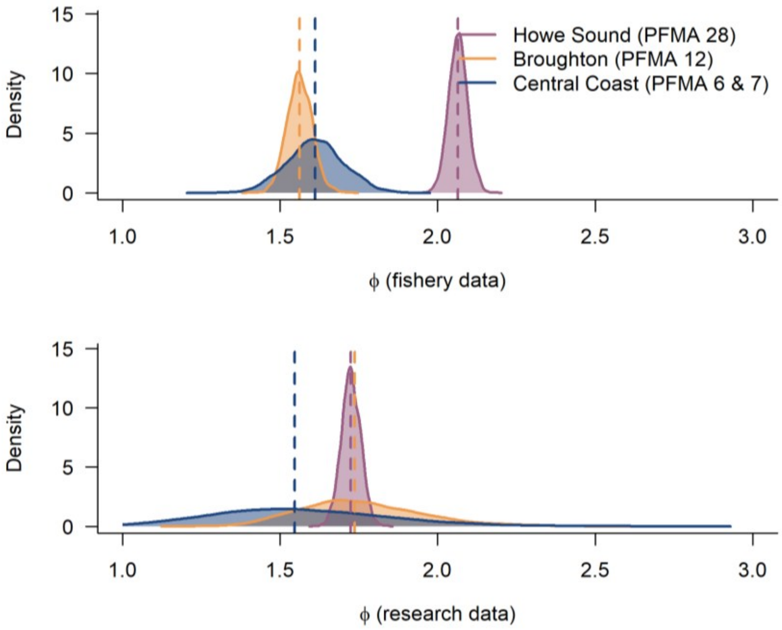

Figure C.8 Posterior distributions of the overdispersion parameter (ϕ_f) from the negative binomial distribution for all three regions.

Dashed lines indicate the median of the distribution. Higher values indicate lower overdispersion between trap-level Spawner Index counts.

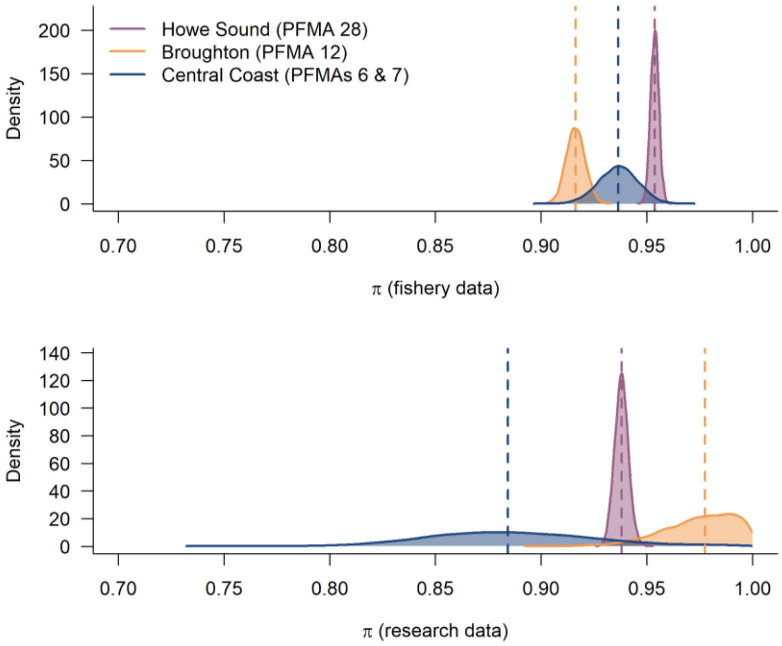

Figure C.9 Posterior distributions of zero-inflation parameter (π_f) for all three regions.

Dashed lines indicate the median estimate of the probability that a trap-level Spawner Index of zero is not a structural zero. The estimated probability of non-structural zeroes is generally above 90% with the exception of the research data from the Central Coast.

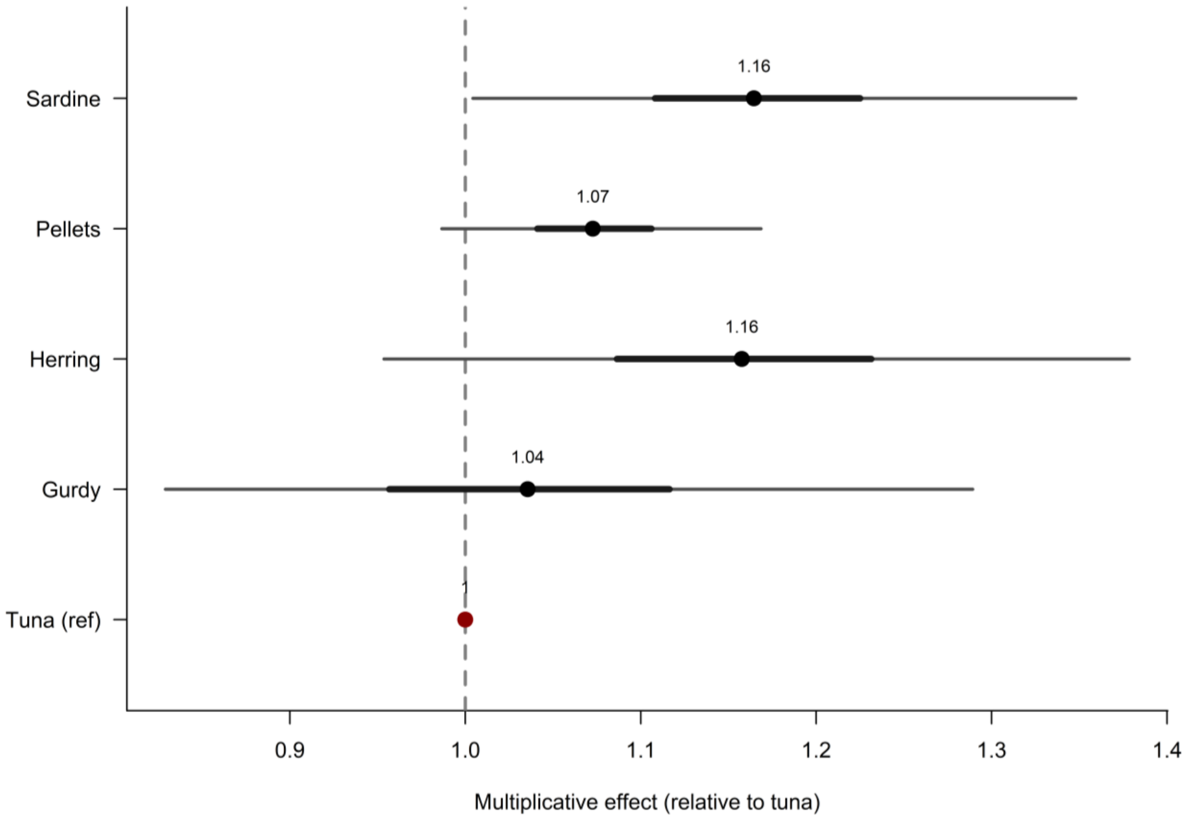

Figure C.10 Estimated bait effects from Howe Sound model.

All bait effects are estimated relative to tuna as a base case, because tuna was the bait used to define initial Spawner Index targets in the 1980s. Multiplicative effects can be interpreted as the proportional increase in the Spawner Index estimated for a given bait type. For example, traps set with pellet bait are estimated to catch 7% more spawners relative to traps baited with tuna. The 95% credible interval overlaps 1 (i.e., indistinguishable from tuna) for all bait types except sardine and the estimated effect of pellet bait (1.07) is lower than previous estimates (1.27, Rutherford et al. 2004).

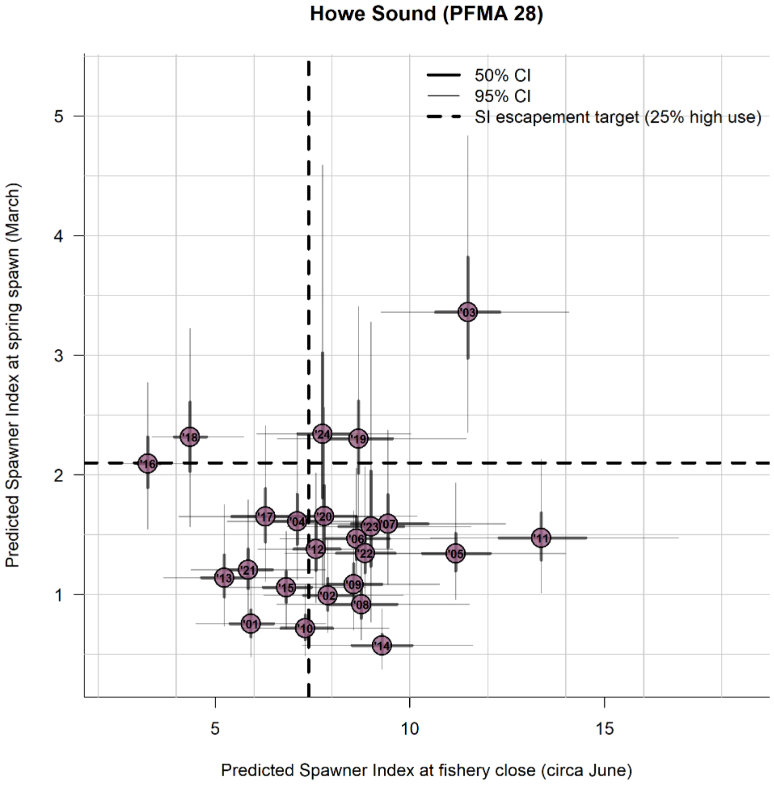

Figure C.11 Predicted Spawner Index at end of March relative to fishery close for Howe Sound.

Points indicate the median predicted Spawner Index on March 31 (y-axis) relative to the predicted Spawner Index on the closing date of the fishery (x-axis). March 31 is the date for which the spot prawn fishery annual spawner escapement target is defined. Text within each point indicates the year (e.g., ’22 indicates predictions for 2022).

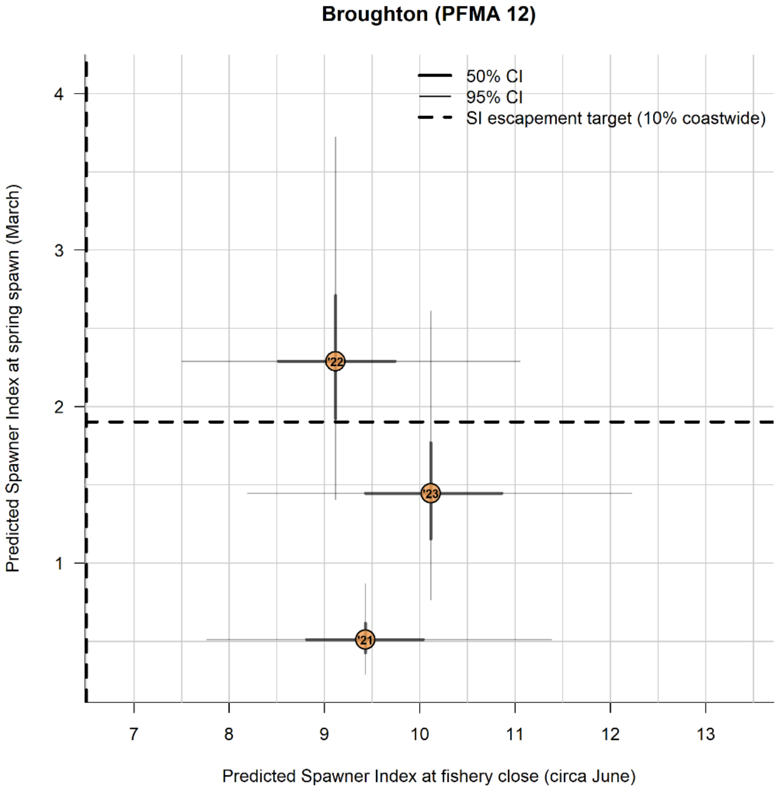

Figure C.12 Predicted Spawner Index at end of March relative to fishery close for the Broughton.

Points indicate the median predicted Spawner Index on March 31 (y-axis) relative to the predicted Spawner Index on the closing date of the fishery (x-axis). March 31 is the date for which the spot prawn fishery annual spawner escapement target is defined. Text within each point indicates the year (e.g., ’22 indicates predictions for 2022).

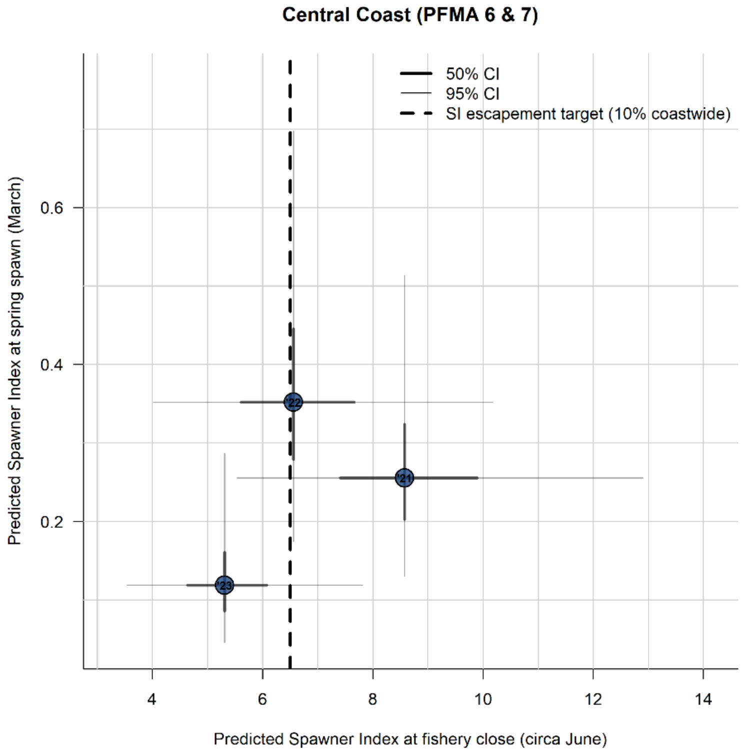

Figure C.13 Predicted Spawner Index at end of March relative to fishery close for the Central Coast.

Points indicate the median predicted Spawner Index on March 31 (y-axis) relative to the predicted Spawner Index on the closing date of the fishery (x-axis). March 31 is the date for which the spot prawn fishery annual spawner escapement target is defined. Text within each point indicates the year (e.g., ’22 indicates predictions for 2022). Note that the spring spawner escapement target (1.9 spawners-per-trap) is not shown because the scale of the y-axis does not include it.

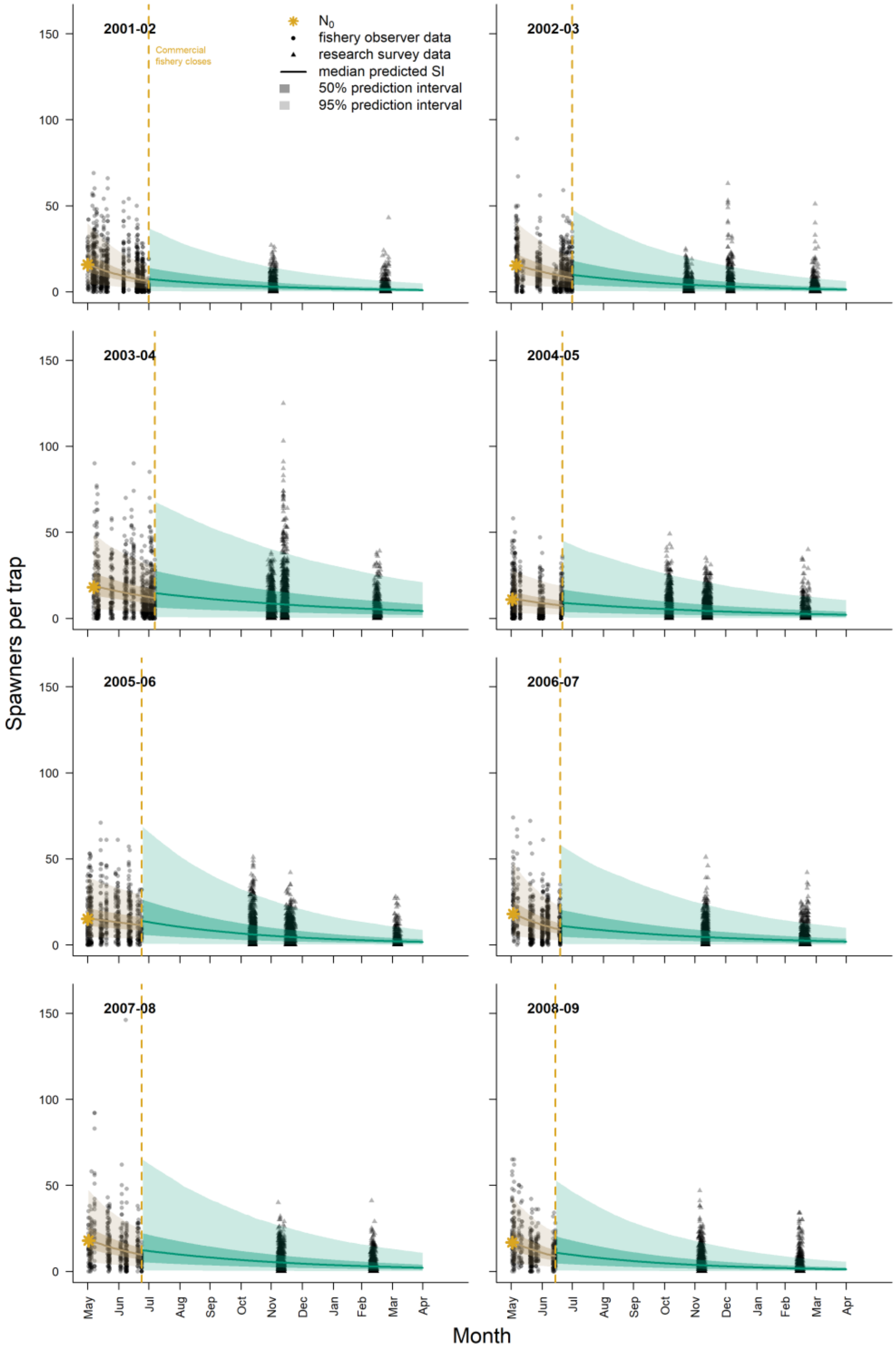

Figure C.14 Spawner Index exponential decay model fit for Howe Sound (2001-2008) including parameter uncertainty and string-level variation.

Solid lines indicate the median predicted Spawner Index on a given day of the year with polygons visualising the 50% and 95% prediction intervals encompassing uncertainty in process parameters and string-level variation estimated by the multiplicative string effect, e^{σ_f}. The disconnect in the prediction interval polygons arises because the model estimates distinct string-level variation depending on the data source (fishery data vs. survey data). Black points (fishery data) or triangles (survey data) indicate raw trap-level Spawner Index counts.

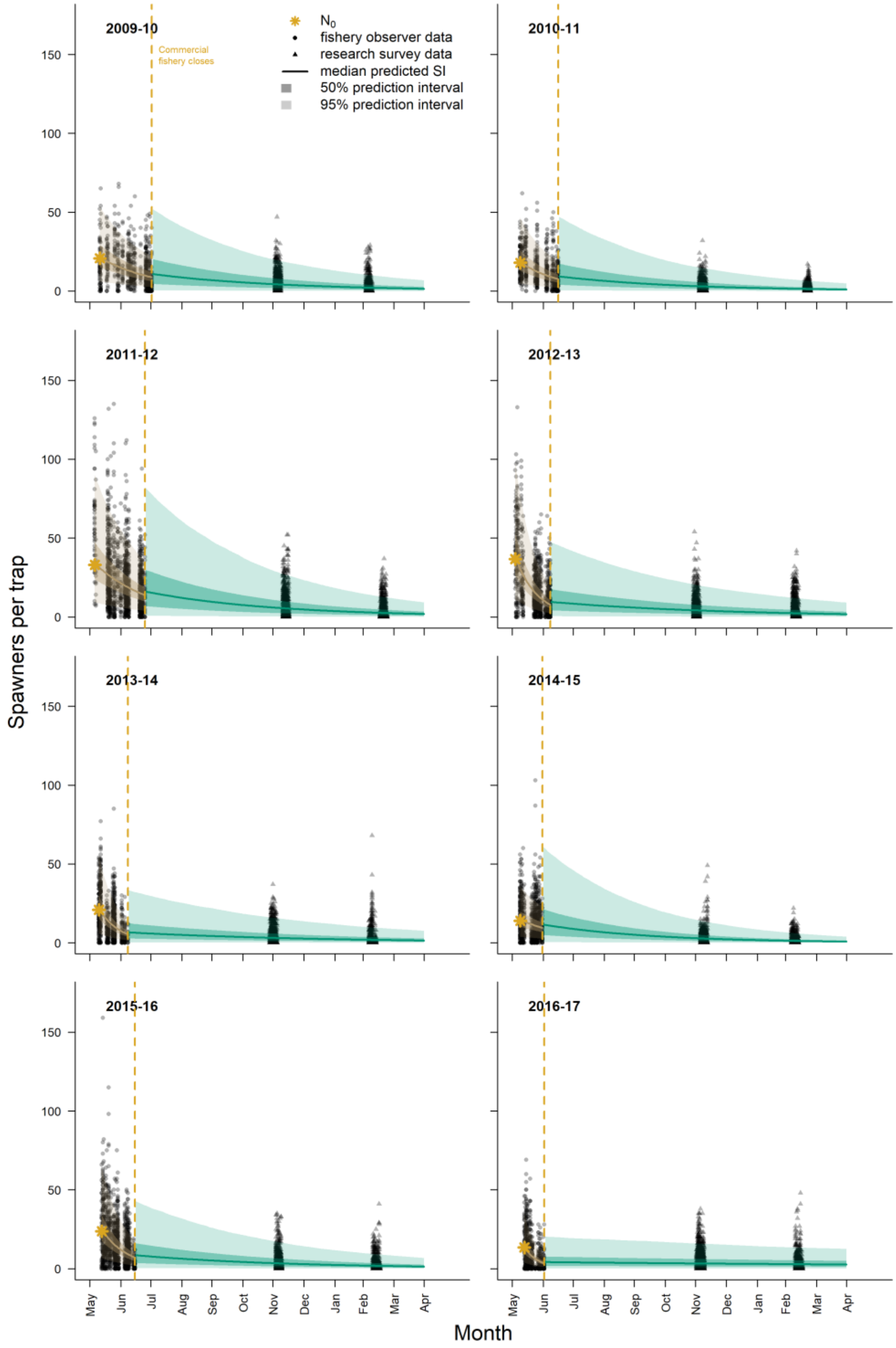

Figure C.15 Spawner Index exponential decay model fit for Howe Sound (2009-2016) including parameter uncertainty and string-level variation.

Solid lines indicate the median predicted Spawner Index on a given day of the year with polygons visualising the 50% and 95% prediction intervals encompassing uncertainty in process parameters and string-level variation estimated by the multiplicative string effect, e^{σ_f}. The disconnect in the prediction interval polygons arises because the model estimates distinct string-level variation depending on the data source (fishery data vs. survey data). Black points (fishery data) or triangles (survey data) indicate raw trap-level Spawner Index counts.

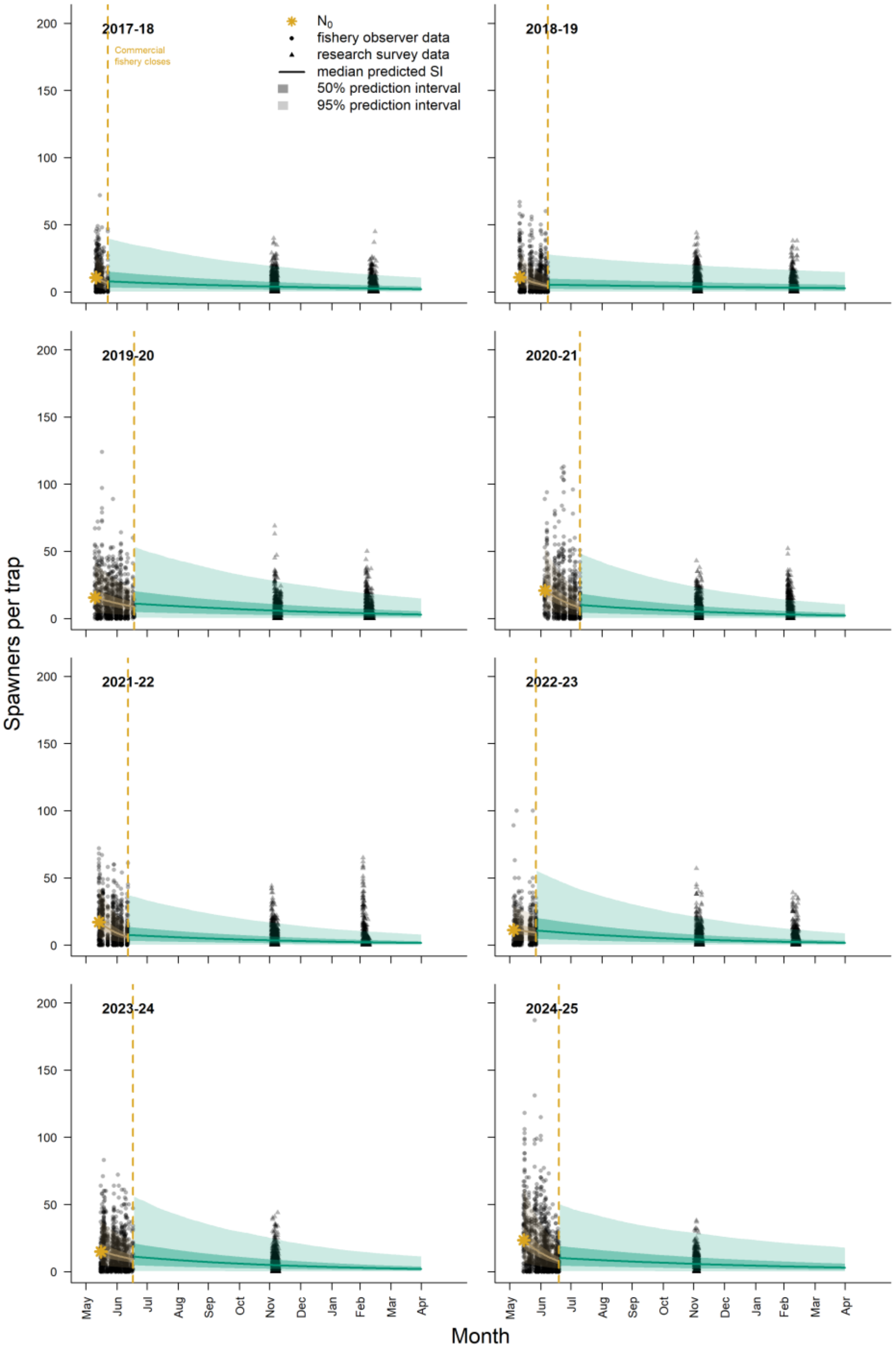

Figure C.16 Spawner Index exponential decay model fit for Howe Sound (2017-2024) including parameter uncertainty and string-level variation.

Solid lines indicate the median predicted Spawner Index on a given day of the year with polygons visualising the 50% and 95% prediction intervals encompassing uncertainty in process parameters and string-level variation estimated by the multiplicative string effect, e^{σ_f}. The disconnect in the prediction interval polygons arises because the model estimates distinct string-level variation depending on the data source (fishery data vs. survey data). Black points (fishery data) or triangles (survey data) indicate raw trap-level Spawner Index counts.

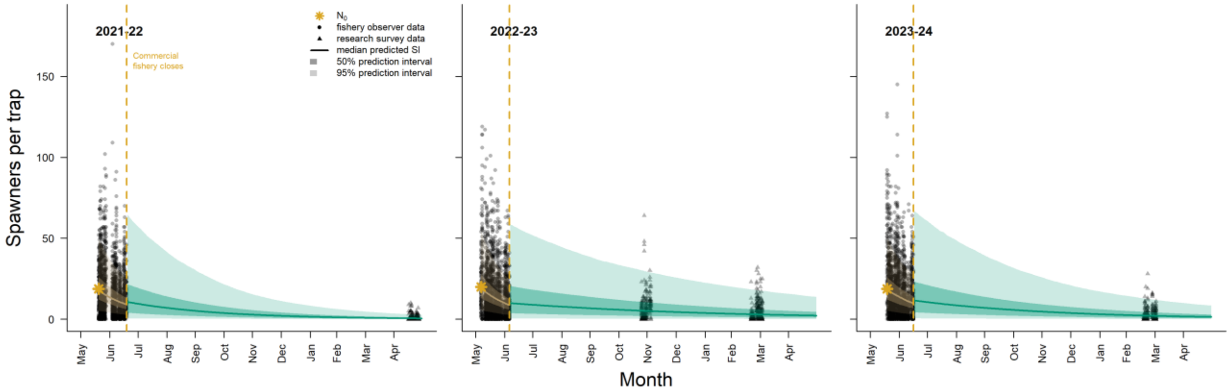

Figure C.17 Spawner Index exponential decay model fit for Broughton (2021-2023) including parameter uncertainty and string-level variation.

Solid lines indicate the median predicted Spawner Index on a given day of the year with polygons visualising the 50% and 95% prediction intervals encompassing uncertainty in process parameters and string-level variation estimated by the multiplicative string effect, e^{σ_f}. The disconnect in the prediction interval polygons arises because the model estimates distinct string-level variation depending on the data source (fishery data vs. survey data). Black points (fishery data) or triangles (survey data) indicate raw trap-level Spawner Index counts.

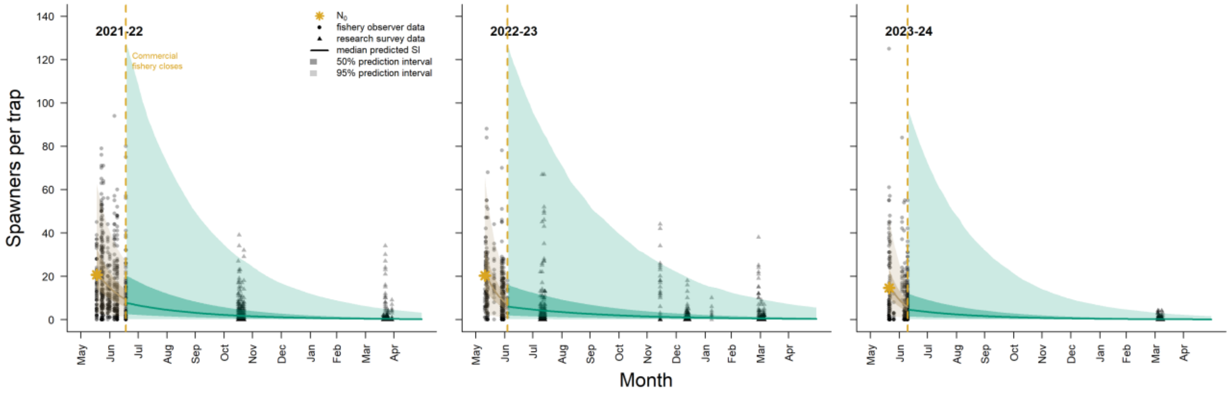

Figure C.18 Spawner Index exponential decay model fit for Central Coast (2021-2023) including parameter uncertainty and string-level variation.

Solid lines indicate the median predicted Spawner Index on a given day of the year with polygons visualising the 50% and 95% prediction intervals encompassing uncertainty in process parameters and string-level variation estimated by the multiplicative string effect, e^{σ_f}. The disconnect in the prediction interval polygons arises because the model estimates distinct string-level variation depending on the data source (fishery data vs. survey data). Black points (fishery data) or triangles (survey data) indicate raw trap-level Spawner Index counts.