Abstract

Catches from bottom longline surveys are used to construct relative abundance indices for many demersal species. Due to their careful design, survey-based relative abundance indices are assumed to be proportional to the true species abundance. However, longlines catches may be affected by interspecific competition, gear saturation, and fine-scale gear and species interactions created by feeding behaviours and habitat preferences. A hook-based relative abundance index, the instantaneous rate of bait loss per species ($\lambda_s$), which accounts for hook competition and gear saturation, may resolve some of the problems with the common catch per unit effort (CPUE) index. I evaluated whether a linear or non-linear relationship exists between the $\lambda_s$ index and abundance, and whether assumptions about bare hooks, species behaviours and fine-scale habitat affect the $\lambda_s$ index. Using longlines targeting Yelloweye Rockfish (Sebastes ruberrimus) and Quillback Rockfish (S. maliger) in the inside waters of Vancouver Island, British Columbia, Canada, as a case study, I compared longline catches with underwater observations of the hooks and surrounding species from a Remotely Operated Vehicle in March ($n = 13$) and August ($n = 12$) of 2010. The results did not refute a linear model between the $\lambda_s$ index and observed density, when compared to a non-linear model, except for the August Yelloweye index. The $\lambda_s$ index did have a better fit with observed density than CPUE for Yelloweye, but not for Quillback. Adding hook-level habitat into the $\lambda_s$ index improved the fit for Yelloweye, but not for Quillback. Additionally, observations showed that bare hooks were mainly due to non-target species, including large invertebrates. The annual $\lambda_s$ index for the rockfish survey was estimated under different scenarios for bare hooks and species interactions, but the trends in the $\lambda_s$ index were robust. Trends in the $\lambda_s$ index differed from CPUE trends in some areas. My research results cast some doubt on the assumption that for a few inshore rockfish the $\lambda_s$ index is consistently linearly related to abundance. Caution needs to be taken in extrapolating these results to other situations, as the experiments occurred in a small area and incorporated limited seasonal and temporal variation.
Lay Summary

Fisheries management often depends on scientific fishing surveys to provide measures of how fish abundance changes over time. However, surveys that use bottom longlines can be affected by fish competing for the limited number of hooks placed on the ocean floor. Using an underwater camera to observe both the longline hooks and the abundance of two common bottom-dwelling species, Yelloweye Rockfish and Quillback Rockfish, I tested if a measure of bait removal by these species consistently matched their observed abundance underwater. Bait removal better matched Yelloweye abundance than other measures and improved when habitat type was considered, but the same was not true for Quillback. These species-specific results call for caution when using this measure of bait removal to track abundance changes. Additionally, hook competition may be lower than suspected, as other frequently caught species appeared to have different habitat than the rockfish.
Preface

The overarching theme of this thesis was developed by me, based on an initial discussion with Lynne Yamanaka, formerly the Inshore Rockfish Program Head at the Pacific Biological Station, Fisheries and Oceans Canada (DFO). My supervisor, Murdoch McAllister, suggested the choice of the exponential model. My supervisor and Marie-Pierre Etienne, a visiting professor from Paris Agro-Tech in Paris, France, provided guidance on the framework of the exponential model. The aims of the thesis and questions in each chapter were developed by me, with advice from my supervisor.

The field experiments in Chapters 2, 3, and 4 were the result of collaboration with Lynne and DFO. I designed the experiments. Ship time was paid for by DFO Science, and DFO hired consultants to watch the video and map the transects from the Remotely Operated Vehicle (ROV). For the ROV video collected during the March experiment, I also watched all the video as one of the reviewers, and was the final editor for the video data. During field operations, I was the Chief Scientist aboard the longlining vessel, and collected all the catch and biological data. Lynne and Karina Cooke from DFO both acted as Chief Scientist aboard the DFO vessel operating the ROV. Lynne and Karina also reviewed the ROV video for habitat while it was live-streaming on the vessel. I calculated the area of the ROV transects, and analyzed all the ROV and longline data from the March experiment.

The August experiment in Chapter 2 was designed in collaboration with Dana Haggarty (at the time, a PhD student in Zoology), as we shared the data collected on the paired fishing vessels. DFO Science paid for the ship time, and DFO hired consultants to watch the video and map the
transects. Dana was the Chief Scientist aboard the DFO vessel operating the ROV. Lynne and I swapped off as Chief Scientist on the DFO vessel operating the longline gear. I analyzed the processed ROV data provided to me by Dana, and analyzed all the longline data.

The data from Annual Inshore Rockfish Longline Survey in Chapter 3 was provided by Lynne and Karina. I was a crew member, and sometimes the Chief Scientist, during some or all of the longline sets in 2008-2012 and again in 2015. I analyzed the data from the survey for Chapter 3.

I wrote the code and performed all the statistical analyses in Chapters 2, 3, and 4. Henry Chen and Md Rashedul Hoque, students in the UBC Fall 2016 STAT 551 course, provided feedback on my proposed statistical methods in Chapter 4 and suggested the use of Generalized Estimation Equations.

I wrote all the parts of the manuscripts in Chapter 2, 3, and 4. DFO provided financial support during the manuscript preparation for Chapter 4.
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<td>Non-linear</td>
</tr>
<tr>
<td>PFMA</td>
<td>Pacific Fishery Management Areas</td>
</tr>
<tr>
<td>PAEK</td>
<td>Polynomial Approximation with Exponential Kernel</td>
</tr>
<tr>
<td>ROV</td>
<td>Remotely Operated Vehicle</td>
</tr>
<tr>
<td>SCUBA</td>
<td>Self-Contained Underwater Breathing Apparatus</td>
</tr>
<tr>
<td>UTM</td>
<td>Universal Transverse Mercator Coordinate System</td>
</tr>
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#### Catch Categories Abbreviations:

- **E**: Bare Hooks
- **O**: Other Species
- **Q**: Quillback Rockfish (*Sebastes maliger*)
- **Y**: Yelloweye Rockfish (*Sebastes ruberrimus*)

#### Habitat Variable Abbreviations:

- **BIO**: Biota
- **DEP**: Depth
- **REL**: Vertical Relief
- **SC**: Substrate-Complexity
List of Symbols

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
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<tr>
<td>$\lambda$</td>
<td>instantaneous rate of bait loss due to all sources (h$^{-1}$)</td>
</tr>
<tr>
<td>$\lambda_s$</td>
<td>instantaneous rate of bait loss per species (h$^{-1}$)</td>
</tr>
<tr>
<td>$\lambda_s^D$</td>
<td>$\lambda_s$ estimated from per set observations made on the deck (h$^{-1}$)</td>
</tr>
<tr>
<td>$\lambda_s^W$</td>
<td>$\lambda_s$ estimated from per hook observations made underwater (h$^{-1}$)</td>
</tr>
<tr>
<td>$\lambda_s^{W-PI}$</td>
<td>per pass $\lambda_s^W$ where all hooks on each ROV pass are included (h$^{-1}$)</td>
</tr>
<tr>
<td>$\lambda_s^{W-PC}$</td>
<td>per pass $\lambda_s^W$ where the hooks included are conditional on the previous ROV pass (h$^{-1}$)</td>
</tr>
<tr>
<td>$\lambda_s^{D-H}$</td>
<td>habitat-adjusted $\lambda_s^D$ index for each hook (h$^{-1}$)</td>
</tr>
<tr>
<td>$\overline{\lambda_s^{D-H}}$</td>
<td>average hook-level $\lambda_s^{D-H}$ value across all hooks on the set</td>
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<tr>
<td>$\lambda_s^{D-H_s}$</td>
<td>set-level intercept for the habitat-adjusted model or $\lambda_s^{D-H}$ at the base level of each habitat variable (h$^{-1}$)</td>
</tr>
<tr>
<td>$\kappa_Y$, $\kappa_Q$</td>
<td>probability of capturing a Yelloweye Rockfish ($Y$) or Quillback Rockfish ($Q$) on the hooks</td>
</tr>
<tr>
<td>$A$</td>
<td>total area of the transect for each ROV pass underwater (m$^2$)</td>
</tr>
<tr>
<td>$a$</td>
<td>intercept for the logistic regression for probability of capture on the hooks</td>
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<tr>
<td>$AIC_c$</td>
<td>Akaike Information Criterion adjusted for small sample sizes</td>
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<td>$B$</td>
<td>coefficients for habitat variable (DEP, SC, BIO, REL) effects in the logistic regression for probability of capture of Yelloweye Rockfish and Quillback Rockfish on the hooks</td>
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<tr>
<td>$C$</td>
<td>total catch of the target species</td>
</tr>
<tr>
<td>$c_s$</td>
<td>coefficient of variation for the observed values of each abundance index</td>
</tr>
<tr>
<td>$D_s$</td>
<td>observed density of a species from the ROV (individuals/100 m$^2$)</td>
</tr>
<tr>
<td>$d$</td>
<td>distance between adjacent fov measurements corrected for the difference in depth (m)</td>
</tr>
<tr>
<td>$dd$</td>
<td>distance between adjacent fov measurements (m)</td>
</tr>
<tr>
<td>$de$</td>
<td>difference in depth between adjacent fov measurements (m)</td>
</tr>
<tr>
<td>$E$</td>
<td>fishing effort</td>
</tr>
<tr>
<td>$fov$</td>
<td>width of the field of view for the ROV or transect strip width (m)</td>
</tr>
<tr>
<td>$G$</td>
<td>abundance of the stock</td>
</tr>
<tr>
<td>$g$</td>
<td>catchability coefficient or constant of proportionality</td>
</tr>
<tr>
<td>$h$</td>
<td>shape parameter for the relationship between the abundance indices and abundance</td>
</tr>
<tr>
<td>$k$</td>
<td>number of model parameters</td>
</tr>
<tr>
<td>$m$</td>
<td>number of fov measurements included in the calculation of each ROV transect area</td>
</tr>
<tr>
<td>$N$</td>
<td>number of baited hooks deployed from the fishing vessel</td>
</tr>
<tr>
<td>$N_B$</td>
<td>number of baited hooks that are retrieved</td>
</tr>
<tr>
<td>$N_s$</td>
<td>number of hooks in category $s$</td>
</tr>
<tr>
<td>$N_Y$</td>
<td>number of hooks that caught a Yelloweye Rockfish</td>
</tr>
<tr>
<td>$N_Q$</td>
<td>number of hooks that caught a Quillback Rockfish</td>
</tr>
<tr>
<td>$N_O$</td>
<td>number of hooks that caught all other species</td>
</tr>
<tr>
<td>$N_E$</td>
<td>number of hooks that had the bait removed but did not catch a species (i.e., bare)</td>
</tr>
<tr>
<td>$N_{s*}$</td>
<td>number of hooks that caught sea stars, when observed on the deck</td>
</tr>
<tr>
<td>$N_{R*}$</td>
<td>predicted number of hooks that caught sea stars on the deck when sea star loss is accounted for</td>
</tr>
</tbody>
</table>
\( N^W_R \) number of hooks that caught sea stars, when observed on ROV Pass 3 underwater

\( q \) slope of the relationship between the abundance index and the observed density (h\(^{-1}\)·100 m\(^2\))

\( P \) number of the ROV Pass underwater

\( p_B \) probability of a hook being baited

\( p_s \) probability of a hook having one of the four categories of catch \( s \)

\( R_{\text{diff}} \) relative difference between the maximum likelihood estimate and Bayesian posterior mode of the \( \lambda^D_s \) for each longline set

\( s \) species category (Yelloweye Rockfish, Quillback Rockfish, other species or bare)

\( t \) soak time, i.e., the time the hooks spent underwater (h)

\( t_P \) time between the end of longline deployment and the end of each ROV pass (h)

\( t_x \) soak time at each hook observation (h)

\( U \) catch per unit effort (CPUE)

\( U^D_s \) catch per unit effort (CPUE) from observations made on the deck, where effort comes from the number of hooks deployed and the soak time of the longline (h\(^{-1}\))

\( v \) intercept in the relationship between the abundance index and observed density which represents the longline catch when the density observed by the ROV is zero (h\(^{-1}\))

\( w \) probability of successfully escaping the hook with the bait

\( X, Y \) coordinates for the position of the ROV (in UTM)

\( z \) proportion of the hooks without catch that are bare (i.e., unbaited) on each longline set

\( zL \) proportion of baited hooks observed on the deck that lost sea stars during retrieval of the longline set
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The completion of this PhD required support from an entire village. I would like to thank my long-time mentor, Lynne Yamanaka, formerly the Inshore Rockfish Program Head at the Pacific Biological Station, Fisheries and Oceans Canada. Without her encouragement, I would not have returned to graduate school to do my PhD. Without her participation, the many field experiments hidden behind this thesis would not have been possible. Without her support, I may not have finished this thesis.

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Go STEM!

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For my parents, Bob and Lynn.
Chapter 1: General Introduction

1.1 Fisheries abundance indices

Fisheries are managed to meet a range of explicit, or implied, management objectives, often aimed at maximizing the sustainable yield for a single species (Hilborn and Walters 1992, Jennings et al. 2001, Maunder et al. 2006b). Stock assessments guide management decisions by providing advice on how fish stocks may respond to different management actions (Hilborn and Walters 1992, Jennings et al. 2001, Walters and Martell 2004). These assessments frequently use catches from commercial fisheries and fishery-independent surveys as abundance indices, in order to determine trends in the stock abundance and to estimate parameters for the assessment, including recruitment and mortality parameters (Gulland 1955, Beverton and Holt 1957, Hilborn and Walters 1992, Jennings et al. 2001, Walters and Martell 2004).

One of the most common catch-based abundance indices is the catch per unit effort (U, CPUE):

\[ U = \frac{C}{E} = g \cdot G \]  

Eq. 1.1

where the ratio of the total catch of the target species (C) and the fishing effort (E) is proportional to the abundance of the stock (G), with a constant catchability (g) (Ricker 1940, Ricker 1944, Gulland 1955, Beverton and Holt 1957). However, non-linear relationships between commercial CPUE and abundance are frequently observed for both pelagic and demersal species (Pope and Garrod 1975, MacCall 1976, Peterman and Steer 1981, Bannernot and Austin 1983, Winters and Wheeler 1985, Angelsen and Olsen 1987, Crecco and Overholtz 1990, Harley et al. 2001, Robinson et al. 2015). Indeed, conditions under which commercial CPUE may no longer be proportional to abundance have been recognized for several decades.
(e.g., Ricker 1940, Gulland 1955, Beverton and Holt 1957, Gulland 1964, Paloheimo and Dickie 1964, Radovich 1976). Several studies have shown that the behavioural response of the fish population to changes in the total abundance can result in a non-linear relationship with commercial CPUE (e.g., Paloheimo and Dickie 1964, Winters and Wheeler 1985, MacCall 1976, Crecco and Overholtz 1990, Rose and Kulka 1999). The theoretical model of Paloheimo and Dickie (1964) indicated that unless the within-school density of schooling species decreases with abundance, then the catchability coefficient will be negatively related to abundance and commercial CPUE will no longer be proportional to abundance. A negative relationship between the catchability coefficient and abundance has been established for Atlantic Cod (Gadus morhua, Pope and Garrod 1975, Rose and Leggett 1991, Swain et al. 1994), Pacific Sardine (Sardinops sagax, MacCall 1976) and Haddock (Melanogrammus aeglefinus, Crecco and Overholtz 1990).

As abundance decreases, many schooling species contract the extent of their overall spatial distribution to maintain the density in their schools, or aggregations, or to maintain the density on particular habitats, such as prey patches (e.g., Winters and Wheeler 1985, Crecco and Overholtz 1990, Rose and Leggett 1991, Swain and Sinclair 1994). It is this density-dependent range contraction that has the greatest effect on the catchability coefficient (Swain and Sinclair 1994). This behaviour can maintain commercial CPUE at high levels as abundance decreases, if fishing vessels are efficient at locating fish aggregations (e.g., see the description of the development of the Pacific Sardine fishery off California in Radovich (1976)). For Atlantic Cod in the Northwest Atlantic, the density of their aggregations actually increased in some areas as their abundance declined, which increased the commercial CPUE (Rose and Kulka 1999). Additionally, fish behaviour, such as territoriality (e.g., Robinson et al. 2015), boldness/timidity (e.g., Biro and Post 2008, Alós et al. 2015) and learning to avoid gear (Fréon et al. 1993) may
cause vulnerability to capture to vary among individuals. Such fish behaviours could cause commercial or survey CPUE to no longer reflect abundance, if the vulnerable individuals are removed first, leaving a pool with increasing numbers of invulnerable individuals. However, in comparing the results of their spatial multispecies model to published stock assessments, Walters and Bonfil (1999) found that while only a small portion of several groundfish stocks appeared to be vulnerable to capture by trawl gear at any time, exchange with areas outside the fishery must happen quickly, as no evidence of local depletion was observed.

For commercial CPUE to be proportional to abundance, fishing effort is assumed to be randomly distributed and each unit of effort is assumed to act independently (Beverton and Holt 1957, Paloheimo and Dickie 1964, Radovich 1976). However, fishing effort is generally non-random, as fishing vessels concentrate their effort on fish aggregations (Paloheimo and Dickie 1964), including overwintering, migrating and spawning aggregations (e.g., Winters and Wheeler 1985, Swain et al. 1994, Fonteneau and Richard 2003). In addition, factors like desirability of the location, fishing costs (e.g., Eales and Wilen 1986, Holland and Sutinen 1999, Salas et al. 2004) and management changes (e.g., Maunder et al. 2006b, Branch and Hilborn 2008, Poos et al. 2009) can all affect decisions on fishing locations and effort allocation. Fishing vessels are expected to efficiently locate aggregations and may share information on the location (Gatewood 1984, Eales and Wilen 1986, Palmer 1991, Ruttan 2003), which creates non-random search patterns and could cause commercial CPUE to no longer be proportional to abundance (e.g., Paloheimo and Dickie 1964, Crecco and Overholtz 1990, Hilborn and Walters 1992, Gaertner and Dreyfus-Leon 2004). Additionally, time spent handling catches (Cooke and Beddington 1984, Hilborn and Walters 1992), angler skill (Bannernot and Austin 1983), misreporting of catches (Pope and Garrod 1975), interactions of fishing operations among
fishing vessels (Gillis and Peterman 1998, Swain and Wade 2003), and saturation of the gear with catch (e.g., Gulland 1955, Murphy 1960, Rothschild 1967, Radovich 1976, Cooke and Beddington 1984) can all result in a non-linear relationship between commercial CPUE and abundance.

A non-linear relationship between commercial CPUE and abundance can result in misinterpretation of the trends in the abundance index. Changes in abundance may be underestimated because the commercial CPUE decreases more slowly than abundance (i.e., hyperstability of the index) or overestimated because the commercial CPUE decreases more quickly than abundance (i.e., hyperdepletion of the index; Hilborn and Walters 1992). Hyperstability has been demonstrated in the CPUE of a number of commercial (MacCall 1976, Crecco and Overholtz 1990, Rose and Kulka 1999, Harley et al. 2001) and recreational fisheries (Peterman and Steer 1981, Bannernot and Austin 1983, Erisman et al. 2011), as has hyperdepletion (Hilborn and Walters 1992, Harley et al. 2001, Fonteneau and Richard 2003, Walters 2003). In a meta-analysis of 209 trawl and seine data sets, Harley et al. (2001) found that most displayed hyperstability (70%), with a few displaying hyperdepletion (30%). Early on, Pope and Garrod (1975) and Ulltang (1980) pointed out that both effort-based and catch-based fisheries management would be affected by a non-linear relationship between commercial CPUE and abundance, due to an erroneous understanding of either the abundance trend or the impact of a unit of effort on different stock sizes. Hyperstability in an abundance index can be particularly dangerous for fisheries management, as serious declines in abundance are not reflected proportionally in the abundance index. Such a situation contributed to the collapse of Atlantic Cod, as spatial aggregation of both the fish and trawl fleet resulted in a hyperstable commercial CPUE index, which together with other factors led to management advice that contributed to the
eventual collapse of the stock (Walters and Maguire 1996, Rose and Kulka 1999).

Many of the issues leading to non-linear relationships between commercial CPUE and abundance are expected to be removed when abundance indices are developed from the catch of fishery-independent surveys (Gulland 1955, Hilborn and Walters 1992, Gunderson 1993, Swain and Wade 2003). A well-designed survey should cover the entire geographic distribution of the species, randomly sample within the survey area and employ a sampling gear to which the target species is completely vulnerable (Hilborn and Walters 1992, Gunderson 1993). Generally, the size of the area surveyed is large enough for spatial heterogeneity to exist in the target species abundance, as survey catch rates can be affected by salinity, temperature and depth (e.g., Smith 1990, Swain et al. 2000). Spatial heterogeneity can be reduced by dividing the survey area into strata where the species abundance is expected to be fairly homogeneous and then sampling separately within each substratum to generate estimates that can be weighted into a final abundance index (Hilborn and Walters 1992, Gunderson 1993, Kimura and Somerton 2006). For example, surveys are often stratified by depth (e.g., Kimura and Zenger 1997, Ault et al. 1999, Lochead and Yamanaka 2007), habitat type (e.g., O’Connell and Carlile 1993, Ault et al. 1999, Yoklavich et al. 2007), or geographic area (e.g., Hilborn and Walters 1992, Kimura and Somerton 2006, Lochead and Yamanaka 2007). However, even if surveys operate consistently over time and changes in fishing operations are corrected for in the time series (e.g., Kimura and Zenger 1997, Pelletier 1998, Somerton and Kimura 2006), survey design cannot correct for issues inherent to the particular type of gear employed in the survey (Gulland 1955, Gunderson 1993) or issues due to changes in the behaviour (Fréon et al. 1993), size, or spatial distribution of the target species (Swain et al. 1994, Walters and Martell 2004). For example, Godø et al. (1999) observed that the fish density in front of the trawl gear affected vulnerability, with greater escape
from the net at lower densities. Additionally, Capelin (*Mallotus villosus*) in the Northwest Atlantic exhibited changes in their vertical distribution and reduced vertical migrations coincident with declines in population abundance, which may have changed their detection in surveys (Mowbray 2002).

### 1.1.1 Abundance indices from bottom longline gear

Surveys employing longline gear may be highly susceptible to issues resulting from the choice of gear. Many authors have noted the potential for longline gear to become saturated (e.g., Gulland 1955, Beverton and Holt 1957, Murphy 1960, Rothschild 1967, Cooke and Beddington 1984, Somerton and Kikkawa 1995, Quinn and Deriso 1999, Ward 2008), which could result in hyperstability in the survey CPUE index, as the index may be insensitive to changes in the abundance at higher densities due to a lack of available hooks. Furthermore, longline catches depend on fish detecting the baited hooks, locating and moving to the hooks, attacking the bait and becoming hooked upon attacking (reviewed in Løkkeborg 1994, Stoner 2004, Løkkeborg *et al.* 2010 and Løkkeborg *et al.* 2014). Laboratory and field studies suggest that the rate of attacks and successful hooking can be quite low (e.g., 1.2 % of observed fish in He (1996)) and depends on the species, possibly due to species-specific differences in prey preferences and feeding behaviour (Løkkeborg *et al.* 2010). Additionally, bait type and size (e.g., Allen 1963, Løkkeborg 1990, Johannessen *et al.* 1993, Løkkeborg and Bjordal 1995, Ingólfsson *et al.* 2017), hook type and size (e.g., Huse and Fernö 1990, Sousa *et al.* 1999, Gregalis *et al.* 2012, Leaman *et al.* 2012), temperature (e.g., Stoner 2004, Stoner and Strum 2004, Stoner *et al.* 2006), light intensity (e.g., Stoner 2003), time of day (e.g., Fernö *et al.* 1986, Løkkeborg *et al.* 1989, Løkkeborg and Pina 1997, Løkkeborg and Fernö 1999, Ward *et al.* 2004), season (e.g., Fernö *et al.* 1986, Løkkeborg
et al. 1989), currents (e.g., Fernö et al. 1986, Løkkeborg et al. 1989, Løkkeborg and Pina 1997), tides (e.g., Løkkeborg et al. 2014), visibility (e.g., Stoner 2004), availability of natural prey (e.g., Bertrand et al. 2002, Steingrund et al. 2009) and hunger (Løkkeborg et al. 1995, Stoner 2003) can all affect the attraction and retention of fish by the longline gear. Several of these variables can be controlled for in the survey design and with a consistent survey protocol over time (Kimura and Somerton 2006). For example, fishing time can be limited to maximize catch and reduce loss of fish from the hooks (e.g., Skud 1978, Ward et al. 2004, Ward and Myers 2007). However, longline catch can also be affected by variation in the species and individuals in the vicinity of the longline gear, due to interactions among individuals of the target species and between the target species and non-target species (reviews by Løkkeborg 1994, Stoner 2004, Løkkeborg et al. 2010). It seems unlikely that the effect of these interactions on the abundance index can be entirely removed by the survey design or by stratification.

Feeding behaviours driven by competition and predation can also influence the catch of longline gear (reviewed in Løkkeborg and Bjordal 1992, Stoner 2004, Løkkeborg et al. 2010). Intraspecific competition for bait has been observed among Pacific Halibut (Hippoglossus stenolepis, Stoner and Ottmar 2004), Atlantic Cod (Løkkeborg and Bjordal 1992), Whiting (Gadus merlangus, Fernö et al. 1986) and Greenland Halibut (Reinhardtius hippoglossoides, Huse et al. 1999). Interspecific competition for bait has been observed between Atlantic Cod and Haddock (Fernö et al. 1986), and between wolfish (Anarhichas sp.), Atlantic Cod and Haddock (Godø et al. 1997). Stoner (2004) classified competition for bait as one of two types: (1) exploitative competition, where some competitors are better at taking the bait than others; and (2) interference competition, where some competitors prevent others from accessing the bait. For example, longline catch rates for Giant Grenadier (Albatrossia pectoralis), Shortraker Rockfish
(Sebastes borealis) and Rougheye Rockfish (S. aleutianus) in the Gulf of Alaska decreased with increasing catches of Sablefish (Anoplopoma fimbria), while trawl catches in the same area did not, likely because Sablefish are more mobile and aggressive, making them a more effective competitor (Rodgveller et al. 2008). Robinson et al. (2015) also observed that competition for bait between two species of groupers (Epinephelidae spp.) resulted in the near exclusion of one species from commercial angling gear. Exploitative competition may also be size-based, where larger individuals can outcompete smaller ones for bait (e.g., Hamley and Skud 1978, Løkkeborg and Bjordal 1992, Engås et al. 1996, Huse et al. 1999, Stoner and Ottmar 2004). Alternatively, some species actively guard the bait and prevent competitors from attacking the baited hooks (Fernö et al. 1986, Løkkeborg et al. 1989, Løkkeborg and Bjordal 1992, Godø et al. 1997).

Competition may also result in increased catches, due to increased activity and attacks on the bait in the presence of other individuals (Stoner and Ottmar 2004) or due to the presence of struggling hooked fish attracting others to attack the longline gear (Fernö et al. 1986, Løkkeborg et al. 1989). Shardlow (1993) saw an exponential increase in the number of encounters between salmon and troll gear as the observed salmon density increased. Additionally, predation risk may influence capture on the longline gear. Foraging arena theory asserts that prey organize into spatially heterogeneous vulnerable and invulnerable pools (e.g., schooling, in shallower habitat, in areas with cover), where exchange to the vulnerable pool and feeding activity depend on the predation risk (Ahrens et al. 2012). Furthermore, foraging arena theory assumes that these predator-prey interactions occur on a fine spatial scale (Walters and Martell 2004, Ahrens et al. 2012). This suggests that distribution of prey along a longline may be patchy, and different patches of habitat along a longline may see different levels of feeding activity due to differences in the predation risk. Additionally, willingness to attack bait may be size-dependent, as habitat
use and diet expand with increasing size due to decreased predation risk (Mittelbach 1986, Love et al. 1991).

Several authors have speculated that interspecific competition and/or gear saturation, will affect the relationship between CPUE for longline gear and abundance (e.g., Gulland 1955, Beverton and Holt 1957, Murphy 1960, Gulland 1964, Rothschild 1967, Ricker 1975, Radovich 1976, Skud 1978, Cooke and Beddington 1984, Stoner 2004, Rodgveller et al. 2008). However, only a few studies have attempted to directly test the relationship between hook and line CPUE and abundance. Richards and Schnute (1986) tested the shape of the relationship between the CPUE from research angling and the density of fish observed using a submersible. Their model included options for the relationship to be non-proportional at low density, high density, or both. However, they found a proportional relationship between the angling CPUE and abundance of Quillback Rockfish (S. maliger), but only at certain depths, when the weather was good for angling. Haggarty and King (2006) also found a proportional relationship between research angling CPUE and the abundance of Copper Rockfish (S. caurinus) observed during SCUBA dive surveys, but did not find a proportional relationship for Quillback. They attributed this to the depth range of their experiment. To my knowledge, only Rodgveller et al. (2011) has empirically tested the relationship between longline CPUE and abundance. However, they did not find a significant proportional relationship between longline CPUE and the pooled density of Shortraker and Rougheye, which was observed with a submersible during their experiment. Although they fit a proportional model to the data, their results showed that longline CPUE was actually lower at higher densities compared with several sets at lower densities. Despite issues like interspecific competition and gear saturation, and the lack of empirical evidence for a proportional relationship between bottom longline survey CPUE and species abundance,
abundance indices for several demersal species are developed from bottom longline gear, including Pacific Halibut (Soderlund et al. 2012), Sablefish (Sigler 2000, Hanselman et al. 2016), Atlantic Halibut (Hippoglossus hippoglossus, Smith 2016), Greenland Halibut (Murua and de Cárdenas 2005, Nygaard 2014), Red Snapper (Lutjanus campechanus, Mitchell et al. 2004), Atlantic Sharpnose Shark (Rhizoprionodon terraenovae) and Bonnethead Shark (Sphyrna tiburo, Pollack and Ingram 2013) and several species of rockfish (Sebastes spp., Harms et al. 2010, Yamanaka et al. 2012a, Yamanaka et al. 2012b). Stock assessments use trends in these indices to provide fisheries management advice on stock size and quotas (e.g., Yamanaka et al. 2012a, Yamanaka et al. 2012b, Pollack and Ingram 2013, den Heyer et al. 2015, Webster and Stewart 2015, Hanselman et al. 2016).

A number of authors have proposed models for longline catches that account for interspecific competition for hooks and/or gear saturation (Gulland 1955, Murphy 1960, Rothschild 1967, Ricker, 1975, Somerton and Kikkawa 1995, Quinn and Deriso 1999). Gulland (1955) developed a deterministic exponential model for longline catches, where the catch depended on the instantaneous rate of rate of capture per hook (or removing available baited hooks). Murphy (1960) considered this model inappropriate for longline gear, as longline catch does not reach an asymptote, but instead has a maximum catch limit based on the number of hooks. He added a parameter for the loss of bait due to hooked fish escaping and a parameter for the bait dropping from the line or the catch of non-target species. Rothschild (1967) built on their models in a multispecies fishery context, assuming that the multiple possible hook states (baited, caught a target species or caught a non-target species) had a multinomial distribution. However, his model did not allow for the loss of species from the hooks once they were caught or account for loss of bait due to other sources. Ricker (1975) extended this model by allowing for bare
hooks (i.e., hooks that returned to the fishing vessel with neither bait nor a species caught on the
hook). In his model, bare hooks were only created by individuals of the target and non-target
species consuming bait without being caught. Ricker (1975) recognized that his model ignored
the possibility of bare hooks due to bait falling off the hooks or due to removal by species that
were not caught on the longline. Quinn and Deriso (1999) proposed a similar exponential model
that included rate parameters for both the capture of all species on the gear and the loss of bait
due to deterioration or uncatchable species like starfish. Similar to earlier models, Somerton and
Kikkawa (1995) accounted for hook competition and gear saturation by modelling longline catch
with a hook-based exponential model.

However, Somerton and Kikkawa (1995) proposed that instead of correcting the longline
CPUE index for the capture of other species (e.g., Rothschild 1967) that the instantaneous rate of
bait loss itself could be used as a relative abundance index that is unaffected by interspecific
competition and gear saturation. The hook-based exponential model for longline catch is derived
from the simple differential equation:

\[
\frac{dN_B}{dt} = -\lambda N_B \quad \text{Eq. 1.2}
\]

where \(\lambda\) is the instantaneous rate of bait loss from the \(N_B\) hooks still baited and fishing at time \(t\).
Over a set of duration \(t\), this model predicts that \(N_B\) hooks will still be baited at time \(t\), with \(N_B\)
given by:

\[
N_B = Ne^{-\lambda t} \quad \text{Eq. 1.3}
\]

where \(N\) is the total number of hooks deployed on the longline. The \(\lambda\) index can be separated into
species-specific components, which are treated as abundance indices for the target species.
Somerton and Kikkawa (1995) estimated the species-specific index (\(\lambda_s\)) in two ways: (1) using
catch composition; and (2) using capture times from hook timers (Somerton et al. 1988) for the target and non-target species, plus soak times for the hooks returning with bait. Soak time is the time that the hooks spend fishing in the water. They found that precision was higher when using capture times from hook timers. Additionally, when \( \lambda_s \) is estimated using catch composition the model does not correct for gear saturation. This means that during long soaks, or soaks when all the bait is removed, the model is only able to provide a lower bound for the estimate of \( \lambda_s \).

An alternative method of accounting for interspecific competition is catch-effort standardization, where the catch of other species can be included as covariates in Generalized Linear Models, Generalized Additive Models or Generalized Linear Mixed Models (e.g., Punt et al. 2001, Maunder and Punt 2004). However, Maunder and Punt (2004) caution against the use of catch covariates when the non-target species are equally influenced by the fishery, as variation in the catch of non-target species catch may obscure annual trends due to abundance of the target species. Additionally, such methods may not reflect the loss of available hooks during fishing due to all other sources of bait loss, including the return of bare hooks.

Some current stock assessments use the \( \lambda_s \) relative abundance index derived from bottom longline surveys (e.g., Yamanaka et al. 2012a, Yamanaka et al. 2012b) or correct regional survey CPUE based on the numbers of hooks returning with bait (e.g., Webster and Stewart 2015). However, the shape of the relationship between the \( \lambda_s \) index and abundance has not been directly tested. Somerton and Kikkawa (1995) found that the \( \lambda_s \) index for Pelagic Armorhead \( (Pseudopenfaceros wheeleri) \) continued to increase while survey CPUE appeared to reach an asymptote, but Haimovici and Ávila-da-Silva (2007) found very little difference between the \( \lambda_s \) index and commercial CPUE, except at the highest densities of one of the three species caught \( (Urophycis mystacea) \). Additionally, Sigler (2000) found that the capture of Sablefish on bottom
longlines only began to decrease exponentially once few baited hooks remained. The $\lambda_s$ index, which presumes that the bait location probability decreases linearly with the number of baited hooks remaining, fit Sablefish capture times from hook timers poorly compared to the model that assumed that the bait location probability decreased linearly only once a certain number of baited hooks remained (Sigler 2000). Sablefish are a mobile predator and apparently efficient at locating baited hooks, even when only a few remain (Sigler 2000). In addition to the lack of empirical evidence for a proportional relationship between the $\lambda_s$ index and abundance, many of the assumptions inherent to the model for the $\lambda_s$ index have not been tested. Finally, the $\lambda_s$ index corrects for gear saturation at the level of each longline set, whereas saturation and patchiness in species distributions are thought to occur on scales smaller than the length of the longline (e.g., Gulland 1955, Huse and Fernö 1990, Somerton and Kikkawa 1995, Ahrens et al. 2012). Clustering of catches along the longline has been seen for pelagic predators (Capello et al. 2013), which could lead to localized saturation.

This thesis focuses on empirically testing the relationship between the $\lambda_s$ index and abundance, as well as some of the model assumptions, using video from a Remotely Operated Vehicle (ROV) and catch from bottom longlines targeting the inshore rockfish species, Yelloweye Rockfish ($S. ruberrimus$) and Quillback Rockfish, in the inside waters of Vancouver Island, British Columbia (BC), Canada, as a case study (Figure 1.1).

1.2 Inshore rockfish

Yelloweye and Quillback in the inside waters of Vancouver Island, provide an excellent case study for testing the influence of interspecific competition, gear saturation and fine-scale variables on the abundance indices from bottom longline gears because of their life history, the
established use of ROVs and other visual methods for surveying rockfish species, and the current fisheries-independent longline survey and abundance indices used in their stock assessments.

Yelloweye and Quillback are very long-lived and slow-growing. Yelloweye in BC have been aged up to 121 years (Yamanaka et al. 2018) with 50% of fish reaching sexual maturity at an age of 17.2-20.3 years, depending on the region (Kronlund and Yamanaka 2001, Yamanaka et al. 2012b). Quillback in BC have been aged up to 95 years (Yamanaka and Lacko 2001), with 50% of fish reaching sexual maturity at an age of 11 years (Yamanaka and Richards 1993). Yelloweye have been recorded up to 91 cm in length, while the maximum recorded size for Quillback is 61 cm (Love et al. 2002). Annual natural mortality rates are very low and estimated at 0.04 yr\(^{-1}\) for Yelloweye (Yamanaka et al. 2018) and 0.06-0.13 yr\(^{-1}\) for Quillback, depending on the management unit (Yamanaka et al. 2012a). This makes these species particularly vulnerable to changes in mortality and slow to recover. Yelloweye and Quillback are demersal, sedentary, and found to associate with complex bottom structure, including boulder fields, rocky reefs, and rugged rock habitat (Richards 1986, O’Connell and Carlile 1993, Murie et al. 1994, Yoklavich et al. 2000, Pacunski and Palsson 2001, Love et al. 2002; Johnson et al. 2003, Yamanaka et al. 2012c, Haggarty et al. 2016), with high vertical relief (Richards 1987, Matthews 1990c, Jagielo et al. 2003, Johnson et al. 2003) and structure-forming biota (Marliave et al. 2009, Yamanaka et al. 2018). They show strong site-fidelity and limited home ranges (Coombs 1979, DeMott 1983, Matthews 1990b, Matthews 1990c). However, home range increases as habitat quality decreases (Matthews 1990b, Matthews 1990c). Their distribution is also influenced by depth (Richards 1986, O’Connell and Carlile 1993, Johnson et al. 2003). Yelloweye in BC are commonly caught between 19 to 251 m (Yamanaka et al. 2006b) and can be found in depths up to 550 m (Hart 1973), while Quillback are most commonly observed between 16 and 182 m (Yamanaka et al.
Individual size increases with depth for these species (Richards 1986, Johnson et al. 2003), as rockfish show an ontogenetic shift in depth (Love et al. 1991). These life history characteristics can make interpretation of survey indices and catch patterns for Yelloweye and Quillback challenging, as their spatial distribution is determined by habitat type and depth, creating patchiness on a both a regional and local spatial scale.

The populations in BC waters represent only a fraction of the distribution of Yelloweye and Quillback. Yelloweye are found from the Aleutian Islands to northern Baja California and Quillback are found from the Gulf of Alaska to southern California (Love et al. 2002). While there is no genetic evidence for more than one population of Quillback in BC (Yamanaka et al. 2006a), there are two populations of Yelloweye (Yamanaka et al. 2006b). The outside population of Yelloweye is located in the waters west of Vancouver Island and extends from southeast Alaska to northern Oregon. The inside population is located in the Strait of Georgia and other waters east of Vancouver Island (Yamanaka et al. 2006b, Figure 1.1). In BC waters, the Quillback population is designated as Threatened by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC, Yamanaka et al. 2012a), while both the inside and outside populations of Yelloweye are designated as Special Concern, and have been listed by the Species at Risk Act in Canada (Yamanaka et al. 2012b). Rockfish in British Columbia are protected by Rockfish Conservation Areas; 164 areas were implemented in 2007 and restrict commercial and recreational fishing (Yamanaka and Logan 2010).

Yelloweye and Quillback in BC are caught by hook and line fisheries coastwise, including commercial, aboriginal and recreational fisheries (Yamanaka and Lacko 2001, Yamanaka et al. 2006a, Yamanaka et al. 2006b). They are caught by both the directed commercial fishery and as bycatch in all other commercial hook and line fisheries on the coast,

Surveys for Yelloweye and Quillback are multispecies (e.g., Lochead and Yamanaka 2007, Olson *et al.* 2016). Yelloweye and Quillback are managed by Fisheries and Oceans Canada (DFO) as part of the inshore rockfish group. This group of species with similar life histories and depth distributions (approximately 0-200 m) also includes Copper Rockfish, China Rockfish (*S. nebulosus*), Tiger Rockfish (*S. nigrocinctus*), and Black Rockfish (*S. melanops*, Yamanaka and Lacko 2001). Several different types of fishery-independent surveys have been used to assess BC inshore rockfish populations. These include hook and line jig surveys in the northern inside waters (1986-1988, 1992, 2004), submersible surveys in the Strait of Georgia (1984, 2003), chartered industry longline vessel surveys of the outside waters population, bycatch in the International Pacific Halibut Commission (IPHC) longline survey, the annual inshore rockfish survey in inside waters (Yamanaka *et al.* 2004, Yamanaka *et al.* 2006a, Yamanaka *et al.* 2006b, Lochead and Yamanaka 2007, Yamanaka and Logan 2010) and recently ROV surveys (Martin *et al.* 2006). ROVs and submarines are often used to survey rockfish species because these species show little to no avoidance to these visual survey methods (Richards and Schnute 1986, Adams *et al.* 1995, Yoklavich *et al.* 2007, Stoner *et al.* 2008).

In the inside waters of British Columbia, relative abundance of the inshore rockfish species, excluding Black Rockfish, is currently indexed by the annual inshore rockfish longline survey. Conducted in August each year, the survey deploys bottom longline gear in random, depth-stratified, 2 km by 2 km blocks of inshore rockfish habitat. The survey covers the inside waters in 2-3 years, sampling 5-8% of the rockfish habitat in total. The most recent stock
assessments for these species use the catch from this annual survey to derive the $\lambda_s$ index (Yamanaka et al. 2012a, Yamanaka et al. 2018). On the survey, Spiny Dogfish comprise greater than 90% of the total catch (by weight) and are assumed to be a major competitor for hooks (Lochead and Yamanaka 2007). Similar to the annual inshore rockfish longline survey, the IPHC longline survey for Pacific Halibut also has large catches of Spiny Dogfish in some areas. Both Hoag et al. (1984) and Kaimmer and St.-Pierre (1993) hypothesized that large catches of Spiny Dogfish reduce the catchability for the target species, Pacific Halibut, through competition for hooks.

1.3 Aims and structure of the thesis

The main assumption of a catch-based abundance index is that the changes in the catch per unit effort of a species are due to proportional changes in the abundance of the species. However, for passive and stationary gears like bottom longlines, fish must react to the baited hooks, so both abiotic (e.g., depth, habitat structure) and biotic (e.g., competitors, predators, prey availability) ecosystem components, as well as properties of the gear (e.g., local saturation), can influence the capture of the target species and confound the influence of abundance on the index. While the potential for these influences are recognized in the literature and attempts are made to account for their effects through survey design, index standardization and the choice of abundance index (e.g., $\lambda_s$), there has been little empirical testing of alternate abundance indices and their assumptions. The main aims of this thesis are to:

(1) empirically test the shape of the relationship between the relative abundance index, $\lambda_s$, which is designed to account for interspecific competition and gear saturation, and species abundance;
(2) empirically test some key assumptions made when using the $\lambda_s$ index, including assumptions about the source of bare hooks and the stationarity of $\lambda_s$ during the soak time; and

(3) improve the $\lambda_s$ index by accounting for fine-scale habitat variables that might contribute to localized saturation or habitat suitability along the longline.

These aims are defined more fully in each of the chapters. The thesis focuses on Yelloweye and Quillback in BC, Canada, as a case study, as the current stock assessments for these species employ the $\lambda_s$ index derived from bottom longlines, and the annual longline survey appears to experience a large amount of interspecific competition for hooks, which should affect the relationship between the index and the abundance. Additionally, rockfish show strong habitat associations, are less mobile than other species caught on bottom longlines (e.g., Sablefish and Pacific Halibut) and are unlikely to be influenced by the use of the ROV when measuring underwater density. The results of this thesis should provide evidence to support or reject the use of the hook-based alternative abundance index ($\lambda_s$), and the choice of model assumptions. Additionally, the results may be used to guide survey design and data collection priorities for strongly habitat-associated species.

- Chapter 2 introduces the $\lambda_s$ relative abundance index, empirically tests whether a linear or non-linear relationship exists between the $\lambda_s$ index and the density of the rockfish species observed with a ROV, and assesses whether the fit of the relationships are an improvement on the nominal CPUE index. A Bayesian framework is used to estimate $\lambda_s$ and maximum likelihood estimation is used to fit the relationships to the indices. The assumption of stationarity of $\lambda_s$ during the soak time is also tested.
• Chapter 3 uses underwater observations of species behaviours and interactions with the longline gear to evaluate assumptions in the $\lambda_s$ index about the source of bare hooks. The underwater observations are used to create corrections for observed species interactions, which are then applied to the rockfish $\lambda_s$ indices from the annual inshore rockfish longline survey to test the influence on temporal trends in the survey indices.

• Chapter 4 investigates habitat variables (depth, substrate type, bottom complexity, vertical relief and biota) that may contribute to local saturation of the longline, by creating patchiness in the capture of Yelloweye and Quillback on a fine spatial scale, i.e., at the hook-level. The Chapter 2 model for the $\lambda_s$ index is extended to include these habitat variables and the habitat-adjusted $\lambda_s$ index is estimated and compared to the unadjusted index to see if the fit to the observed rockfish density improves. Additionally, correspondence analysis is used to identify species, or groups of species, with fine-scale habitat distributions that are similar to, or contrast with, those of Yelloweye and Quillback.
Figure 1.1. Location of the Yelloweye Rockfish (*Sebastes ruberrimus*) inside waters population off Vancouver Island, British Columbia, Canada. The solid blue lines are the northern and southern boundaries separating the inside and outside waters populations. The solid black line is the Canada-USA border.
Chapter 2: An Empirical Evaluation of Key Assumptions of a Relative Abundance Index, the Instantaneous Rate of Bait Loss

2.1 Introduction

For bottom-dwelling fish, the catch from fisheries-independent longline surveys and commercial fisheries is often used to create relative abundance indices (e.g., Mitchell et al. 2004, Murua and de Cárdenas 2005, Harms et al. 2010, Soderlund et al. 2012, Yamanaka et al. 2012b, Pollack and Ingram 2013, Nygaard 2014, Menezes et al. 2015, Hanselman et al. 2016, Smith 2016). Stock assessments use trends in these indices to provide fisheries management advice on stock size and quotas (e.g., Yamanaka et al. 2012a, Yamanaka et al. 2012b, den Heyer et al. 2015, Webster and Stewart 2015, Hanselman et al. 2016). Appropriate advice relies on the assumption that these indices are proportional to the true population abundance. However, this assumption can be incorrect for the common index, catch per unit effort (CPUE), when CPUE comes from commercial trawls (Pope and Garrod 1975, Harley et al. 2001), commercial purse seines (MacCall 1976), sport angling fisheries (Peterman and Steer 1981, Bannernot and Austin 1983) or from bottom longline surveys (Rodgveller et al. 2011). The instantaneous rate of bait loss per species ($\lambda_s$) has been proposed as an unbiased alternative to longline CPUE (Murphy 1960, Rothschild 1967, Somerton and Kikkawa 1995). Although, the $\lambda_s$ index is currently used in stock assessments (Yamanaka et al. 2012a, Yamanaka et al. 2012b), the assumption that $\lambda_s$ is proportional to population abundance (i.e., a linear relationship with an intercept of zero) has not been directly tested.

Many factors besides population abundance can influence the capture of bottom-dwelling fish and change the relationship between population abundance and the relative abundance
indices. Changes in the spatial behaviour of either the fish population or the fishing fleet can cause a commercial CPUE index to no longer proportionately reflect abundance (e.g., Rose and Leggett 1991, Maunder et al. 2006b). The commercial CPUE index may become hyperstable, declining more slowly than the population abundance (e.g., Crecco and Overholtz 1990, Harley et al. 2001). For example, as the population of northern cod (Gadus morhua) declined, increased spatial aggregation of both the fish and trawl fleet resulted in a hyperstable commercial CPUE index; this led to management advice that contributed to the eventual collapse of the stock (Rose and Kulka 1999). Carefully designed fisheries-independent surveys that cover the entire species geographic distribution of the species and apply consistent sampling protocols should avoid such hyperstable behaviour in the survey CPUE index (Hilborn and Walters 1992, Gunderson 1993). However, careful survey design will not necessarily correct for issues that are specific to the type of fishing gear.

Longline CPUE is affected by both interspecific competition for a limited number of hooks and gear saturation (e.g., Beverton and Holt 1957, Murphy 1960). When multiple species are caught on a longline, competition from non-target species can cause underestimation of the CPUE index for the target species (Rothschild 1967). Similarly, saturation of a high percentage of the hooks can lead to underestimation of the CPUE index at high levels of fish abundance. As abundance approaches the minimum level required to saturate the hooks, the CPUE index becomes insensitive to changes in the abundance. A longline index that accounts for all of the species caught and for gear saturation can help resolve these issues.

Unlike CPUE, the $\lambda_s$ index can account for all the hooks on the longline that return with catch, i.e., the total number of occupied hooks or the total longline catch. As the number of occupied hooks increases, the total abundance of all species is also expected to increase. $\lambda_s$ is
calculated from the catch of each species in proportion to the total catch or from the precise capture time for each hook (Somerton and Kikkawa 1995). For smaller catches, \( \lambda_s \) is consistent with CPUE, but as the catch increases, CPUE increases at a slower rate than \( \lambda_s \) (Somerton and Kikkawa 1995). This discrepancy between \( \lambda_s \) and CPUE may be species-specific (Haimovici and Ávila-da-Silva 2007).

One concern about the application of the \( \lambda_s \) index is that \( \lambda_s \) is assumed to be relatively constant over the soak time, which is the time the longline is fishing. However, previous studies estimating \( \lambda_s \) from precise capture times from hook timers found that \( \lambda_s \) both increased and decreased over the soak time (Somerton and Kikkawa 1995, Sigler 2000). This becomes important when extending the use of the \( \lambda_s \) index to commercial longline fisheries, where soak times can vary widely. For example, longline sets with longer soak times might result in all the hooks becoming saturated with fish or in increased fish loss from the hooks (e.g., Ward et al. 2004), which could bias \( \lambda_s \) relative to sets with shorter soak times. In such situations, \( \lambda_s \) would not reflect species abundance alone, but would also depend on soak time. Since there is a lack of knowledge about how \( \lambda_s \) might vary over the soak time, it is assumed to be constant.

To examine the hypothesis that \( \lambda_s \) is a better index than CPUE because it corrects for interspecific competition and saturation of the hooks, I used a Remotely Operated Vehicle (ROV) to observe fish density and longline catch per hook underwater. I used Yelloweye Rockfish (\textit{Sebastes ruberrimus}) and Quillback Rockfish (\textit{S. maliger}), in British Columbia (BC), Canada, as a case study because the management of these species already uses a \( \lambda_s \) index from a fisheries-independent bottom longline survey. This longline survey shows high levels of interspecific competition from a non-target species, Spiny Dogfish (\textit{Squalus acanthias}); Spiny Dogfish can occupy greater than 50% of all the hooks deployed on the survey (Lochead and
Yamanaka 2007). Additionally, rockfish generally show little to no avoidance during visual surveys (Richards and Schnute 1986, Adams et al. 1995, Yoklavich et al. 2007, Stoner et al. 2008). I predicted that: 1) there is a linear relationship between $\lambda_s$ and observed fish density; 2) $\lambda_s$ shows a better fit with observed fish density than CPUE, as measured by the coefficient of determination ($R^2$); and 3) $\lambda_s$ is not constant over the soak time. I tested these predictions by estimating the $\lambda_s$ index in a Bayesian framework, and then fitting the relationship between the $\lambda_s$ estimates and fish density using maximum likelihood estimation. I used model selection (Akaike Information Criterion) to determine whether the best model for the relationship was linear (with an intercept) or non-linear (with an intercept).

2.2 Methods

2.2.1 Data collection

To test the hypothesis that $\lambda_s$ is a better index of relative abundance than CPUE, I conducted two different field experiments; the first experiment occurred in March 2010, and the second occurred in August 2010, during the annual rockfish longline survey (Lochead and Yamanaka 2007). The second experiment was added because the levels of interspecific competition and bait loss during the March experiment were much lower than the levels previously observed on the annual rockfish survey. In both experiments, bottom longline fishing was used to catch Yelloweye and Quillback, and the ROV was used to observe total fish density. However, due to ship time constraints, the design of the two experiments differed. In the March experiment, the ROV was deployed during the longline fishing; this allowed the ROV to view both the longline hooks and the surrounding fish density. In the August experiment, the ROV
was deployed and retrieved before the longline fishing started, so the ROV could only view the fish density prior to longline fishing.

In the March experiment, 13 longline sets were fished in the Strait of Georgia area of BC, Canada, during daylight hours (Figure 2.1). During these sets, a commercial fishing vessel deployed the longline gear, while a government research vessel deployed the ROV. The captain of the commercial vessel selected fishing sites where he expected the combined abundance of Yelloweye, Quillback and Spiny Dogfish to differ, creating variation in the level of interspecific competition for hooks.

In the August experiment, 12 longline sets were fished in the Discovery Islands, Johnstone Strait and Queen Charlotte Strait areas of BC (Figure 2.1). During these sets, a government research vessel deployed the longline gear, while another government research vessel deployed the ROV. Due to the multiple objectives of the annual rockfish survey, I could only use fishing sites within the randomly-selected survey blocks that were also adjacent to Rockfish Conservation Areas (Yamanaka and Logan 2010).

2.2.1.1 Longline fishing

In both the March and August experiments, the fishing vessels deployed weighted snap longline gear with 11/32 inch diameter copolymer leaded groundline in 550 m skates. Each set had 225 #13 circle hooks. The hooks were baited with Argentinean squid (Illex sp.), and snapped onto the groundline with approximately 1.8 m of spacing between the hooks. Each longline set was deployed for approximately 120 min (range of 115-123 min). At the end of this soak time, the longline was retrieved and the state of each hook was recorded as baited, bare, species caught or unknown (i.e., the hook was missing). This allowed me to calculate CPUE and $\lambda_D$ from the
catch recorded on the deck of the vessel (Table 2.1). $\lambda_s^{D}$ indicates where $\lambda_s$ is estimated from the per set observations made on the deck.

2.2.1.2 ROV operations

To observe the density of Yelloweye and Quillback, Fisheries and Ocean Canada's (DFO) Deep Ocean Engineering Phantom HD2+2 ROV mounted with a Sony EVI 300 Zoom video camera was deployed. The position of the ROV (in UTM) was recorded every second (in GMT), as the transponder on the ROV communicated with the hydrophone pole held underneath the vessel. Haggarty et al. (2017) details the standard operations of this ROV for rockfish surveys.

In the March experiment, the ROV was deployed directly after the longline was released from the fishing vessel. During the soak time, the ROV passed over the entire length of the longline three times (Pass 1, Pass 2 and Pass 3). Each pass of the ROV took around 30 minutes (32.3 ± 4.5 min, ± standard deviation). During each pass, the ROV observed the state of each hook underwater; this gave captures times for each hook, which I used to estimate $\lambda_s^{W}$ (Table 2.1). $\lambda_s^{W}$ indicates where $\lambda_s$ is estimated from the per hook observations made underwater. I believed these underwater estimates would be more precise than the estimates from catch composition observed on deck, as Somerton and Kikkawa (1995) showed that adding capture times increased the precision of their $\lambda_s$ estimates.

In the August experiment, the ROV was deployed an average of 17.3 ± 13.0 h before the longline started fishing. The ROV transects lasted 52.4 ± 17.5 min. The ROV typically travelled perpendicular to the shore and from deep to shallow waters (Haggarty et al. 2017).
2.2.2 Analysis

2.2.2.1 Fish density

For each longline set, I calculated the density of Yelloweye and Quillback as the number of individuals seen on the video, divided by the total area surveyed by the ROV (m$^2$) and multiplied by 100 to get the observed density per 100 m$^2$. I included fish caught on the hooks in the observed density for the March experiment. Detailed methods for calculating the observed density are in Appendix A. I expected that the observed rockfish density would increase around the longline over time. Using the “lm” and “anova” functions in the base R stats package (R Core Team 2017), I tested if the timing of the ROV passes ($t_P$) had an effect ($\beta_{tP}$) on the observed density ($D$) of each rockfish species category $s$ on set $i$ ($D_{s,P,i}$), using the model:

$$\log(D_{s,P,i}) = \alpha + \beta_s + \beta_i + \beta_{tP} \cdot t_P + \varepsilon$$  
Eq. 2.1

where $t_P$ was the time when the pass over the longline gear finished, $\alpha$ was the intercept of the linear model, $\beta_s$ was the effect of the rockfish species on the observed density, $\beta_i$ was the effect of the longline set number on the observed density and $\varepsilon$ is the error in the model. Due to a few sets with zero density, a small constant ($1 \times 10^{-25}$) was added to the observed density (Kimura and Somerton 2006). The time when the pass finished did not have a significant effect on the observed density of Yelloweye or Quillback observed during the March experiment ($F_{1,63} = 1.92$, $p = 0.17$). Therefore, for the March experiment, I averaged the density observed on the three ROV passes to get the best estimate of observed density. The August experiment had only one pass along the transect; this provided a single observation of the density.
2.2.2.2 Relative abundance indices

Based on the exponential models of Rothschild (1967) and Somerton and Kikkawa (1995), λ represents the instantaneous rate of bait loss from all sources,

\[ \frac{dN_B}{dt} = -\lambda N_B \]  \hspace{1cm} \text{Eq. 2.2}

which integrates to:

\[ N_B = Ne^{-\lambda t} \]  \hspace{1cm} \text{Eq. 2.3}

where \( N \) is the number of baited hooks deployed from the fishing vessel at the start of the longline set and \( N_B \) is the number of baited hooks that are retrieved at the end of the soak time \( t \). λ is assumed to be the sum of \( \lambda_s \) for the catch of each category \( s \). This means that the number of hooks in category \( s \) at time \( t \) (\( N_s \)) can be used to determine the species-specific instantaneous rate of bait loss \( \lambda_s \) as:

\[ N_s = N \frac{\lambda_s}{\lambda} \left(1 - e^{-\lambda_s} \right) \]  \hspace{1cm} \text{Eq. 2.4}

The analytical solution for the maximum likelihood estimation (MLE) of \( \lambda_s \) is shown in Table 2.1. However, the estimates reported in this chapter are the posterior medians from Bayesian estimation of \( \lambda_s \). Bayesian estimation was used instead of MLE due to the complexity of estimating uncertainty in the \( \lambda_s \) parameters using bootstrapping and repeated numerical optimization with this data. Appendix B compares the MLE of \( \lambda_s \) to the mode of the Bayesian posterior for \( \lambda_s \) (Table B.1 - Table B.3). For the March and August experiments, I included four different categories (\( s \)) as catch: Yelloweye (\( Y \)), Quillback (\( Q \)), all other species (\( O \)) and hooks.
that had the bait removed but had not caught a species (i.e., were bare, \( E \)). \( \lambda \) is the sum of the \( \lambda_s \) categories:

\[
\lambda = \sum \lambda_s = \lambda_y + \lambda_o + \lambda_d + \lambda_E \tag{2.5}
\]

For each set in the March and August experiments, I calculated CPUE (\( U_s^D \)) and estimated the \( \lambda_s \) from the number of occurrences of category \( s \), observed when the longline returned to the deck of the fishing vessel (\( \lambda_s^D \)) (see equations in Table 2.1). For each set in the March experiment, I also estimated \( \lambda_s \) from the multiple hook observations underwater (\( \lambda_s^W \)). There were no underwater hook observations during the August experiment. The \( U_s^D \), \( \lambda_s^D \) and \( \lambda_s^W \) all represent the number of individuals of category \( s \) caught on the set. However, \( \lambda_s^D \) and \( \lambda_s^W \) account for varying captures of other species (\( \sum N_s \)) (Table 2.1).

While \( U_s^D \) and \( \lambda_s^D \) were estimated from the total catch during the longline soak time (\( \tau \)), \( \lambda_s^W \) was estimated from the underwater hook observations. For each set, I combined the hook observations from the three ROV passes into a single dataset. I expected that combining all the observations would increase the precision of the \( \lambda_s^W \) estimates. I accounted for the repeated observation of the hooks by including only hooks that remained baited at the end of the previous pass, as a new experiment. All observations from the first ROV pass (Pass 1) along the longline were included, but for the second (Pass 2) and third (Pass 3) ROV passes, hooks that had caught something, or were bare on the previous pass were removed. Estimating \( \lambda_s^W \) required a soak time for each hook observation (\( \tau_s \)). I used the clock time from the ROV video to calculate the time between release of the hook from the deck and the underwater observation. Hook observations where \( \tau_s \) could not be calculated, or the ROV was off-transect, were excluded.
To test the prediction that \( \lambda_s \) is not constant during the soak time, I estimated \( \lambda_s^W \) for the first and third ROV passes using the per pass hook observations in two different ways. First, I treated each pass as a sequential measurement of \( \lambda_s^W \) (\( \lambda_s^{W-PI} \)). All of the hooks observed on each pass were included in the estimate of \( \lambda_s^{W-PI} \). Second, I attempted to remove the influence of the previous passes by using only the hooks that remained baited at the end of the previous pass (\( \lambda_s^{W-PC} \)). In both cases, \( t_s \) was the time interval between on-deck deployment of the hook and observation of the hook underwater. \( \lambda_s^{W-PI} \) represents the \( \lambda_s \) estimated from the total bait loss occurring during a shorter (Pass 1) and a longer (Pass 3) soak time. \( \lambda_s^{W-PC} \) represents the \( \lambda_s \) estimated only from bait loss occurring early (Pass 1) or late (Pass 3) in the soak time.

### 2.2.2.3 Bayesian estimation

I used a Bayesian methodology to estimate the posterior median \( \lambda_s^D \) and \( \lambda_s^W \) (including \( \lambda_s^{W-PI} \) and \( \lambda_s^{W-PC} \)) for each longline set. I assumed that at soak time \( t \), the number of hooks that were still baited (\( N_B \)) or had caught a Yelloweye (\( N_Y \)), Quillback (\( N_Q \)), another species (\( N_O \)) or were bare (\( N_E \)), followed a Multinomial distribution:

\[
\left( N_B, N_Y, N_Q, N_O, N_E \right) \sim M(N, p = (p_B, p_Y, p_Q, p_O, p_E))
\]

where \( p \) is the probability of a hook being baited (\( p_B \)) or in one of the four categories of catch (\( p_s \)), and is specified as:

\[
p_B = e^{-\lambda_s t}
\]

\[
p_s = \frac{\lambda_s}{\lambda} \left( 1 - e^{-\lambda t} \right)
\]
with

$$p_B + p_Y + p_Q + p_O + p_E = 1$$  \hspace{1cm} \text{Eq. 2.9}

For $\lambda^w_s$, where the hook observations from the three ROV passes were combined together, each hook was treated as an individual trial. Each hook was recorded as being baited or in one category of catch at time $t_s$ (e.g., 0, 1, 0, 0, 0 for a Yelloweye on the hook), the soak time for the observed hook, and followed the Multinomial distribution:

$$\left(N_B, N_Y, N_Q, N_O, N_E\right) \sim M\left(1, p = (p_B, p_Y, p_Q, p_O, p_E)\right)$$  \hspace{1cm} \text{Eq. 2.10}

For hook observations from the second and third ROV passes, I made the probabilities in the vector $p$ (Eqs. 2.7 - 2.8) conditional on the previous pass by adjusting the hook soak times ($t_s$ values). For hooks observed on Pass 2 and Pass 3, $t_s$ was the time since the hook was observed on the previous pass, instead of the time since the hook left the deck. For example, for observations from Pass 2, I calculated the conditional probability of a hook being baited on Pass 2, given it was baited on Pass 1 ($p_{B|B_{\text{Pass 1}}}$) by modifying Eq. 2.7 as:

$$p_{B|\text{Pass 2}|B_{\text{Pass 1}}} = e^{-\lambda \left(t_s^{\text{Pass 2}} - t_s^{\text{Pass 1}}\right)}$$  \hspace{1cm} \text{Eq. 2.11}

I estimated the posterior median $\lambda^B_s$ and $\lambda^w_s$ using WinBUGS 1.4 (Lunn et al. 2000) called from within the R statistical software (R Core Team 2017) using the R2WinBUGS package (Sturtz et al. 2005). I set the prior distribution for each $\lambda_s$ as:

$$\lambda_s \sim \text{exponential (7.5 h}^{-1}\text{)}$$  \hspace{1cm} \text{Eq. 2.12}
which provided a prior distribution with a realistic maximum, while ensuring that the instantaneous rate of bait loss could not be negative. I selected a rate parameter of 7.5 h\(^{-1}\) as this resulted in a post-model pre-data distribution (McAllister 2014) mean of 0.4 for \(p_B\); this is similar to the average proportion of baited hooks on the British Columbia fisheries-independent longline survey (Lochead and Yamanaka 2007). I tested for sensitivity of the posterior distributions to the prior rate parameter, by changing the prior rate parameter to 0.17 h\(^{-1}\) (mean \(p_B = 3.08 \times 10^{-5}\)) and 25 h\(^{-1}\) (mean \(p_B = 0.73\)), and estimating \(\lambda^0_s\) for each set (Appendix B, Figure B.1 - Figure B.12). I used Markov Chain Monte Carlo (MCMC) methods to take 200,000 samples (two Markov chains) from the joint posterior distribution for the \(\lambda_s\) parameters, after removing the first 15,000 samples from each chain. For each MCMC run, I checked whether the chains had approached a stationary distribution using the Gelman-Rubin convergence statistics in the R coda package (Plummer et al. 2006). The Gelman-Rubin convergence statistics (Gelman et al. 2004) were <1.1 for all parameters. I also tested that the posterior distribution was approximated with sufficient precision (MC error was less than 5% of the posterior standard deviation (Powers and Xie 2008)) and the chains showed satisfactory mixing (i.e., the chains did not show strong autocorrelation). Finally, I visually inspected the trace plots and posterior distributions of each parameter under the base conditions (Appendix B, Figure B.13 - Figure B.24).

### 2.2.2.4 Model fits for the relative abundance indices and observed density

To test the first prediction, that a linear relationship exists between the median posterior estimates of \(\lambda_s\) and the observed rockfish density \((D_s)\), I fit both linear:

\[
\lambda_s = q_s \cdot D_s + v_s
\]  

Eq. 2.13
\[ U_s = q_s \cdot D_s + v_s \]  
Eq. 2.14

and non-linear asymptotic models:

\[ \lambda_s = q_s \cdot D_s^h + v_s \]  
Eq. 2.15

\[ U_s = q_s \cdot D_s^h + v_s \]  
Eq. 2.16

for both the posterior median \( \lambda_s \) and CPUE \( (U_s) \) and compared the parameter values and model fits. \( q \) is the slope of the relationship between the relative abundance index and the observed density, \( h \) is the shape parameter, to account for hyperstability or hyperdepletion (Hilborn and Walters 1992), and the intercept \( (v) \) accounts for rockfish captures when zero rockfish were observed by the ROV. Due to the design of the March and August experiments, I fit a linear model with an intercept instead of a proportional model without an intercept. I assumed that rockfish could still be caught by the longline when zero rockfish were observed by the ROV because the ROV might not have observed all the fish in the area sampled by the longline, and because some sets in the August experiment had a large delay between the ROV observation and the longline fishing. I estimated the model parameters using maximum likelihood estimation. All three parameters were constrained to be non-negative. I constrained \( v \) to be non-negative in order to prevent the models from predicting negative values for the response variables, \( \lambda_s \) and \( U_s \). Additionally, \( v \) was constrained to be non-zero \( (v \geq 1 \times 10^{-18}) \), where necessary to arrive at a stable solution. Due to the small sample sizes at higher observed densities, the variances of the residuals showed heteroscedasticity when assuming a normal distribution for \( \lambda_s \) and \( U_s \). I corrected this by using weighted-MLE, where the error in the predicted values of \( \lambda_s \) and \( U_s \) for each set \( j \) was treated as normally distributed with a variance \( (\sigma^2_{s,j}) \) of:
\[ \sigma^2_{s,j} = (c_s \cdot \text{predicted} \lambda_{s,j})^2 \]  
\[ \sigma^2_{s,j} = (c_s \cdot \text{predicted} U_{s,j})^2 \]

where \( c_s \) is the coefficient of variation for all the observed values of the index and is estimated along with the other parameters (see McAllister et al. 1994). I selected the best model by comparing Akaike Information Criterion (AIC) values (Akaike 1992) corrected for bias due to small sample sizes (AIC\(_c\)) as:

\[ AIC_c = AIC + \frac{2k^2 + 2k}{n - k - 1} \]

where \( n \) is the sample size and \( k \) is the number of parameters in the model (Burnham and Anderson 2002).

To test the second prediction that \( \lambda_s \) has a better fit, than CPUE \( (U_s^D) \), with the observed rockfish density, I computed the coefficient of determination \( (R^2) \) for both the linear and non-linear models and compared them between the two indices. The \( R^2 \) values represent the variance in the \( \lambda_s \) and CPUE \( (U_s) \) indices that can be explained by the variance in the observed rockfish density.

Finally, I tested the third prediction, that \( \lambda_s \) is not constant over the soak time, by comparing the posterior median estimates of \( \lambda_s^W \) for Pass 1 and Pass 3, for both the \( \lambda_s^{W-PL} \) and \( \lambda_s^{W-PC} \) data treatments. Using the “t.test” function in the base R stats package (R Core Team 2017), I used a paired t-test to determine whether the posterior median estimates of \( \lambda_s^{W-PL} \) and \( \lambda_s^{W-PC} \) indices differed significantly between Pass 1 and Pass 3 for Yelloweye and Quillback.
2.3 Results

During the March experiment, the ROV observed more Quillback (2.9 individuals per 100 m$^2$) than Yelloweye (1.3 individuals per 100 m$^2$) on average for all three passes; density was observed concurrently with the longline fishing and included fish caught on hooks. Yelloweye density varied more than Quillback density; the coefficients of variation (CV) were 71.7% and 63.1%, respectively. Similarly, during the August experiment, a higher density of Quillback (1.5 individuals per 100 m$^2$) than Yelloweye (0.1 individuals per 100 m$^2$) was observed; density was observed prior to the longline fishing. Again, Yelloweye density varied more (CV = 128.1%) than Quillback density (CV = 83.4%). However, these densities were lower and more variable than those observed in March, particularly for Yelloweye. On most sets in March, more Yelloweye and Quillback were observed than caught on the longline. In August, more Quillback were observed than caught, but more Yelloweye were caught than were observed on the transects.

Despite differences in the mean observed density, the mean number of Quillback and Yelloweye caught were similar. In the March experiment, an average of 8.2 ± 5.1 Quillback (± standard deviation) and 8.6 ± 4.7 Yelloweye were caught per set. In the August experiment, an average of 3.5 ± 2.5 Quillback and 3.3 ± 5.6 Yelloweye were caught per set. Across all the sets, a larger number of hooks returned bare in the August experiment (38.1%), than in the March experiment (27.4%), with a higher mean number of Spiny Dogfish caught in the August experiment (39.5 ± 41.3 Spiny Dogfish per set), than in the March experiment (13.3 ± 14.2 Spiny Dogfish per set).

In the March experiment, the model fits tended to weakly support the linear relationship between the $\chi^2_0$ (Table 2.2, Figure 2.2, Figure 2.3) or $\chi^2_w$ indices (Table 2.2, Figure 2.4) and the
observed rockfish density. For both Yelloweye and Quillback, the AICc values were smaller for the linear model; the difference in the AICc values was greater for Quillback than for Yelloweye (Table 2.2). However, the model fits between the between the \( \lambda^D \) or the \( \lambda^W \) indices and the observed density were weak for both species \((R^2 \leq 0.30)\). In the August experiment, the model fits supported a non-linear relationship between \( \lambda^D \) and the observed Yelloweye density, with smaller AICc values for the non-linear model (Table 2.2, Figure 2.2). For Quillback, the model fits between \( \lambda^D \) and the observed Quillback density were weak and the AICc was smaller for the linear model (Table 2.2, Figure 2.3). Although the August experiment provides some evidence for a non-linear relationship between \( \lambda^D \) and the observed Yelloweye density, the present results do not strongly distinguish between a linear or non-linear relationship between \( \lambda \) and the observed density of either rockfish species.

For both Yelloweye and Quillback, the posterior medians of \( \lambda^W \) were slightly larger than the estimates from deck data \((\lambda^D)\) (Figure 2.5). However, the \( \lambda^W \) and \( \lambda^D \) estimates were strongly correlated (Figure 2.5). The results were the same for other species (Figure C.1). However, while the posterior medians of \( \lambda^W \) for the bare hooks category were strongly correlated with those for \( \lambda^D \), the \( \lambda^D \) posterior medians were larger (Figure C.1).

The relationship between CPUE \((U^D)\) and the observed rockfish density was also inconsistent between the two experiments. In the March experiment, the AICc value for the linear model was smaller for both Yelloweye and Quillback (Table 2.2). In the August experiment, the AICc value for the non-linear model was marginally smaller for Yelloweye (Table 2.2). Although the AICc value for the linear model was smaller for Quillback, the model fits were weak again and differed only slightly between the linear and non-linear models (Table 2.2, Figure 2.3).
Despite the lack of consistent support for either model, both the March and August experiments showed that for Yelloweye, $\lambda^D_s$ had a better fit with the observed fish density than CPUE ($U^D_s$); the $R^2$ values for $\lambda^D_s$ were higher than for $U^D_s$ for both the linear and non-linear models (Table 2.3). The Quillback $\lambda^D_s$ index did not show a better fit than $U^D_s$ with the observed fish density and the difference in the $R^2$ values was much smaller between the linear and non-linear models (Table 2.3).

The estimated parameters of the linear and non-linear models varied by experiment and rockfish species, particularly for $h$ and $q$. For the March experiment, the estimates of $h$ (the shape parameter) in the non-linear model were all less than one for $\lambda^D_s$, $\lambda^W_s$ and $U^D_s$ (Table 2.3), indicating the observed rockfish density declined faster than the indices (hyperstability) for both Yelloweye and Quillback. However, for the August experiment, Yelloweye $h$ values were greater than one for both $\lambda^D_s$ and $U^D_s$ (Table 2.3), indicating that the indices declined faster than the observed density (hyperdepletion). The corresponding $h$ estimates for Quillback in the August experiment were zero (Table 2.3), indicating no response by the indices as the observed density decreased. However, $h$ was constrained to be non-negative. The estimates of $q$ (the slope) for Quillback were lower than those for Yelloweye for both the linear and non-linear models, reflecting that a greater number of Quillback were observed by the ROV, but similar numbers of Quillback and Yelloweye were caught. Additionally, for Yelloweye, the $q$ estimates were higher for August experiments than for the March experiments, reflecting that a greater number of Yelloweye were caught than observed by the ROV (Table 2.3).

Estimates of the posterior median of $\lambda^W_s$ ($\lambda^{W-PI}_s$ and $\lambda^{W-PC}_s$) generally decreased over the soak time, during the March experiment. The posterior medians estimated from the third pass
over the longline (Pass 3 $\lambda_y^{W-PI}$ and $\lambda_y^{W-PC}$) were consistently lower than the estimates from the first pass over the longline (Pass 1 $\lambda_y^{W-PI}$ and $\lambda_y^{W-PC}$) (Figure 2.6). These differences were significant for $\lambda_y^{W-PI}$ for Yelloweye (mean difference $\text{Pass 1-Pass 3} = 0.03 \text{ h}^{-1}$, paired $t(12) = 3.36$, $p = 0.01$) and Quillback (mean difference $\text{Pass 1-Pass 3} = 0.01 \text{ h}^{-1}$, paired $t(12) = 2.64$, $p = 0.02$), and for $\lambda_y^{W-PC}$ for Yelloweye (mean difference $\text{Pass 1-Pass 3} = 0.05 \text{ h}^{-1}$, paired $t(12) = 4.57$, $p < 0.001$) and Quillback (mean difference $\text{Pass 1-Pass 3} = 0.03 \text{ h}^{-1}$, paired $t(12) = 4.92$, $p < 0.001$). On average, the first pass ended $39.2 \pm 7.6 \text{ min}$ after longline deployment, while the third pass ended $111.4 \pm 4.3 \text{ min}$ after longline deployment. The result was similar whether all hooks on the pass were included ($\lambda_y^{W-PI}$) or some hooks on the pass were excluded ($\lambda_y^{W-PC}$) (Figure 2.6). However, the fit of the relationship between the posterior medians from Pass 3 and Pass 1 was more variable when hooks were excluded (Figure 2.6).

The posterior distributions for $\lambda_y$ were more precise for the March experiment than for the August experiment, for both Yelloweye and Quillback (Figure 2.7). The posterior precision was similar between the March and August experiments for other species and bare hooks, except for $\lambda_y^W$ for bare hooks (Figure C.2). In March, the posterior precision was similar between $\lambda_y^W$ and $\lambda_y^D$, except for the bare hooks category (Figure 2.7, Figure C.2). For the posterior distributions of Pass 1 $\lambda_y^{W-PI}$, Pass 3 $\lambda_y^{W-PI}$ and Pass 3 $\lambda_y^{W-PC}$, the CV varied without a consistent pattern, except that estimates that included all the hooks on the pass ($\lambda_y^{W-PI}$) were more precise than those that removed some hooks ($\lambda_y^{W-PC}$), with Pass 3 $\lambda_y^{W-PI}$ being most precise (Figure 2.7, Figure C.2). The posterior distributions were minimally affected by the choice of prior rate parameter, except for sets where the gear was near saturation (e.g., Set 2, Figure B.11).
2.4 Discussion

Relative abundance indices from fisheries-independent surveys are often assumed to change proportionally with the abundance of the target species. However, on longline surveys, competition from non-target species may cause underestimation of the CPUE index when their catches are high (Rothschild 1967, Somerton and Kikkawa 1995). The instantaneous rate of bait loss index, $\lambda_s$, is thought to correct for this issue by accounting for all the hooks that return without bait. Using field experiments, I tested the validity of key assumptions about the relative abundance indices, $\lambda_s$ and CPUE, for Yelloweye and Quillback. In these experiments, rockfish density was observed using a ROV.

For both rockfish species, the March experiment did not refute the linear model for the relationship between $\lambda_s$ ($\lambda^D_s$ or $\lambda^W_s$) and the observed rockfish density, when compared with the non-linear model. Neither did the August experiment for Quillback. In contrast, the August experiment refuted the linear model to favour the non-linear model, over the small range of Yelloweye densities observed. The experiments supported my prediction that $\lambda_s$ has a better fit with observed density than CPUE, but only for Yelloweye. Finally, as predicted, $\lambda_s$ was not constant during the soak time, decreasing between the first and last observations of the longline underwater.

The linear model was generally weakly favoured over the non-linear model as better describing the relationship between $\lambda_s$ (or CPUE) and observed density, except for the August experiment, which favoured a non-linear relationship between $\lambda_s$ and Yelloweye density. The $\text{AIC}_c$ for the linear model was generally smaller than the $\text{AIC}_c$ for the non-linear model due to the increased penalty for the extra parameter in the non-linear model at the small sample sizes in the experiments. The lack of strong support for the linear model is consistent with Rodgveller et
al. (2011); they did not find a significant proportional relationship between longline CPUE and the observed density of deepwater rockfish, despite a larger sample size. The rockfish densities observed in my experiments were similar to those of Rodgveller et al. (2011), except for the August Yelloweye densities, which were much smaller. Although the March and August experiments produced non-linear models with different shapes for the Yelloweye $\lambda_s$ and $U_s$ (i.e., hyperstability with $h < 1$ for March and hyperdepletion with $h > 1$ for August), I expect the March experiment to produce more accurate results than the August experiment. Given that the ROV operations occurred at the same time as the longline fishing during the March experiment, the ROV could observe the fish around the longline, including those attracted to the bait scent (see reviews in Stoner 2004, Løkkeborg et al. 2014). Additionally, the ROV repeatedly observed the fish density around each hook. The timing and repeated observations likely improved the accuracy of the observed density in March. During the August experiment, the ROV operations preceded the longline fishing by up to 47.5 hours, so the ROV did not view the longline. Fish attracted to the longline by the bait scent would not have been seen by the ROV. This may have caused the observed density to be underestimated relative to the density sampled by the longline, particularly for highly mobile species. This would compress the model fit with $\lambda_s$ over a smaller range of rockfish densities, and could be why the August experiment supports a non-linear relationship for Yelloweye $\lambda_s$, with very high $\lambda_s$ values at small Yelloweye densities. This increases the possibility that the non-linear relationship between Yelloweye $\lambda_s$ and the Yelloweye densities observed in August is driven by observation error rather than fish behaviour.

When fitting the relationship between $\lambda_s$ and observed density, I assumed that the ROV measured the rockfish density without error, except for the intercept ($\nu$) which accounted for rockfish captures when zero rockfish were observed by the ROV. However, a limited vertical
field of view (Trenkel et al. 2004), hidden biomass (Willis 2001) and attraction or avoidance by fish outside the camera view (Trenkel et al. 2004, Stoner et al. 2008) can all introduce observation error into visual sampling methods. Richards and Schnute (1986) accounted for observation error in their underwater count data by using an error-in-variables approach to fit their model between angling CPUE and the observed density of Quillback. However, the results of their error-in-variables approach did not differ from their ordinary least squares approach for single-species models.

Due to the small sample size, few replicates existed to separate the effects of rockfish density on the $\lambda_s$ and CPUE indices from the effects of environmental variables. For example, the on-bottom temperature of the sets ranged from 7.7 - 10.6 °C during the August experiment, but was similar across sets (8.4 - 8.7 °C) during the March experiment. Temperature influences the activity rate, swimming speed and feeding motivation of fish and can change the rate at which they encounter the longline, and the rate at which they attack and consume bait (see review in Stoner 2004, Stoner and Sturm 2004, Stoner et al. 2006). Other variables, including tides, current, light intensity, visibility, availability of natural prey and habitat type (e.g., complexity) also influence feeding behaviour and attraction to baited hooks (see reviews in Stoner 2004 and Løkkeborg et al. 2014). Environmental conditions likely varied more among the sets in the August experiment, than in the March experiment. In the March experiment, the sites were selected by an experienced commercial fisherman in a relatively small area. In the August experiment, the sites were randomly selected blocks of rockfish habitat, as part of the annual rockfish longline survey (Lochead and Yamanaka 2007). Set locations were separated by much greater distances, than during the March experiment, and the ROV observations preceded the longline fishing by up to 47.5 hours for some sets in the August experiment. The observed
density and longline catches may have occurred under very different environmental conditions (e.g., currents, light levels) in the August experiment. Additionally, habitat type and depth also affect rockfish distribution, with greater densities associated with more complex bottom types, particularly boulder-fields (Richards 1986, O'Connell and Carlile 1993, Johnson et al. 2003).

Depths in the March and August experiments were similar, with an average depth of 68.39 m in March (range of 45.35 m - 107.28 m) and an average depth of 70.34 m in August (range of 55.19 m - 94.21 m). Given the methods of site selection, I believe that the habitat type in both experiments was suitable for Quillback and Yelloweye. However, differences in depth, habitat type and other environmental variables between the longline sets could influence $\lambda_s$ and introduce uncertainty into the relationship with the observed density.

The observed relationship between $\lambda_s$ ($\lambda_s^D$ or $\lambda_s^W$) and the rockfish densities may be due to inadequate sampling at high levels of hook competition. Although, the range of rockfish densities and catch rates were greatest during the March experiment, both experiments had few sets at high rockfish densities. In the August experiment, the maximum observed density of Yelloweye was almost an order of magnitude smaller than in the March experiment. In both experiments, this made it more difficult to distinguish the shape of the relationship between observed density and $\lambda_s$, as hyperstability in the indices should be most visible at high densities. Additionally, the experiments had lower interspecific competition for the hooks than expected. The overall number of hooks returning with catch or with the bait removed (bare) was only 27.4% (March) and 38.1% (August). This is lower than the 43.9% (August 2010) and 62.8% (August 2011) of hooks returning with catch, or without bait, during the annual rockfish longline survey. Sometimes greater than 50% of the hooks on this survey had dogfish (Lohead and Yamanaka 2007). The $\lambda_s$ index is expected to perform better than CPUE at high levels of catch,
when the gear may become saturated (Somerton and Kikkawa 1995, Haimovici and Ávila-da-Silva 2007). However, for Yelloweye, \( \lambda_s \) showed a better fit than CPUE, over the range of observed densities, suggesting that hook competition may affect Yelloweye indices at lower catch rates. In contrast, the fit between \( \lambda_s \) and CPUE differed only marginally for Quillback, even though the range of densities observed was larger than that of Yelloweye.

Although the design of the experiments and the small sample sizes may limit the inferences that can be made from the data, the \( \lambda_s \) indices for Quillback still showed a poorer fit to the observed density, than did the \( \lambda_s \) for Yelloweye. The \( \lambda_s \) indices appeared insensitive to changes in Quillback density, even though the observed density was two to 10 times greater than the observed Yelloweye density. One hypothesis for this relates to the size of these rockfish species. In fitting the relationship between \( \lambda_s \) and the observed density, I assumed that all the observed rockfish could be caught, as did Rodgveller et al. (2011). However, Richards and Schnute (1986) excluded rockfish with a fork length less than 20 cm from their observed density for experiments with angling gear, and Haggarty and King (2006) excluded rockfish with a fork length less than 15 cm. Longline size selectivity depends on the size of the hook (Sousa et al. 1999, Gregalis et al. 2012, Leaman et al. 2012) and the size of the bait (Løkkeborg 1990, Løkkeborg and Bjordal 1995, Ingólfsson et al. 2017). The size selectivity of the longline gear used in my experiments is unknown (Yamanaka et al. 2012b), but Yelloweye grow to a larger maximum size than Quillback (Love et al. 2002). The Yelloweye caught averaged 43.6 ± 9.3 cm (± standard deviation) in total length, while the Quillback were 35.9 cm ± 3.1 cm. Larger Yelloweye may also be dominant when feeding, preventing some Quillback from taking hooks. Large fish can outcompete smaller fish (Hamley and Skud 1978, Engås et al. 1996, Stoner and Ottmar 2004) and may chase them away from hooks (Løkkeborg and Bjordal 1992). For
example, Atlantic Cod (*Gadus morhua*) have been observed to chase Whiting (*Gadus merlangus*) away from hooks (Fernö *et al.* 1986), and wolffish (*Anarhichas* sp.) actively guard baited hooks and chase away other species (Godø *et al.* 1997). Additionally, larger fish may move farther than smaller fish to find baited hooks (Mittelbach 1986). Small Pacific Halibut (*Hippoglossus stenolepis*) are caught less when hooks are widely spaced, suggesting that smaller fish travel less for bait (Hamley and Skud 1978). Sablefish (*Anoplopoma fimbria*), a more mobile predator, can outcompete Shortraker Rockfish (*S. borealis*) and Roughey Rockfish (*S. aleutianus*) for hooks (Rodgveller *et al.* 2008). Catch rates of these rockfish species decline when Sablefish are present. Sablefish are even effective at finding bait when few baited hooks remain (Sigler 2000). Additionally, Kaimmer (1999) found that Yelloweye had higher hooking success, relative to the number of bites, than Quillback. If a greater proportion of the Yelloweye observed were able to take the baited hooks, this may partially explain the difference in the model fits for the two species. This is also consistent with the lower estimates of the slope (*q*) for Quillback than Yelloweye in the linear and non-linear model fits. Furthermore, Quillback and Yelloweye size varies by depth, with larger fish found at deeper depths (Richards 1986). Since larger fish are more likely to take hooks, the proportion of the Quillback able to take hooks could increase with depth. *λs* could appear insensitive to changes in the Quillback density due to the set depth and the selectivity of the gear.

A second hypothesis for the poor model fits and apparent insensitivity of *λs* to the observed Quillback density is related to a suspected hook-aggregating behaviour of Quillback. During the March experiment, I noticed groups of Quillback around the hooks on some sets. I did not observe similar hook-aggregating behaviour by Yelloweye, although they were sometimes found in small multispecies groups. Johnson *et al.* (2003) also noted that Quillback
often aggregate into small groups. Fish sampled by longlines regularly have patchy distributions due to schooling (Gulland 1955). A patchy spatial distribution is expected for many rockfish, due to their preference for specific habitat types (Richards 1986, O’Connell and Carlile 1993, Anderson and Yoklavich 2007, Johnson et al. 2003, Haggarty et al. 2016). However, this hook-aggregating behaviour by Quillback could increase their patchiness, in comparison with Yelloweye. I noticed that Quillback in these groups were often not caught on nearby hooks, which were spaced only 1.8 m apart. This means that Quillback that form small groups may only move a short distance to find baited hooks. Quillback do have small home ranges (less than 10 m$^2$) when on high quality habitat (Matthews 1990b). These behaviours could lead to localized saturation of the longline, where hooks near these small groups capture Quillback, but adjacent hooks remain baited. Spatial variation at the level of individual hooks or small groups of hooks cannot be accounted for by the $\lambda_s$ index, which corrects for gear saturation at the level of the entire longline. Gear saturation at the level of individual hooks could mask changes in the relationship between the $\lambda_s$ index and fish density over time, leading to bias in the trends in survey and commercial longline indices.

In addition to the $\lambda_s$ index lacking a consistent relationship with the observed density, I found that $\lambda_s$ changed over the 120 minute soak time. Sablefish capture rates, an analog for $\lambda_s$, also decrease slowly with soak time and then more rapidly when only 20 - 30% of the hooks remain baited (Sigler 2000). Sigler (2000) attributed this to a reduction in the fish encountering the longline over time. Sablefish encounter rate appears to track the decrease in the bait scent concentration at the outer edge of the dispersal plume. Somerton and Kikkawa (1995) also found that $\lambda_s$ for Pelagic Armorhead ($Pseudopentaceros wheeleri$) first increased and then decreased. Non-stationarity in $\lambda_s$ could bias the $\lambda_s$ index, if applied to commercial or survey catch data.
where the soak time varies across sets or is difficult to estimate or measure for the gear. For example, Sigler (2000) found that a longline soaked for three hours, versus seven hours, showed little difference in the CPUE, regardless of the density of the target species. In this case, the $\lambda_s$ index would be underestimated for the seven-hour soak time. Stock assessments using $\lambda_s$ as the index for commercial fisheries or surveys that have a systematic increase or decrease in soak time could show a biased time trend.

When estimating the $\lambda_s$ index, the assumption about how to treat the bare hooks that return without bait or catch could also create bias in the index. Since bare hooks reduce the effective sample size of the longline and increase variability in the abundance indices, it is important to account for them in the $\lambda_s$ index. I treated bare hooks as a separate species category, since little was known about the source of the bare hooks. Although unlikely for these rockfish species, this method could bias the $\lambda_s$ index for the target species, if the target species is responsible for a disproportionately large or small number of the bare hooks, relative to the other species caught. Somerton and Kikkawa (1995) attributed bare hooks to the target and non-target species in equal proportion to their catch. Webster and Stewart (2015) handled bare hooks on the Pacific Halibut longline survey in a similar way, by correcting for total hook competition in their weight-based abundance index based on the percent of hooks that return with bait. However, if the target species is responsible for more, or less, of the bare hooks than other species, then these methods could underestimate or overestimate the $\lambda_s$ index, respectively. These methods also overestimate hook competition if there are other sources of bare hooks, besides the species caught on the line. These sources could include the mechanical loss of bait, while setting or hauling back the longline, or bait removed by invertebrates that are not caught on the hooks. For example, crabs have been observed to remove bait from longline hooks (High 1980). If an
invisible source of bait loss, invertebrates could create bias in the time trends of the $\lambda_s$ index, if there are changes in their abundance over time that are not accounted for in the calculation of $\lambda_s$. This is a potential problem for the stock assessment of Yelloweye and Quillback in BC. In recent years, populations of large predatory starfish, which can be frequently caught during the survey (Lochead and Yamanaka 2007), have declined drastically due to a sea star wasting disease (Hewson et al. 2014, Eisenlord et al. 2016). Additionally, crab populations can vary highly from year to year, as with the local population of Dungeness Crab (*Metacarcinus magister*) (Zhang and Dunham 2013).

The present results suggest that while the $\lambda_s$ index may have a better fit than CPUE to the observed density, it may not have a clear linear relationship with target species density. Trends in $\lambda_s$ may be biased by differences in the soak time and assumptions about the bare hooks on the longline. Therefore, caution should be taken when using $\lambda_s$ as an index of abundance. Careful survey design should correct for a number of the sources of hyperstability or hyperdepletion in relative abundance indices (Hilborn and Walters 1992, Gunderson 1993) and spatial and temporal effects are often corrected by standardization and/or imputation of data (Maunder and Punt 2004, Carruthers et al. 2011). However, some issues at the level of the longline, like interspecific competition for hooks, size selectivity, localized gear saturation from species-specific behaviour and trends in the source of bare hooks may not be accounted for in the estimation of the relative abundance indices and may introduce bias into the trends. Future work should focus on whether these issues significantly bias the time trends of the indices and whether such biases can be corrected.
Table 2.1. Model parameters and variables used for the relative abundance indices and for the linear and non-linear model fits to observed density.

<table>
<thead>
<tr>
<th>Term</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Deck Observations</strong></td>
<td></td>
</tr>
<tr>
<td>$t$</td>
<td>Soak time for the set (h), the total time the hooks spend in the water.</td>
</tr>
<tr>
<td>$N$</td>
<td>Number of baited hooks deployed on the longline (total hooks).</td>
</tr>
<tr>
<td>$N_B$</td>
<td>Number of hooks returning to the deck with bait at time $t$.</td>
</tr>
<tr>
<td>$N_s$</td>
<td>Number of hooks returning to the deck, at time $t$, with a catch of category $s$. The four categories include catches of Yelloweye Rockfish ($Y$), Quillback Rockfish ($Q$), or other species ($O$), and bare hooks ($E$).</td>
</tr>
<tr>
<td><strong>Derived variables</strong></td>
<td></td>
</tr>
<tr>
<td>$U_s^D$</td>
<td>Catch per unit effort (CPUE) of category $s$ (h$^{-1}$), based on set-level observations of total catch on the deck of the fishing vessel.</td>
</tr>
<tr>
<td>$\lambda_s^D$</td>
<td>Maximum likelihood estimate of the total instantaneous rate of bait loss (h$^{-1}$), based on set-level observations of total catch on the deck of the fishing vessel.</td>
</tr>
<tr>
<td>$\lambda_s^D$</td>
<td>Maximum likelihood estimate of the instantaneous rate of bait loss due to category $s$ (h$^{-1}$), based on set-level observations of total catch on the deck of the fishing vessel.</td>
</tr>
<tr>
<td><strong>Underwater Observations</strong></td>
<td></td>
</tr>
<tr>
<td>$t_x$</td>
<td>Soak time (h) for each hook, calculated as the time between the hook leaving the deck of the fishing vessel and observation by the ROV.</td>
</tr>
<tr>
<td>$\lambda_s^W$</td>
<td>Estimate of the bait loss due to category $s$ (h$^{-1}$), based on hook-level observations. Hook observations from pass two and pass three are treated as conditional on the previous pass by modifying $t_x$.</td>
</tr>
<tr>
<td>$\lambda_s^{W-PI}$, $\lambda_s^{W-PC}$</td>
<td>Per pass estimate of the bait loss due to category $s$ (h$^{-1}$), based on underwater hook-level observations of catch. $t_x$ is not modified. For $W-PI$, passes are treated as sequential experiments. For $W-PC$, passes are conditional on the previous pass and only some hook observations are included.</td>
</tr>
<tr>
<td>$D_s$</td>
<td>Observed rockfish density. The number of individuals observed underwater with the ROV, divided by the total area surveyed by the ROV (individuals /100 m$^2$).</td>
</tr>
<tr>
<td><strong>Linear and non-linear model parameters</strong></td>
<td></td>
</tr>
<tr>
<td>$q_s$</td>
<td>Slope of the relationship between the relative abundance index and the observed density (h$^{-1}$·100 m$^2$).</td>
</tr>
<tr>
<td>$v_s$</td>
<td>Intercept representing longline catch when the density observed by the ROV is zero, constrained to be non-negative (h$^{-1}$).</td>
</tr>
<tr>
<td>$h_s$</td>
<td>Shape parameter for the non-linear model.</td>
</tr>
</tbody>
</table>
Table 2.2. Coefficient of determination ($R^2$) and difference in the Akaike Information Criterion values corrected for small sample size (AICc) for the linear (Eqs. 2.13 - 2.14) and non-linear (Eqs. 2.15 - 2.16) model fits between observed rockfish density and the relative abundance indices. The AICc differences are shown as the linear model AICc minus the non-linear model AICc (L-NL).

<table>
<thead>
<tr>
<th>Species</th>
<th>Index</th>
<th>Experiment</th>
<th>Linear model</th>
<th>Non-linear model</th>
<th>AICc (L-NL)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Yelloweye Rockfish</td>
<td>$\lambda_s^W$</td>
<td>March</td>
<td>0.30</td>
<td>0.64</td>
<td>-2.06</td>
</tr>
<tr>
<td></td>
<td>$\lambda_s^D$</td>
<td>March</td>
<td>0.06</td>
<td>0.57</td>
<td>-1.47</td>
</tr>
<tr>
<td></td>
<td></td>
<td>August</td>
<td>0.61</td>
<td>0.98</td>
<td>15.61</td>
</tr>
<tr>
<td></td>
<td>$U_s^D$</td>
<td>March</td>
<td>0.00</td>
<td>0.30</td>
<td>-4.06</td>
</tr>
<tr>
<td></td>
<td></td>
<td>August</td>
<td>0.49</td>
<td>0.78</td>
<td>0.55</td>
</tr>
<tr>
<td>Quillback Rockfish</td>
<td>$\lambda_s^W$</td>
<td>March</td>
<td>0.17</td>
<td>0.23</td>
<td>-3.00</td>
</tr>
<tr>
<td></td>
<td>$\lambda_s^D$</td>
<td>March</td>
<td>0.23</td>
<td>0.24</td>
<td>-2.64</td>
</tr>
<tr>
<td></td>
<td></td>
<td>August</td>
<td>0.00</td>
<td>0.00</td>
<td>-4.71</td>
</tr>
<tr>
<td></td>
<td>$U_s^D$</td>
<td>March</td>
<td>0.21</td>
<td>0.25</td>
<td>-3.09</td>
</tr>
<tr>
<td></td>
<td></td>
<td>August</td>
<td>0.00</td>
<td>0.00</td>
<td>-4.71</td>
</tr>
</tbody>
</table>
Table 2.3. Parameter estimates for the linear (Eqs. 2.13 - 2.14) and non-linear (Eqs. 2.15 - 2.16) model fits between observed rockfish density and the relative abundance indices.

<table>
<thead>
<tr>
<th>Species</th>
<th>Index</th>
<th>Experiment</th>
<th>Model</th>
<th>Parameters</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>$q$</td>
</tr>
<tr>
<td>Yelloweye Rockfish</td>
<td>$\lambda_s^W$</td>
<td>March</td>
<td>Linear</td>
<td>0.024</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Non-linear</td>
<td>0.027</td>
</tr>
<tr>
<td></td>
<td>$\lambda_s^D$</td>
<td>March</td>
<td>Linear</td>
<td>0.019</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Non-linear</td>
<td>0.021</td>
</tr>
<tr>
<td></td>
<td></td>
<td>March</td>
<td>Linear</td>
<td>0.117</td>
</tr>
<tr>
<td></td>
<td></td>
<td>March</td>
<td>Non-linear</td>
<td>1.203</td>
</tr>
<tr>
<td></td>
<td>$U_s^D$</td>
<td>March</td>
<td>Linear</td>
<td>0.015</td>
</tr>
<tr>
<td></td>
<td></td>
<td>March</td>
<td>Non-linear</td>
<td>0.015</td>
</tr>
<tr>
<td></td>
<td></td>
<td>August</td>
<td>Linear</td>
<td>0.035</td>
</tr>
<tr>
<td></td>
<td></td>
<td>August</td>
<td>Non-linear</td>
<td>0.201</td>
</tr>
<tr>
<td>Quillback Rockfish</td>
<td>$\lambda_s^W$</td>
<td>March</td>
<td>Linear</td>
<td>0.003</td>
</tr>
<tr>
<td></td>
<td></td>
<td>March</td>
<td>Non-linear</td>
<td>0.019</td>
</tr>
<tr>
<td></td>
<td>$\lambda_s^D$</td>
<td>March</td>
<td>Linear</td>
<td>0.003</td>
</tr>
<tr>
<td></td>
<td></td>
<td>March</td>
<td>Non-linear</td>
<td>0.013</td>
</tr>
<tr>
<td></td>
<td></td>
<td>August</td>
<td>Linear</td>
<td>0.000</td>
</tr>
<tr>
<td></td>
<td></td>
<td>August</td>
<td>Non-linear</td>
<td>0.000</td>
</tr>
<tr>
<td></td>
<td>$U_s^D$</td>
<td>March</td>
<td>Linear</td>
<td>0.003</td>
</tr>
<tr>
<td></td>
<td></td>
<td>March</td>
<td>Non-linear</td>
<td>0.010</td>
</tr>
<tr>
<td></td>
<td></td>
<td>August</td>
<td>Linear</td>
<td>0.000</td>
</tr>
<tr>
<td></td>
<td></td>
<td>August</td>
<td>Non-linear</td>
<td>0.008</td>
</tr>
</tbody>
</table>
Figure 2.1. Location of paired longline fishing sets and Remotely Operated Vehicle transects in the (A) March 2010 (n = 13) and (B) August 2010 (n = 12) experiments.
Figure 2.2. Linear (solid line) and non-linear (dashed line) model fits for the relationship between the relative abundance indices, $\lambda_s^D$ (posterior median) and $U_s^D$, and the mean observed density of Yelloweye Rockfish. The relative abundance indices were estimated from catch data observed on the deck of the vessel. Density was observed by the ROV during the March (three passes along the longline, $n = 13$) and August (one pass along the transect, $n = 12$) experiments.
Figure 2.3. Linear (solid line) and non-linear (dashed line) model fits for the relationship between the relative abundance indices, $\lambda^D_s$ (posterior median) and $U^D_s$, and the mean observed density of Quillback Rockfish. The relative abundance indices were estimated from catch data observed on the deck of the vessel. Density was observed by the ROV during the March (three passes along the longline, $n = 13$) and August (one pass along the transect, $n = 12$) experiments. For August, the linear and non-linear model fits for $\lambda^D_s$ are identical.
Figure 2.4. Linear (solid line) and non-linear (dashed line) model fits for the relationship between the relative abundance index, $\lambda_s^W$ (posterior median), and the mean observed density of Yelloweye Rockfish and Quillback Rockfish. The relative abundance indices were estimated from multiple observations of the hooks underwater. Density was observed by the ROV during the March experiment (three passes along the longline, $n = 13$).
Figure 2.5. Estimates of the relative abundance index $\lambda_s$ (posterior medians) from catch data observed on the deck of the vessel ($\lambda_s^D$) and from multiple observations of the hooks underwater ($\lambda_s^W$) for Yelloweye Rockfish (left panel) and Quillback Rockfish (right panel). The solid line is the best fitting linear model and the dashed line is the 1:1 line. Observations from the March experiment (three passes along the longline, $n = 13$).
Figure 2.6. Estimates of the relative abundance index $\lambda_s^W$ (posterior medians) for Yelloweye Rockfish (left column) and Quillback Rockfish (right column) at two different times during the longline set: the first (Pass 1); and third (Pass 3) pass over the hooks by the ROV. Estimates treated observations during Pass 3 as either independent ($\lambda_s^{W-PI}$, top row) or conditional on the previous pass ($\lambda_s^{W-PC}$, bottom row). The solid line is the best fitting linear model and the dashed line is the 1:1 line. The relative abundance indices were estimated from multiple observations of each hook underwater during the March experiment (three passes along the longline, $n = 13$).
Figure 2.7. Coefficient of variation (%) for the precision of the posterior distribution of $\lambda_s$ across all longline sets in the March ($n = 13$) and August ($n = 12$) experiments for Yelloweye Rockfish (top row) and Quillback Rockfish (bottom row). $\lambda_s^D$ was estimated from catch observed on the deck of the vessel, $\lambda_s^W$ from multiple observations of the hooks underwater during three passes (Pass 1, Pass 2, and Pass 3) over the longline. $\lambda_s^{W-PI}$ used all the hooks viewed in each pass over the longline, while $\lambda_s^{W-PC}$ used a reduced number based on catch in the previous pass.
Chapter 3: Evaluating Assumptions about Species Behaviours and Competitive Interactions and their Influence on a Relative Abundance Index, the Instantaneous Rate of Bait Loss

3.1 Introduction

Species-specific feeding behaviours and competitive interactions influence the catch of baited gears like longlines (reviews in Løkkeborg 1994, Stoner 2004, Løkkeborg et al. 2010, Løkkeborg et al. 2014), as well as the number of bare hooks, i.e., those hooks returning with neither bait nor catch (Shomura 1955, Johnstone and Hawkins 1981, He 1996). Many factors, for example, social facilitation behaviour that increases attacks on the bait when a fish is hooked (Fernö et al. 1986, Løkkeborg et al. 1989, Stoner and Ottmar 2004), interspecific competition (Fernö et al. 1986, Kaimmer and St-Pierre 1993, Rodgveller et al. 2008) and bait defense behaviours (Løkkeborg et al. 1989, Løkkeborg and Bjordal 1992, Godø et al. 1997), can all influence which species are caught on the longline hooks. Escape of some species from the hooks (He 1996), and bait scavenging by large invertebrates (High 1980) can remove bait and result in bare hooks returning to the longline vessel. Nevertheless, catches from fisheries-independent bottom longline surveys are used as relative abundance indices in stock assessments (e.g., Yamanaka et al. 2012a, Yamanaka et al. 2012b, Pollack and Ingram 2013, den Heyer et al. 2015, Webster and Stewart 2015, Hanselman et al. 2016). I hypothesized that fish and invertebrate behaviours that influence longline catches change the relative abundance index of the target species and may alter the temporal trends of the index. Typically, the species assumed to affect longline catches are limited to those observed aboard the fishing vessel (Somerton and Kikkawa 1995), but other species may also influence the longline catches and the number of bare
hooks (High 1980, Grimes et al. 1982). Accounting for both observed and unobserved species may be necessary to correct for their influence on the relative abundance indices. I designed a field experiment which used a Remotely Operated Vehicle (ROV) to directly observe all the species influencing longline catches, and to guide where appropriate adjustments for species behaviours and competitive interactions needed to be made to the methods for abundance index calculation.

Since stock assessments use trends in relative abundance indices to inform fisheries management advice on stock size and harvest controls (Yamanaka et al. 2012a, Yamanaka et al. 2012b, Pollack and Ingram 2013, den Heyer et al. 2015, Webster and Stewart 2015, Hanselman et al. 2016), relative abundance indices uncorrected for inconsistencies due to species behaviours and competitive interactions could result in inappropriate management advice, particularly if there is a temporal trend in the effects. This may happen if the abundance of a non-target species that strongly influences the longline catches changes over time. Both Punsly and Nakano (1992) and Stoner (2004) speculated that species behaviours in response to environmental conditions (e.g., temperature, competitors, etc.) could have a greater effect on catch than species abundance, and that abundance indices uncorrected for environmental effects may only index feeding conditions for the target species and their competitors.

Additionally, changes in the number of bare hooks across years (e.g., Ward and Myers 2007) could alter the temporal trends of a relative abundance index, as bare hooks will affect catch rates. For example, shrimp and crab have been observed to remove bait from longlines (High 1980) and local populations of Dungeness crab can vary highly from year to year (Zhang and Dunham 2013), which could cause the number of bare hooks to change from year to year. Bare hooks also reduce the effective fishing power of the longline, by reducing the number of
available hooks (Ward and Myers 2007). This decreases the effective sample size of the longline set and causes increased uncertainty in the relative abundance indices used in the stock assessment. Accounting for the species behaviours and competitive interactions responsible for the bare hooks can be difficult, since bare hooks can result from removal of the bait by a species or from mechanical removal during release or retrieval of the longline by the fishing vessel (Shomura 1955, Shepard et al. 1975, Skud 1978, High 1980, Boggs 1992). Mechanical removal can include the loss of bait due to rough seas (Shepard et al. 1975) or due to contact of the hooks with the ocean floor. Also, the species responsible for removing bait may or may not be caught on the longline, as with invertebrate scavengers (High 1980) or bottom fish species (He 1996). Furthermore, information on the number of bare hooks returning may not be recorded (Ward and Myers 2007, Smith 2016).

Many relative abundance indices from fishery-independent surveys are not corrected for the influence of species behaviours and competitive interactions or for the number of bare hooks (e.g., Mitchell et al. 2004, Murua and Cárdenas 2005, Harms et al. 2010, Pollack and Ingram 2013, Nygaard 2014, Smith 2016). In contrast, Yamanaka et al. (2012a and 2012b) and Webster and Stewart (2015) attempt to correct for competitive interactions and the return of bare hooks using the instantaneous rate of bait loss per species index ($\lambda_s$) or a correction based on $\lambda_s$. $\lambda_s$ accounts for the catch of non-target species to correct for the influence of interspecific competition due to the non-target species observed aboard the fishing vessel (Murphy 1960, Rothschild 1967, Somerton and Kikkawa 1995, Chapter 2). Correcting for the number of bare hooks in the $\lambda_s$ index requires making an assumption about the sources of bait removal. Such assumptions include splitting the bare hooks between target and non-target species equally (Yamanaka et al. 2012a) or based on their relative proportions in the catch (Somerton and
Kikkawa 1995), or assuming that one species, either the target or non-target species, is better at removing bait. Most often, bare hooks are assumed to be caused by non-target species only (Bjordal 1983, Hovgård and Lassen 2000, Webster et al. 2011, Yamanaka et al. 2018). However, there exists little empirical evidence to justify the selection of one assumption over the other, an important selection if temporal trends in relative abundance indices, like $\lambda$, are sensitive to assumptions about the source of bare hooks.

I conducted a field experiment to test my hypothesis that the species behaviours and competitive interactions that influence longline catches change the relative abundance index of the target species and may alter the temporal trends of the index. During this experiment, a ROV directly viewed bottom longlines underwater during longline fishing for inshore rockfish. Inshore rockfish include Yelloweye Rockfish (*Sebastes ruberrimus*), Quillback Rockfish (*S. maliger*), Copper Rockfish (*S. caurinus*), Tiger Rockfish (*S. nigrocinctus*), China Rockfish (*S. nebulosus*) and Black Rockfish (*S. melanops*). The experiment followed the survey methods of the Fisheries and Oceans Canada (DFO) annual inshore rockfish survey in British Columbia, Canada, as a case study, because this annual survey has a multispecies catch, extremely high interspecific competition from Spiny Dogfish (*Squalus acanthias*) (Lochead and Yamanaka 2007) and variation in the number of bare hooks per set. I predicted that: (1) the directly observed sources of bare hooks would primarily be due to species behaviours and competitive interactions from Spiny Dogfish, the main non-target species on the inshore rockfish survey; (2) mechanical bait removal would result in fewer bare hooks than bait removal bait by species; (3) a relationship exists between the proportion of bare hooks observed on the deck of the fishing vessel and the catch of species observed to be the sources of bare hooks; and (4) correcting for observed species behaviours and competitive interactions, including bare hooks, would change the temporal trends
for the inshore rockfish $\lambda_s$ indices. I tested these predictions by comparing multiple observations of the longline hooks underwater to observations on the deck and testing for statistical differences. I used these underwater observations to create adjustments for the influence of some species behaviours and competitive interactions on both the Yelloweye and Quillback $\lambda_s$ indices and estimated both the corrected and uncorrected $\lambda_s$ in a Bayesian framework.

3.2 Methods

3.2.1 Data collection

To understand how species feeding behaviours and competitive interactions affect bottom longline catches and influence the resulting relative abundance indices, I conducted a field experiment during March 2010 in Nanoose Bay and Northwest Bay in the Strait of Georgia, British Columbia (BC), Canada (Figure 2.1). During the March experiment, 13 longline fishing sets were observed underwater by a ROV deployed directly after the longline was released. A commercial fishing vessel deployed the longline gear, while a government research vessel deployed the ROV. During the fishing sets, I observed the state of each longline hook (225 per set) at four different observation periods: three times underwater, while the ROV passed along the length of the longline (Pass 1, Pass 2 and Pass 3), and once as the hooks were retrieved on the deck of the fishing vessel. During each of the four observations, the hooks were recorded as having bait, having caught a species, being bare (i.e., with neither bait nor a species on the hook), or as unknown (i.e., the hook was missing). For hooks that caught a species, I identified fish and invertebrates to the species level, whenever possible. During the underwater ROV observations, I also recorded the time that each hook was observed. Details of the fishing and ROV operations can be found in the Methods section of Chapter 2 (Sections 2.2.1.1 and 2.2.1.2) and Appendix A.
3.2.2 Observed sources of bare hooks

To identify the sources of the bare hooks, I determined the observation period when each hook was first observed bare (Pass 1, Pass 2, Pass 3, or on the deck) and then looked at the state of the hook during the previous ROV pass. If a species was observed on the hook during the previous ROV pass, I considered this species to be the probable source of bait removal. Hooks observed to be bare during the first ROV pass underwater had only been previously observed during release of the longline from the fishing vessel and the source of bait removal for these hooks could not be determined.

To investigate if mechanical removal of bait during release and retrieval of the longline led to fewer bare hooks than removal by species, I compared the bait removal rate between the four hook observation periods. The observation periods were separated into times when the longline hooks were both stationary and observed (Pass 2 and Pass 3 underwater) and times when the longline hooks were either moving, or were stationary and unobserved (Pass 1 and on the deck). Pass 1 was the first observation of the hooks underwater after the longline was released from the fishing vessel. Pass 3 was the last observation underwater before the longline was retrieved on the deck of the fishing vessel. I assumed that mechanical removal of bait only occurred when the longline hooks were moving. For each longline set, the bait removal rate between observations periods was calculated as the number of new bare hooks divided by the average time since each hook was last observed. On Pass 2, for example, the average time since the hooks were last observed ($\Delta t_{i,Pass2}^{Pass2} = \frac{\sum_{j} t_{ij}^{Pass2} - t_{ij}^{Pass4}}{N}$) was calculated as:

Eq. 3.1
where $N$ is the number of baited hooks released from the fishing vessel during the longline set, $t_{x}^{\text{Pass2}}$ is the time interval between on-deck deployment of hook $j$ and observation underwater during Pass 2, and $t_{x}^{\text{Pass1}}$ is the time interval between on-deck deployment and underwater observation during Pass 1, the previous ROV pass. For hooks observed on the deck during release or retrieval, the time was recorded only for the first and last hooks on the longline. I assumed that the hooks were brought onto the deck, or released from the deck, at a constant rate. The times for these hook observations ($t_{x}$) were calculated as the time difference (h) between the release/retrieval of the first hook and release/retrieval of the last hook on the longline, divided by the total number of hooks ($N$). I tested whether the log of the bait removal rate differed significantly between the four observation periods (Pass 1, Pass 2, Pass 3, and on the deck) using the "lm" and “anova” functions in the R base stats package (R Core Team 2017). Due to a few observations where the bait removal rate was zero, a small constant ($1 \times 10^{-25}$) was added to all the bait removal rates (Kimura and Somerton 2006). Both set and pass were included in the General Linear Model as fixed factors. I could not test whether there was a significant interaction between set and pass due to the limited number of sets and observations. For all the statistical tests, I examined whether the residuals were normal, independent and homogeneous by looking for patterns in the plots of the residuals and fitted values.

3.2.3 Determining sources of bare hooks from catch observed only on the deck

To assess the relationship between the bare hooks observed on the deck and the catch composition, I investigated species that were identified as probable sources of bare hooks from the ROV video and were also caught on the deck during the March 2010 experiment. For each longline set, the proportion of the hooks without catch that were unbaited ($z$) was calculated as
the number of bare hooks \((N_E)\) relative to the total number of hooks that could have returned without bait (i.e., baited hooks \((N_B)\) plus the bare hooks \((N_E)\)):

\[
z = \frac{N_E}{N_E + N_B}
\]

Eq. 3.2

I tested whether this proportion of bare hooks could be predicted by the number of hooks catching species category \(s\) \((N_s)\), or by the mean observed density of the species \((D_s)\), by fitting a logistic regression (binomial error distribution) to the logit-transformed proportions:

\[
\log\left(\frac{z}{1-z}\right) = \alpha + \beta_{N_s} \cdot N_s + \epsilon
\]

Eq. 3.3

\[
\log\left(\frac{z}{1-z}\right) = \alpha + \beta_{D_s} \cdot D_s + \epsilon
\]

Eq. 3.4

I fit the logistic regression, and tested for statistical significance using the "glm" and "anova" functions in the R base stats package (R Core Team 2017) to test the \(\chi^2\)-distributed difference in the residual deviance with a Likelihood Ratio test. I also calculated McFadden's pseudo-\(R^2\) as a measure of model strength (McFadden 1974). McFadden's pseudo-\(R^2\) uses the ratio of the log likelihoods for the model being estimated \((L(M))\) and the intercept only model \((L(0))\):

\[
R^2 = 1 - \frac{L(M)}{L(0)}
\]

Eq. 3.5

and represents the explained variance.

As the March 2010 experiment only included 13 longline sets and the maximum proportion of bare hooks observed was less than 0.25, I also fit logistic regressions to data from the annual inshore rockfish longline survey. The annual inshore rockfish longline survey has
operated for 13 years (2003-2005, 2007-2016) in the inside waters east of Vancouver Island
(Figure 3.1). During the survey, the state of each hook was recorded as it returned to the deck
(bait, species caught, bare, or unknown) and catch was identified to the species level where
possible. The longline specifications are the same as those described in the Methods of Chapter 2
(see Methods section 2.2.1.1). Longline fishing operations were consistent across survey years
(e.g., hook type, bait type, longline material and length, method of deployment), with the only
difference being set location and vessel crew (see Lohead and Yamanaka 2007 for details).
However, survey areas changed during two time periods: in 2007, when no-take Rockfish
Conservation Areas (RCAs) were expanded (Yamanaka and Logan 2010), and in 2010, when the
survey was restricted to sample only the genetically-unique inside waters population of
Yelloweye between Port McNeill and Victoria (Yamanaka et al. 2012b, Figure 1.1). For the
logistic regressions, I used survey longline sets from 2003 to 2015, restricted to those from the
DFO Pacific fishery management areas (PFMA) that were frequently sampled during the survey
years (n = 701) (Figure 3.1).

3.2.4 Correcting for the effect of observed species behaviours and competitive
interactions

3.2.4.1 Assumptions about the sources of bare hooks

Based on the observed sources of bare hooks and the results of the logistic regressions, I
tested whether different assumptions about the source of bare hooks altered the temporal trends
in the estimated instantaneous rate of bait loss per species ($\lambda_D$) index of the annual inshore
rockfish longline survey. $\lambda_D$ indicates that the $\lambda_s$ index is estimated from observations made on
the deck of the vessel. I split the annual inshore rockfish longline survey data by PFMA (Figure
3.1) and estimated $\lambda_i^D$ for Yelloweye and Quillback in each PFMA area because I expected
different trends among the PFMA areas. This treatment is consistent with recent stock
assessments for Yelloweye in this region (Yamanaka et al. 2012b, Yamanaka et al. 2018). I
estimated $\lambda_i^D$ under three different assumptions about the source of bare hooks: (1) bare hooks
were ignored and excluded from the catch; (2) bare hooks were due equally to all species caught
on the hooks, including Yelloweye, Quillback and Spiny Dogfish, or the fraction of fish that took
the bait and escaped was assumed to be identical for all species; and (3) bare hooks were due
only to species other than Yelloweye and Quillback, which included Spiny Dogfish. In all three
assumptions about bare hooks, Yelloweye ($\lambda_Y^D$), Quillback ($\lambda_Q^D$) and other species ($\lambda_O^D$)
contribute to the total instantaneous rate of bait loss ($\lambda^D$):

$$\lambda^D = \sum_x \lambda_x^D = \lambda_Y^D + \lambda_Q^D + \lambda_O^D$$

Eq. 3.6

To estimate the posterior median $\lambda_i^D$ for Yelloweye and Quillback, I used a similar
Bayesian methodology to Chapter 2 (Methods section 2.2.2.3). I assumed that at the end of the
longline soak time $t$, the number of hooks that were still baited ($N_B$) or had caught a Yelloweye
($N_Y$), Quillback ($N_Q$), another species ($N_O$) or were bare ($N_E$), followed a Multinomial
distribution:

$$(N_B, N_Y, N_Q, N_O, N_E) \sim M(N, p = (p_B, p_Y, p_Q, p_O, p_E))$$

Eq. 3.7

where $p$ is the probability of a hook being baited ($p_B$, Eq. 2.7, Methods section 2.2.2.3) or in one
of the four categories of catch ($p_x$), or three categories of catch when bare hooks were excluded
from the model under assumption number one:
\( (N_B, N_Y, N_Q, N_O) \sim M(N, p = (p_B, p_Y, p_Q, p_O)) \)  

Eq. 3.8

The sum of \( p_s \) across all the categories of catch must equal one. Estimating \( p_s \) depended on the assumption about the source of the bare hooks. When the bare hooks were excluded from the catch, \( p_s \) for all three categories of catch was:

\[ p_s = \frac{\lambda_s}{\lambda} (1 - e^{-\lambda t}) \]  

Eq. 3.9

When the bare hooks were attributed to a particular species then \( p_s \) for that category of catch \( s \) was:

\[ p_s = (1 - w) \frac{\lambda_s}{\lambda} (1 - e^{-\lambda t}) \]  

Eq. 3.10

and the probability of a hook being bare (\( p_E \)) was:

\[ p_E = w (1 - e^{-\lambda t}) \]  

Eq. 3.11

where \( w \) was the probability that the source of the bare hooks would successfully escape with the bait.

To compare the temporal trends in \( \lambda_s^D \) for each survey area, I estimated the posterior median of the annual \( \lambda_s^D \) for each of the three different bare hook assumptions using WinBUGS 1.4 (Lunn et al. 2000) called from within the R statistical software (R Core Team 2017) with the R2WinBUGS package (Sturtz et al. 2005). I also compared the posterior median \( \lambda_s^D \) estimates to the annual mean nominal catch per unit effort (CPUE, mean \( U_s^D \), see Table 2.1) calculated from all the sets in that survey area.
3.2.4.2 Correcting for sea star loss during longline retrieval

While identifying the sources of bare hooks from the March 2010 experiment, I found that although 130 individual sea stars (Astroidea spp.) were observed on hooks underwater on ROV Pass 3, 88 of these sea stars were lost from the hooks before the longline reached the deck. The loss of these sea stars did not result in any bare hooks. I observed that large sea stars could entirely cover baited hooks underwater, making the hooks inaccessible to other species. As 68% of sea stars on hooks were lost and the bait was retained, this source of hook competition would not be included in the bare hooks catch category. This could potentially create an artificially low λs index for Yelloweye and Quillback on longline sets with sea stars. To test whether this hidden sea star behaviour and competitive interaction changed the temporal trends in the estimated λs indices for Yelloweye and Quillback, I compared the annual λs indices for the rockfish longline survey to an index adjusted for sea star loss (λs*).

To determine a correction for the hidden hook competition due to the loss of sea stars, I fit a logistic regression (binomial Generalized Linear Model (GLM), Zuur et al. 2009), between the logit-transformed proportion of baited hooks observed on deck that lost sea stars during gear retrieval (zL) and the number of sea stars observed on the deck (NR) during the March 2010 experiment:

\[
\log\left(\frac{zL}{1-zL}\right) = \alpha + \beta_{NR} \cdot N_R + \varepsilon
\]

Eq. 3.12

For each set, the proportion of baited hooks, observed on the deck, that lost sea stars during gear retrieval was calculated from the number of sea stars observed on Pass 3 underwater (NW) and
the number of sea stars ($N_R^D$) and baited hooks ($N_B$) observed on the deck:

$$zL = \frac{N_R^W - N_R^D}{N_B} \quad \text{Eq. 3.13}$$

I fit the logistic regression using the "glm" function in the R base stats package (R Core Team 2017) to obtain the regression coefficients (Figure 3.2). As the March 2010 experiment only included 13 longline sets in a small geographical area (Figure 2.1), I fit logistic regressions to $zL$ values two times (scenario 1) and four times as high (scenario 2) as observed in the March 2010 experiment (Figure 3.2). I used the regression coefficients from the three models to adjust the number of sea stars caught during the annual inshore rockfish longline survey for sea star loss as:

$$N_R^{D*} = \left( \frac{e^{\alpha + N_R^D \beta N_R^D}}{1 + e^{\alpha + N_R^D \beta N_R^D}} \cdot N_B \right) + N_R^D \quad \text{Eq. 3.14}$$

and estimated the adjusted index ($\lambda_i^{D*}$) from these new sea star counts ($N_R^{D*}$). I tested the temporal trends in the posterior median $\lambda_i^D$ indices for Yelloweye and Quillback for sensitivity to increased sea star loss, by estimating the adjusted index ($\lambda_i^{D*}$) when the sea star loss was increased by two and four times.

To estimate the posterior medians of the annual $\lambda_i^D$ and $\lambda_i^{D*}$ (adjusted for sea star loss) for Yelloweye and Quillback in each survey area, I used the total instantaneous rate of bait loss ($\lambda^D$) described in Chapter 2 (Methods section 2.2.2.2). I treated bare hooks ($\lambda_E^D$) as a separate category of catch, in addition to Yelloweye ($\lambda_Y^D$), Quillback ($\lambda_Q^D$) and other species ($\lambda_O^D$):

$$\lambda^D = \sum_s \lambda_i^D = \lambda_Y^D + \lambda_Q^D + \lambda_O^D + \lambda_E^D \quad \text{Eq. 3.15}$$
and used the same Bayesian methodology for estimating the posterior median $\lambda_s^D$ in Chapter 2 (see Methods section 2.2.2.3). I estimated the posterior medians of the annual $\lambda_s^D$ and $\lambda_s^{D*}$ (adjusted for sea star loss) using WinBUGS 1.4 (Lunn et al. 2000) called from within the R statistical software (R Core Team 2017) by the R2WinBUGS package (Sturtz et al. 2005). The temporal trends in posterior median $\lambda_s^D$ and $\lambda_s^{D*}$ (adjusted for sea star loss) were compared to those of the annual mean nominal CPUE, calculated from all the sets in that PFMA area (mean $U_s^D$, see Table 2.1).

3.2.4.3 Bayesian estimation

For the $\lambda_s^D$ indices estimated under the three different bare hook assumptions, I set the prior distribution as:

$$\lambda_s^D \sim \text{exponential (5.4 h}^{-1}\text{)}$$  \hspace{1cm} \text{Eq. 3.16}

for each $\lambda_s^D$. The prior distribution for $w$, the probability that the source of the bare hooks would successfully escape with the bait, was:

$$w \sim \text{beta (2, 6)}$$  \hspace{1cm} \text{Eq. 3.17}

when the bare hooks were attributed equally to all species caught on the hooks, including Yelloweye, Quillback and Spiny Dogfish, and:

$$w \sim \text{beta (2, 2)}$$  \hspace{1cm} \text{Eq. 3.18}

when bare hooks were due only to species other than Yelloweye and Quillback, which included Spiny Dogfish. For the models adjusting for sea star loss, I set the prior distribution of each $\lambda_s^D$
and $\lambda_r^{D^e}$ (adjusted for sea star loss) as:

$$\lambda_r^{D^e} \sim \text{exponential} \ (7.5 \ h^{-1}) \quad \text{Eq. 3.19}$$

The prior distributions were specified to maintain a realistic maximum, while ensuring that the instantaneous rate of bait loss could not be negative. I selected these rate parameters because they created a post-model pre-data distribution (McAllister 2014) with a mean close to 0.4 for $p_B$. This is similar to the proportion of hooks that returns with bait on the British Columbia fisheries-independent longline survey (Lochead and Yamanaka 2007). Additionally, the posterior mean $\lambda_r^{D^e}$ was relatively equal for all the categories of catch. 200,000 samples were taken from the joint posterior distribution for the $\lambda_r^{D^e}$ parameters using Markov Chain Monte Carlo (MCMC) methods (two Markov chains). Prior to taking the samples, the first 15,000 samples from each chain were removed as a burn-in period. To check that the chains had approached a stationary distribution, the Gelman-Rubin convergence statistics (Gelman et al. 2004) were calculated for each MCMC run, using the R coda package (Plummer et al. 2006). The Gelman-Rubin convergence statistics were <1.1 for all parameters. In addition, the posterior distributions (Appendix D, Figure D.1-Figure D.28), trace plots and autocorrelation plots were inspected for each parameter to ensure that the chains showed satisfactory mixing and there was no strong autocorrelation within the chains. I also tested that the posterior distribution was approximated with sufficient precision (MC error was less than 5% of the posterior standard deviation (Powers and Xie 2008)).
3.3 Results

3.3.1 Field observations of species behaviours and interactions affecting longline catch

To determine the sources of the bare hooks, I made repeated observations of the longline hooks in March 2010: three observations with the ROV underwater and one observation on the deck during longline retrieval. I found probable sources of bait removal by predation for 14%, or 33, of the 239 hooks observed to be bare during the 13 longline sets (Table 3.1). For these 33 bare hooks, a fish or large invertebrate was observed hooked, or feeding on the bait, during the previous ROV observation of the hook. This included six Spiny Dogfish (18%), three Yelloweye (9%), one Quillback (3%), one Pacific Cod (*Gadus macrocephalus*, 3%), seven Giant Pacific Octopuses (*Enteroctopus dofleini*, 21%) and 15 crabs or groups of crabs (*Cancridae* sp., *Lithodoidea* spp., *Majidae* sp., *Oregoniidae* sp., 46%), particularly Brown Box Crabs (*Lopholithodes foraminatus*) (11 of the 15 observations of crabs) (Table 3.1). While crabs and Giant Pacific Octopuses accounted for 67% of the probable sources of bait removal, only one Giant Pacific Octopus and zero crabs were seen on the deck. For 71% of the 239 hooks, I could not observe a probable source of bait removal, as the hooks had either bait (162 hooks, 68%) or were not observed (7 hooks, 3%) during the previous pass over the longline (Table 3.1).

Despite few observations of probable sources of bait removal due to species escaping with the bait, I observed that a large number of sea stars escaped from the hooks while the bait remained on the hook. This loss of sea stars occurred after the third ROV observation of the hooks underwater, but before the observation of the hooks on the deck. Across all 13 longline sets in the March 2010 experiment, 130 sea stars (*Crossaster papposus, Evasterias trochelii, Luidia foliolata, Mediaster aequalis, Orthasterias koehleri, Pisaster brevispinus, Pycnopodia*
*helianthoides* and *Stylasterias forreri*) were observed on the baited hooks during the third ROV pass underwater, but only 42 (32%) of these sea stars (*Luidia foliata*, *Pycnopodia helianthoides* and *Stylasterias forreri*) were observed on the deck. However, all the hooks observed to lose a sea star returned to the deck with the bait on the hook. A logistic regression between the logit-transformed proportion of baited hooks that lost sea stars during gear retrieval and the number of sea stars observed on the deck had a slope of 0.074 ± 0.096 (± standard error) and an intercept of -3.758 ± 1.930 (*n* = 13).

To analyze whether mechanical loss during longline release and retrieval resulted in fewer bare hooks than removal of the bait by species, I looked at when most of the bare hooks were first observed. In the March 2010 experiment, the average time that bare hooks were first observed varied between the sets (Table 3.2). For the sets with the most bare hooks, the mean time of observation was around the halfway point of the set (60 min). The shortest and longest mean times of observation came from sets with less than two bare hooks (Table 3.2). The 95% confidence intervals did not overlap for some of the sets. Over all 13 sets, 66% of the 239 bare hooks were first observed during one of the three observations periods underwater (Pass 1, Pass 2 and Pass 3 in Table 3.1). The other 34% were first observed on the deck, meaning bait removal occurred between the last observation underwater (Pass 3) and the observation during retrieval of the longline on the deck (Table 3.1). Of the bare hooks first observed underwater, 24% (37 of the 157 bare hooks) were already bare by the first underwater observation of the gear (Pass 1), meaning bait removal occurred sometime between the release of the baited hooks from the deck and the first observation with the ROV. Taken together, almost 50% of the hooks became bare during periods where the longline was either moving or was stationary and unobserved (Pass 1 and deck observations in Table 3.1). Five of the 13 sets did show the highest bait removal rate
during periods where the gear was either moving, or stationary and unobserved (Figure 3.3). However, across all the sets, there was no significant difference in the bait removal rate (number of bare hooks/h) between observation periods when the longline was stationary and observed (Pass 2 and Pass 3), and periods when the longline was either moving, or was stationary and unobserved (Pass 1 and on the deck) ($F_{3,36} = 0.20, p = 0.89$) (Figure 3.3). Set number did not have a significant effect on the bait removal rate ($F_{12,36} = 1.99, p = 0.06$), but trends across the observation periods varied between the sets.

To assess if there was a relationship between the proportion of bare hooks observed on the deck and the catch on the deck, I focused on the species most frequently observed as probable sources of bait removal (from Table 3.1) that were also commonly caught on the deck in the March 2010 experiment. The most frequent sources of bare hooks that were also commonly caught on the deck were Spiny Dogfish, Yelloweye and Quillback (Table 3.1). I combined Yelloweye and Quillback catches with the catches of the three other inshore rockfish species: Copper, Tiger and China. In the March 2010 experiment, the proportion of bare hooks significantly increased as the catch of Spiny Dogfish (logistic regression, $\chi^2 = 36.61, df = 1, p < 2.2 \times 10^{-16}$, McFadden's pseudo-$R^2 = 0.54$), inshore rockfish ($\chi^2 = 128.82, df = 1, p = 3.02 \times 10^{-5}$, McFadden's pseudo-$R^2 = 0.09$), or other species, including Spiny Dogfish ($\chi^2 = 77.44, df = 1, p < 2.2 \times 10^{-16}$, McFadden's pseudo-$R^2 = 0.34$) increased (Figure 3.4). The proportion of bare hooks also increased as the mean observed density of inshore rockfish increased ($\chi^2 = 131.73, df = 1, p = 1.4 \times 10^{-4}$, McFadden's pseudo-$R^2 = 0.07$) (Figure 3.4). However, the model that included the catch of Spiny Dogfish as the explanatory variable had the greatest likelihood when compared to an intercept-only null model (McFadden's pseudo-$R^2 = 0.54$), whereas the models including inshore rockfish had much lower pseudo-$R^2$ values (Figure 3.4).
Similar results were obtained from logistic regressions between the proportion of bare hooks and the catch of Spiny Dogfish, inshore rockfish and total other species, for the sets of the annual inshore rockfish longline survey (Figure 3.5). The proportion of bare hooks on the survey sets significantly increased as the catch of Spiny Dogfish (logistic regression, $\chi^2 = 31933$, $df = 1$, $p < 2.2 \times 10^{-16}$, McFadden's pseudo-$R^2 = 0.43$), or other species, including Spiny Dogfish ($\chi^2 = 27517$, $df = 1$, $p < 2.2 \times 10^{-16}$, McFadden's pseudo-$R^2 = 0.50$) or excluding Spiny Dogfish ($\chi^2 = 58489$, $df = 1$, $p = 3.3 \times 10^{-13}$, McFadden's pseudo-$R^2 = 8.6 \times 10^{-4}$) increased (Figure 3.5).

However, the proportion of bare hooks decreased as the catch of inshore rockfish increased ($\chi^2 = 52861$, $df = 1$, $p < 2.2 \times 10^{-16}$, McFadden's pseudo-$R^2 = 0.09$) (Figure 3.5). All relationships were statistically significant due to the large sample size ($n = 701$ sets). However, the models that included the catch of Spiny Dogfish as an explanatory variable had the greatest likelihood when compared to an intercept-only null model (McFadden's pseudo-$R^2 = 0.43$ (Spiny Dogfish only), 0.50 (other species, including Spiny Dogfish)) (Figure 3.5). The models including inshore rockfish and other species (excluding Spiny Dogfish) had a likelihood similar to the intercept-only null model (McFadden's pseudo-$R^2 = 0.09$ and $8.6 \times 10^{-4}$ respectively). When the sets were split into each survey area (i.e., PFMA 12, 13, 14, 15, 16, 17 and 28), most of the relationships remained the same. The proportion of bare hooks decreased in all areas as the catch of inshore rockfish increased (Figure 3.6) and increased in all areas as the catch of Spiny Dogfish (Figure 3.7) or other species, including Spiny dogfish increased (Figure 3.8). However, the proportion of bare hooks did not increase as the catch of other species, excluding Spiny Dogfish, increased except in Area 12 (Figure 3.9). When all the survey sets were combined, adding other species to the Spiny Dogfish catch increased the likelihood of the model compared to the null intercept-only model (McFadden's pseudo-$R^2$ went from 0.43 to 0.50) (Figure 3.5). However, when the
sets were divided by area, the likelihood only increased slightly in some areas (Areas 14, 16 and 28) and actually decreased slightly in some areas (Areas 13, 15 and 17) (Figure 3.7 - Figure 3.8). Only Area 12 showed a similar increase (McFadden's pseudo-$R^2$ went from 0.29 to 0.40) (Figure 3.7 - Figure 3.8).

3.3.2 Effect of accounting for species behaviours and interactions on trends in longline relative abundance indices

To test whether different assumptions about the source of bare hooks altered the temporal trends in the estimated $\lambda_s^D$ index, I compared the Yelloweye and Quillback $\lambda_s^D$ indices estimated when bare hooks were: (1) excluded from the catch; (2) equally due to the escape of all species on the hooks; and (3) only due to species other than Yelloweye and Quillback. For the annual rockfish longline survey, the trends in estimated mean-scaled $\lambda_s^D$ index were similar regardless of the assumption about bare hooks, for both Yelloweye and Quillback (Figure 3.10 - Figure 3.11). Mean-scaled $\lambda_s^D$ was very similar when bare hooks were excluded or treated as coming from other species, but higher when bare hooks were also attributed to Yelloweye and Quillback (Figure 3.10 - Figure 3.11). Trends in the mean nominal CPUE per area (mean $U_s^D$ divided by the mean for the entire time series) were also similar to the mean-scaled $\lambda_s^D$ trends for Yelloweye and Quillback, except in two areas (PFMAs 14 and 15) (Figure 3.10 - Figure 3.11).

Temporal trends in the estimated $\lambda_s^D$ index were affected little when the catch on the annual longline survey was adjusted for sea star loss during gear retrieval (Figure 3.12 - Figure 3.13). In all areas, the 95% Bayesian credible interval for $\lambda_s^{D*}$ (adjusted for sea star loss) encompassed the unadjusted $\lambda_s^D$ index for both Yelloweye and Quillback (shaded areas in Figure 3.8).
3.12 and Figure 3.13). Adjusting the $\lambda_s^D$ index for an increase in the proportion of sea stars lost by two and four times (Figure 3.2) did not change the temporal trends in $\lambda_s^{DP}$ (adjusted for sea star loss) for either Yelloweye or Quillback (Figure 3.14 - Figure 3.15). In all areas, the 95% Bayesian credible interval for $\lambda_s^{DP}$ (adjusted for four times the sea star loss) still encompassed the unadjusted $\lambda_s^D$ index for both Yelloweye and Quillback (shared areas in Figure 3.14 and Figure 3.15).

3.4 Discussion

The main assumption when using catch as a relative abundance index is that the catch rate of the target species is proportional to the species abundance (Ricker 1940, Ricker 1944, Gulland 1955, Beverton and Holt 1955). However, species-specific feeding behaviours and competitive interactions can influence the longline catch (reviews in Løkkeborg 1994, Stoner 2004, Løkkeborg et al. 2010, Løkkeborg et al. 2014) and the number of bare hooks returning (Shomura 1955, Johnstone and Hawkins 1981, He 1996), which could change the relative abundance index of the target species and might alter the temporal trends of the index. To identify species whose behaviours and competitive interactions might affect the $\lambda_s$ relative abundance index for inshore rockfish, an ROV was used to observe the longline hooks underwater, during an experiment in March 2010. I chose the $\lambda_s$ index because it attempts to account for interspecific competition and saturation of the hooks with catch (Murphy 1960, Rothschild 1967, Somerton and Kikkawa 1995) and is used in current stock assessments (Yamanaka et al. 2012a, Yamanaka et al. 2012b, den Heyer et al. 2015, Webster and Stewart 2015, Yamanaka et al. 2018). I found that while the number of Spiny Dogfish caught on the deck was generally the best predictor of the proportion of bare hooks returning to the deck, Spiny
Dogfish was only one of the probable sources of bare hooks identified with the ROV video. Large invertebrates, like crabs and Giant Pacific Octopus, were more frequently observed than Spiny Dogfish as the probable sources of bare hooks, but were rarely observed on the deck. Bait removal by species appeared to be equally likely or greater than mechanical removal. Bait removal during periods when the longline was moving, or was stationary but unobserved, was not higher than at other times. Furthermore, large sea stars, which cover the baited hooks and ingest the bait and hook together, were observed to be frequently lost from the longline during gear retrieval, while the bait was retained. Correcting for the observed species behaviours and competitive interactions, including the loss of sea stars and the source of bare hooks, did not markedly change the temporal trends in $\lambda_i^D$ for the annual inshore rockfish longline survey for either Yelloweye or Quillback. However, annual mean nominal CPUE (mean $U_i^D$) trends did differ from $\lambda_i^D$ trends in some areas (PFMAs) of the annual inshore rockfish longline survey.

Different assumptions about the source of bare hooks did not markedly change the temporal trends in $\lambda_i^D$, but the value of $\lambda_i^D$ did change, and $\lambda_i^D$ trends were different from $U_i^D$ in some areas. When some of the bare hooks were assumed to be due to Yelloweye and Quillback escaping, the catch attributed to those species increased and the $\lambda_i^D$ estimates increased by $1.28 \pm 0.16$ times (± standard deviation) relative to when bare hooks were excluded, and by $1.48 \pm 0.22$ times compared to when bare hooks were assumed to be due to species other than Yelloweye or Quillback. Hoag et al. (1984) and Kaimmer and St.-Pierre (1993) hypothesized that large catches of Spiny Dogfish in some areas reduced the catchability of the target species, Pacific Halibut, through competition for hooks. In the same geographic area, longline catches had a much higher percentage of Spiny Dogfish relative to Pacific Halibut than did trawl catches. If trawl
catchability is similar for both species, this may suggest that Spiny Dogfish are preventing Pacific Halibut from accessing longline hooks. For Area 14 of the annual longline survey, the trends in mean $U_s^D$ did differ from $\lambda_s^D$ for both Yelloweye and Quillback. Area 14 had the highest mean number of Spiny Dogfish caught per set. Without empirical evidence to support the assumptions used to attribute bare hooks to either the target species or non-target species, the $\lambda_s$ index could be overestimated or underestimated annually, depending on the choice of assumption. This could be further complicated by fluctuations in the abundance of non-target species contributing to bare hooks.

The ROV observations during the March 2010 experiment provide empirical evidence for evaluating assumptions about the source of bare hooks. Inshore rockfish, including Yelloweye and Quillback, appeared to be the source for some of the bare hooks in the March 2010 experiment. However, other non-target species contributed to a greater number of the bare hooks. Of the species commonly observed on the deck, Spiny Dogfish was the probable source of bait removal for the greatest number of hooks. Additionally, the proportion of bare hooks on the deck increased significantly as the number of Spiny Dogfish caught increased, both for the March 2010 experiment and for all areas on the annual inshore rockfish longline survey. Some sets on the survey showed saturation of all the hooks from a combination of Spiny Dogfish and bare hooks. Sets on the annual longline survey were never saturated by a combination of bare hooks and inshore rockfish, or other species, and the proportion of bare hooks actually decreased at the highest levels of inshore rockfish catch. Camera studies and stomach samples from halibut longline gear also suggest that dogfish are efficient at bait removal (Kaimmer and Stoner 2008). Based on the large catches of Spiny Dogfish on the annual inshore rockfish longline survey (Lochead and Yamanaka 2007), this species may make the greatest number of attacks on the
baited hooks. If Spiny Dogfish make the greatest number of attacks on baited hooks and the bait is removed as some of these Spiny Dogfish subsequently escape, it is credible that Spiny Dogfish could be responsible for a large number of the bare hooks.

Although I only infrequently observed Spiny Dogfish underwater, due to their avoidance of the ROV once detected (my observations, Matlock et al. 1991, Trenkel et al. 2004), I hypothesize that Spiny Dogfish would be more likely to attack the hooks, due to their greater mobility than species like inshore rockfish. Dogfish, which are often found in schools (Hart, 1973) throughout the entire water column (Hoag et al. 1984), feed on a wide variety of organisms (Jones and Geen 1977, Tanasichuk et al. 1991), determining location of prey based on scent (Parker, 1913) and are attracted, by scent, to areas where food abundance is high (Hart 1973). More mobile bait competitors tend to outcompete less mobile ones. For example, Sablefish (Anoplopoma fimbria) outcompete deepwater rockfish species for hooks (Rodgveller et al. 2008) and larger Pacific Halibut outcompete smaller ones (Hamley and Skud 1978, Stoner and Ottmar 2004), similar to larger tuna and billfishes competing for pelagic longline hooks (Ward 2008). This is likely due to differences in their swimming speeds (Hart 1993) and lower aggressiveness in smaller fish (Stoner and Ottmar 2004). Additionally, Johnstone and Hawkins (1981) found that Small-Spotted Catshark (Scyliorhinus canicula) were more likely to be hooked than competing Atlantic Cod (Gadus morhua) and Saithe (Pollachius virens), but equally likely to escape the hooks, indicating that a greater number of attacks could result in more bare hooks.

If Spiny Dogfish are responsible for the majority of the bare hooks on the inshore rockfish longline survey, but bare hooks are allocated to species based on their proportion in the catch, then $\lambda_s$ for inshore rockfish species would consistently be overestimated in the presence of Spiny Dogfish.
The ROV observations of the longline underwater also revealed that species that are rarely observed on the deck might contribute to a greater number of bare hooks than species that are frequently caught and brought to the deck. During the March 2010 experiment, crabs and Giant Pacific Octopus were observed as the probable sources of bait removal three times more often than Spiny Dogfish, but I only observed one Giant Pacific Octopus, and zero crabs, on the deck of the fishing vessel. Crabs have been observed to remove bait from bottom longlines, during submarine (High 1980, Grimes et al. 1982) and fixed camera observations (He 1996). Grimes et al. (1982) observed that crabs and starfish together removed 50% of the longline bait in four hours. Octopuses have been observed to attack hooked fish, but not baited hooks (Erzini et al. 1996). This may also be true for some of the large Giant Pacific Octopuses that I observed during the March 2010 experiment. The one Giant Pacific Octopus caught and brought to the deck was in the process of trying to remove a Quillback from the hook and I observed at least one other underwater that appeared to be wrapped around a fish. I also observed very small octopuses directly on the bait, which resulted in bare hooks in the subsequent ROV observations. It could be possible that I more frequently observed large invertebrates, like crabs and Giant Pacific Octopuses, as the probable source of bare hooks because they may be slower at removing bait from hooks than Spiny Dogfish or other fish. Alternatively, rather than being the main cause of bare hooks, higher Spiny Dogfish catches could indicate that the longline hooks are on habitat favorable for large invertebrates that are capable of removing bait. For example, Area 17, which showed the weakest relationship between the number of Spiny Dogfish caught and the proportion of bare hooks observed on the deck, had the highest mean number of bare hooks per set, and was the area where most of the March 2010 longline sets were conducted. Additionally, the three areas of the longline survey with the highest mean number of bare hooks per set (Areas
(12, 14 and 17) also had the highest mean number of sea stars caught. Although sea stars were not observed to remove bait during the March 2010 experiment, these observations could indicate higher bait removal by large invertebrates in these areas, as observed with the ROV during the March 2010 experiment in Areas 14 and 17. Ultimately, if these unobserved invertebrates are a substantial source of the bare hooks, then indices estimated from assumptions based on the species observed on the deck (e.g., Somerton and Kikkawa 1995, Yamanaka et al. 2012a, Yamanaka et al. 2012b) would tend to overestimate the $\lambda_s$ index for the target species by incorrectly attributing bare hooks to the target species. These incorrect assumptions could also obscure temporal trends in the $\lambda_s$ index, as some crab species, and Giant Pacific Octopus, appear to have large annual fluctuations (Hartwick et al. 1984; Zhang and Dunham 2013), which could cause overestimation of the target species index to vary from year to year.

Bait removal due to mechanical sources, i.e., during the release and retrieval of the longline or dragging the longline along the bottom, may also influence the $\lambda_s$ index, but cannot typically be separated from other sources of bare hooks. I did not observe a significant difference in the bait removal rate during periods when the longline hooks were settled on the bottom and stationary and when the longline hooks were either moving, or were stationary and unobserved. Skud (1978) did observe bait loss on the vessel as the bottom longline was being released, but did not quantify the bait loss. However, Shepard et al. (1975) concluded that about 2% of the hooks lost their bait or became tangled during release of a pelagic longline. In the March 2010 experiment, bait loss in the period between the release of the longline from the vessel and the first observation with the ROV underwater was generally not higher than in other observation periods. Additionally, I did not observe the loss of bait on the deck as the longline was being released into the water. Ward and Myers (2007) suggested that gear retrieval was not a
significant source of bait loss, based on their best-fitting model to explain bait loss from pelagic longlines. However, from my observations, five of the 13 sets in the March 2010 experiment showed a higher bait removal rate in the period when the longline was returning to the deck than in other periods. This could be due to species escaping rather than a mechanical source. The highest loss of species resulting in bare hooks occurred between the third ROV pass underwater and the observation on the deck. Perhaps more species escape with the bait as the longline is being retrieved, similar to the loss of sea stars from the hooks during gear retrieval.

The ROV observations of the longline showed that almost 70% of the sea stars covering the baited hooks underwater were lost as the longline was pulled back to the deck. As none of these sea stars removed the bait, their influence on the available number of hooks would not be accounted for in the catch or in the assumptions about bare hooks, even when assuming bare hooks were only due to species other than Yelloweye and Quillback. To adjust the catches on the annual longline survey for this hidden competition, I used the catches predicted by a logistic regression between the proportion of sea stars lost and the number of sea stars observed on the deck during the March 2010 experiment. If baited hooks that were actually unavailable underwater due to sea stars are included as baited hooks, rather than as catch, then the total instantaneous rate of bait loss for the set ($\lambda$) and the $\lambda_s$ indices would be underestimated. This potential bias in the $\lambda_s$ indices could vary from year to year, particularly as the abundance of large sea stars has decreased in recent years due to a sea star wasting disease (Hewson et al. 2014, Eisenlord et al. 2016). This variation in available hooks created by sea star competition could obscure the true temporal trends for the $\lambda_s$ index. However, accounting for these hidden sea stars caused little change in the Yelloweye or Quillback $\lambda_s^D$ index for all the survey areas (PFMAs), even when sea star loss was increased four times. The minimal impact of the sea star
loss on the $\lambda_s$ indices may be due to differences in the habitat preferences of Yelloweye, Quillback and sea stars. For example, during the March 2010 experiment, the highest densities of the large Sunflower Star (*Pycnopodia helianthoides*) were on sandy bottoms where few Yelloweye and Quillback were found. Yelloweye and Quillback prefer more complex bottom types, particularly boulder-fields (Richards 1986, O’Connell and Carlile 1993, Murie *et al.* 1994, Martin *et al.* 2006, Yamanaka *et al.* 2012c, Haggarty *et al.* 2016). While Sunflower Stars can be found on many habitat types (Britton-Simmons *et al.* 2012), the largest Sunflower Stars tend to be on softer bottoms (Shivji *et al.* 1983). Large Sunflower Stars move faster than small ones, with speeds of approximately 36 m/h (Montgomery 2014) and are capable of moving to the bait relatively quickly when near the hooks. Hidden competition from sea stars could be more important when estimating the $\lambda_s$ index for species caught on softer bottoms.

During the March 2010 experiment, the ROV observations of the sources of bare hooks and the loss of species from the longline were limited by the small sample size, both in terms of the number of sets and the repeated observation of each hook underwater. As the ROV was continually moving along the longline, I only had three observations of each hook underwater. The length of time between the observations was also highly variable. Some hooks were viewed twice in rapid succession, as the ROV turned at the end of the longline, and other hooks had a much longer time gap between the observations. With such infrequent observation of each hook, I missed many of the bait removal events and the ones I did observe may not be a representative sample. For example, if I was more likely to view bait removals by crabs and Giant Pacific Octopuses due to their methods of bait removal, then I would overestimate their contribution to the number of bare hooks. An alternate method would be to use hook timers (Somerton *et al.* 1988) to measure the time each hook was first attacked. Then the times for bare hooks could be
compared to the times when different species were caught on the hooks (Somerton and Kikkawa 1995). However, my methods have an advantage over hook timers in that I directly observed the hooks underwater. Although hook timers should accurately measure the timing of hook attacks, and potentially bait removal, only the species caught on the deck could be considered as the sources of bare hooks. Large invertebrates, such as the crabs, octopuses and sea stars would be remain as hidden influences, which could result in attributing too many bare hooks to the target species and overestimating the relative abundance index, $\lambda_s$. Additionally, I treated each observation as independent, but this is unlikely to be true, as hooked fish can increase the interest of unhooked fish (Fernö et al. 1986, Løkkeborg et al. 1989, Stoner and Ottmar 2004).

A variety of species behaviours and competitive interactions from the target and non-target fish species and large invertebrates, as well as mechanical processes, appear to contribute to competition for hooks and result in bare hooks. However, the extent of some of these sources can only be fully observed underwater. Corrections to the relative abundance indices for the influence of hook competition and bare hooks usually relies on assumptions based on the species observed on the deck (Somerton and Kikkawa 1995, Yamanaka et al. 2012a, Yamanaka et al. 2012b). This has the potential to change the relative abundance index of the target species and alter the temporal trends of the index. If the sources of competition and bare hooks are unknown, the most conservative approach would be to avoid attributing bare hooks to the target species (e.g., Bjordal 1983, Hovgård and Lassen 2000, Yamanaka et al. 2018), as this would provide the minimum estimate of the relative abundance index. However, empirical studies like this one can help to provide evidence for the choice of these assumptions. For the inshore rockfish survey, bare hooks should be attributed to other species more frequently than is assumed from on-deck observations. Future studies should work to understand fish community influencing the longline.
More accurate observations could be obtained by pairing underwater cameras and hook timers or perhaps by using sonar paired with the ROV, as applied by Rose et al. (2005). Additionally, simulation studies that investigate the potential impact of hidden sources of bare hooks and hook competition on the relative abundance indices, the management parameters and the resulting management advice would improve our understanding of the necessity of correcting for hidden processes.
Table 3.1. Probable sources of bare hooks for the March 2010 experiment, based on three observations of the hooks underwater by the ROV (Pass 1, Pass 2, Pass 3) and one observation of the hooks on the deck during longline retrieval. Bait removal sources were determined by looking at the state of each hook on the ROV pass previous to when the hook was first observed to be bare.

<table>
<thead>
<tr>
<th>Species</th>
<th>New bare hooks</th>
<th>Not observed</th>
<th>Bait</th>
<th>Total Species</th>
<th>Spiny Dogfish</th>
<th>Yelloweye Rockfish</th>
<th>Quillback Rockfish</th>
<th>Pacific Cod</th>
<th>Crabs</th>
<th>Giant Pacific Octopus</th>
</tr>
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<tbody>
<tr>
<td>Pass 1</td>
<td>37</td>
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<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Pass 2</td>
<td>70</td>
<td>65</td>
<td>1</td>
<td>4</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Pass 3</td>
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<td>2</td>
<td>8</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td>Deck</td>
<td>82</td>
<td>57</td>
<td>4</td>
<td>21</td>
<td>4</td>
<td>3</td>
<td>1</td>
<td>1</td>
<td>10</td>
<td>2</td>
</tr>
<tr>
<td>Total</td>
<td>239</td>
<td>162</td>
<td>7</td>
<td>33</td>
<td>6</td>
<td>3</td>
<td>1</td>
<td>1</td>
<td>15</td>
<td>7</td>
</tr>
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</table>
Table 3.2. Mean ($\mu$) and standard deviation ($\sigma$) for the time (min) that bare hooks were first observed underwater on each longline set in the March 2010 experiment. Data from all three ROV passes are combined and $n$ is the total number of newly bare hooks observed underwater for each set.

<table>
<thead>
<tr>
<th>Set</th>
<th>$n$</th>
<th>$\mu$</th>
<th>$\sigma$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>16</td>
<td>69.8</td>
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</tr>
<tr>
<td>2</td>
<td>12</td>
<td>44.9</td>
<td>24.8</td>
</tr>
<tr>
<td>3</td>
<td>23</td>
<td>63.2</td>
<td>29.0</td>
</tr>
<tr>
<td>4</td>
<td>15</td>
<td>63.1</td>
<td>27.9</td>
</tr>
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<td>5</td>
<td>24</td>
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</tr>
<tr>
<td>7</td>
<td>23</td>
<td>79.1</td>
<td>26.3</td>
</tr>
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<td>8</td>
<td>4</td>
<td>53.7</td>
<td>52.3</td>
</tr>
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<td>9</td>
<td>6</td>
<td>63.9</td>
<td>28.7</td>
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<tr>
<td>10</td>
<td>5</td>
<td>88.4</td>
<td>24.9</td>
</tr>
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<td>11</td>
<td>8</td>
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<td>32.1</td>
</tr>
<tr>
<td>12</td>
<td>2</td>
<td>39.9</td>
<td>14.0</td>
</tr>
<tr>
<td>13</td>
<td>1</td>
<td>104.6</td>
<td>-</td>
</tr>
</tbody>
</table>
Figure 3.1. Pacific fishery management areas (PFMAs, Fisheries and Oceans Canada) that were frequently sampled during the years of the annual inshore rockfish longline survey (2003-2005, 2007-2015). The survey operates in the Canadian waters inside Vancouver Island.
Figure 3.2. Proportion of the baited hooks observed on the deck that lost seas stars during gear retrieval in the March 2010 experiment (Base case). Loss was determined by comparing underwater hook observations, using the ROV, to the hook observations on-deck. To test scenarios where sea star loss might be greater than observed in the March 2010 experiment, the proportion of baited hooks that lost sea stars was increased two times (blue line) and four times (red line). Regression coefficients from the logistic model fits to the logit-transformed proportion data were used to adjust for potential sea star loss on survey longline sets.
Figure 3.3. During the March 2010 experiment, mechanical removal did not appear to be the main source of bare hooks on the longline. Bait removal rates (number of bare hooks / h) between observation periods were not consistently higher when the gear was either moving, or stationary and unobserved (periods one and four) than when it was stationary (periods two and three). The first three observation periods occurred underwater with the Remotely Operated Vehicle, while the fourth observation occurred on the deck as the longline was retrieved by the fishing vessel. Bare hooks were only counted when they were first observed to be bare.
Figure 3.4. The proportion of the hooks without catch that returned bare (i.e., unbaited), observed on the deck during the March 2010 experiment ($n = 13$ sets). This proportion of bare hooks had a significant logistic relationship (solid line) with the number of Spiny Dogfish, inshore rockfish and other species (including Spiny Dogfish) caught on the set, and with the mean observed density of inshore rockfish. McFadden's pseudo-$R^2$ (Eq. 3.5) was largest for the model with Spiny Dogfish only (0.54).
Figure 3.5. The proportion of the hooks without catch that returned bare (i.e., unbaited), observed on the deck during the annual inshore rockfish longline survey (2003-2005, 2007-2015) \((n = 701\) sets). This proportion of bare hooks showed a positive logistic relationship (solid line) with the number of Spiny Dogfish and other species (including or excluding Spiny Dogfish) caught on the set, but not with the number of inshore rockfish caught. McFadden's pseudo- \(R^2\) (Eq. 3.5) was largest for the Spiny Dogfish alone (0.43) and for other species including Spiny Dogfish (0.50).
Figure 3.6. The proportion of the hooks without catch that returned bare (i.e., unbaited), observed on the deck in each survey area (PFMAs) during the annual inshore rockfish longline survey (2003-2005, 2007-2015) \((n = 701\) sets). In all areas, this proportion of bare hooks showed a negative logistic relationship (solid line) with the number of inshore rockfish caught on the set. McFadden's pseudo-\(R^2\) (Eq. 3.5) was less than 0.28 in all areas.
Figure 3.7. The proportion of the hooks without catch that returned bare (i.e., unbaited), observed on the deck in each survey area (PFMAs) during the annual inshore rockfish longline survey (2003-2005, 2007-2015) \((n = 701\) sets). In all areas, this proportion of bare hooks showed a positive logistic relationship (solid line) with the number of Spiny Dogfish caught on the set. McFadden's pseudo-\(R^2\) (Eq. 3.5) was higher than 0.5 in several areas.
Figure 3.8. The proportion of the hooks without catch that returned bare (i.e., unbaited), observed on the deck in each survey area (PFMAs) during the annual inshore rockfish longline survey (2003-2005, 2007-2015) ($n = 701$ sets). In all areas, the proportion of bare hooks showed a positive logistic relationship (solid line) with the number of other species (including Spiny Dogfish, but excluding inshore rockfish) caught on the set. McFadden's pseudo-$R^2$ (Eq. 3.5) was higher than 0.5 in several areas.
Figure 3.9. The proportion of the hooks without catch that returned bare (i.e., unbaited), observed on the deck in each survey area (PFMAs) during the annual inshore rockfish longline survey (2003-2005, 2007-2015) ($n = 701$ sets). In all areas, except Area 12, this proportion of bare hooks showed a negative logistic relationship (solid line) with the number of other species (excluding Spiny Dogfish and inshore rockfish) caught on the set. McFadden's pseudo-$R^2$ (Eq. 3.5) was smaller than 0.11 in all areas.
Figure 3.10. Temporal trends of the mean-scaled Yelloweye Rockfish relative abundance indices, $\lambda_s^D$ (posterior median divided by the mean of the series) and $U_s^D$ (mean nominal CPUE per area divided by the mean of the series) under different assumptions about the source of bare hooks. Longline sets are from the annual inshore rockfish longline survey (2003-2005, 2007-2015) in survey areas (PFMAs) frequently sampled over the survey years ($n = 701$ sets). The shaded area represents the Bayesian 95% credible interval when $\lambda_s^D$ was estimated under the assumption that only other species (excluding Yelloweye Rockfish and Quillback Rockfish) are assumed to be the source of bare hooks.
Figure 3.11. Temporal trends of the mean-scaled Quillback Rockfish relative abundance indices, $\lambda^D_s$ (posterior median divided by the mean of the series) and $U^D_s$ (mean nominal CPUE per area divided by the mean of the series) under different assumptions about the source of bare hooks. Longline sets are from the annual inshore rockfish longline survey (2003-2005, 2007-2015) in survey areas (PFMAs) frequently sampled over the survey years ($n = 701$ sets). The shaded area represents the Bayesian 95% credible interval when $\lambda^D_s$ was estimated under the assumption that only other species (excluding Yelloweye Rockfish and Quillback Rockfish) are assumed to be the source of bare hooks.
Figure 3.12. Temporal trends in the mean-scaled Yelloweye Rockfish relative abundance index \( \lambda_s^D \) (posterior median divided by the mean of the series), when the catch data was adjusted for sea star loss during gear retrieval (\( \lambda_s^{D^a} \), blue line). \( \lambda_s^{D^a} \) trends are compared with those of the unadjusted \( \lambda_s^D \) (black line) and the mean nominal CPUE per area (mean \( U_s^D \) divided by the mean of the series, turquoise line). Longline sets are from the annual inshore rockfish longline survey (2003-2005, 2007-2015) in survey areas (PFMAs) frequently sampled over the survey years (\( n = 701 \) sets). The shaded area represents the Bayesian 95% credible interval for \( \lambda_s^{D^a} \), the index adjusted for sea star loss.
Figure 3.13. Temporal trends in the mean-scaled Quillback Rockfish relative abundance index $\lambda_s^D$ (posterior medians divided by the mean of the series), when the catch data was adjusted for sea star loss during gear retrieval ($\lambda_s^{Da}$, blue line). $\lambda_s^{Da}$ trends are compared with those of the unadjusted $\lambda_s^D$ (black line) and the mean nominal CPUE per area (mean $U_s^D$ divided by the mean of the series, turquoise line). Longline sets are from the annual inshore rockfish longline survey (2003-2005, 2007-2015) in survey areas (PFMAs) frequently sampled over the survey years ($n = 701$ sets). The shaded area represents the Bayesian 95% credible interval for $\lambda_s^{Da}$, the index adjusted for sea star loss.
Figure 3.14. Temporal trends in the mean-scaled Yelloweye Rockfish relative abundance index \( \lambda_s^D \) (posterior medians divided by the mean of the series), when the catch data was adjusted for a sea star loss four times greater than observed in the March 2010 experiment (\( \lambda_s^{D_a} \), blue line). \( \lambda_s^{D_a} \) trends are compared with those of the unadjusted \( \lambda_s^D \) (black line) and the mean nominal CPUE per area (mean \( U_s^D \) divided by the mean of the series, turquoise line). Longline sets are from the annual inshore rockfish longline survey (2003-2005, 2007-2015) in survey areas (PFMAs) frequently sampled over the survey years (\( n = 701 \) sets). The shaded area represents the Bayesian 95% credible interval for \( \lambda_s^{D_a} \), the index adjusted for sea star loss.
Figure 3.15. Temporal trends in the mean-scaled Quillback Rockfish relative abundance index $\lambda_s^D$ (posterior medians divided by the mean of the series), when the catch data was adjusted for a sea star loss four times greater than observed in the March 2010 experiment ($\lambda_s^{D^a}$, blue line). $\lambda_s^{D^a}$ trends are compared with those of the unadjusted $\lambda_s^D$ (black line) and the mean nominal CPUE per area (mean $U_s^D$ divided by the mean of the series, turquoise line). Longline sets are from the annual inshore rockfish longline survey (2003-2005, 2007-2015) in survey areas (PFMAs) frequently sampled over the survey years ($n = 701$ sets). The shaded area represents the Bayesian 95% credible interval for $\lambda_s^{D^a}$, the index adjusted for sea star loss.
Chapter 4: Evaluating the Impact of Fine-scale Habitat Variation on a Hook-based Abundance Index Developed from Bottom Longline Catches

4.1 Introduction

Management advice for many demersal species relies on tuning assessment models to abundance indices derived from the catch of fisheries-independent surveys (e.g., Yamanaka et al. 2012b, Webster and Stewart 2015, Hanselman et al. 2016). However, habitat variation can increase bias and uncertainty in these abundance indices (e.g., biomass estimates for trawls; Rooper and Martin 2012, Shelton et al. 2014), as habitat variation influences the distribution and abundance of demersal species (e.g., Day and Pearcy 1968, Carlson and Straty 1981, Friedlander and Parrish 1998, Laidig et al. 2009) and creates patchiness and spatial variation in species catches (e.g., Chester et al. 1984, Husebø et al. 2002, Wieland et al. 2009, Stobart et al. 2012). If ignored, habitat variation may result in survey-derived abundance indices that do not reflect the true trends in the abundance of the species (Cordue 2007, Shelton et al. 2014) and may lead to erroneous management advice. Most research has focused on correcting abundance indices for variation in habitat between survey set locations (e.g., Rooper and Martin 2012, Thorson and Ward 2013, Shelton et al. 2014), but for strongly habitat-associated species, habitat variation within each set may further affect catch rates (Stobart et al. 2012, Carrasquilla-Henao et al. in prep.).

For longline surveys, variation in species density (i.e., at the hook-level or for groups of hooks) is hypothesized to create local saturation along the longline gear (Gulland 1955, Huse and Fernö 1990, Somerton and Kikkawa 1995), which may result in the abundance indices no longer accurately reflecting the species density. Clustering of catches has been observed on pelagic
longlines (Capello et al. 2013). For strongly habitat-associated species, patchiness of habitat along the longline could lead to uncertainty in the abundance indices that may not be accounted for at the set-level. Using directs observations of catch and habitat at the hook-level, this chapter aims to empirically test the influence of hook-level habitat variation on the capture of two inshore rockfish species, Yelloweye Rockfish (Sebastes ruberrimus) and Quillback Rockfish (S. maliger), and to assess whether correcting for hook-level variation improves the fit and precision of their abundance indices.

Rockfish species show strong habitat associations and rockfish distributions vary at multiple spatial scales (Anderson and Yoklavich 2007, Anderson et al. 2009), including distribution on larger scales, due to depth and substrate type (Richards 1986, Matthews 1990a), and distribution on smaller scales, due to complexity of the substrate (e.g., crevices and holes; Murie et al. 1994, Pacunski and Palsson 2001) and the presence of structure-forming biota, like sponges (Cook et al. 2008, Marliave et al. 2009, Du Preez and Tunnicliffe 2011) and kelp (Richards 1987). Both Yelloweye and Quillback are demersal and associate with complex bottom structure, including boulder fields and rocky reefs (Richards 1986, O’Connell and Carlile 1993, Johnson et al. 2003), but separate somewhat by depth (Richards 1986). Additionally, rockfish show high site fidelity on rocky reefs (Coombs 1979, DeMott 1983, Matthews 1990b), although home range appears to depend on habitat quality (Matthews 1990c). Combined, these characteristics contribute to a patchy spatial distribution for rockfish, and make rockfish an ideal group for studying fine-scale habitat effects on longline abundance indices.

Few studies have assessed the impact of fine-scale patchiness in species distributions on the abundance indices derived from fishery-independent bottom longlines surveys. Instead, survey design-based methods are used to minimize habitat effects. Surveys can be designed to
sample a specific substratum (e.g., a depth ranges or substrate type), based on prior knowledge about the target species distributions, and to return habitat-specific abundance indices from catches or observations within the substratum (e.g., Lohead and Yamanaka 2007, Yoklavich et al. 2007). However, habitat variation within substrata, due to patchiness in habitat quality for example, can still create variation in the abundance indices (Shelton et al. 2014) and may occur at scales smaller than the set-level (Rooper and Martin 2012). An alternative approach is to correct for habitat effects in longline catch data that has already been collected (e.g., Ward and Myers 2005, Maunder et al. 2006a). This includes methods of standardizing for habitat effects at the hook-level. Stobart et al. (2012) used GPS coordinates to retrieve hook-level substrate type from multibeam-sonar maps, and for species with strong habitat associations, removed hooks on unfavourable habitat before calculating catch per unit effort (CPUE). Hinton and Nakano (1996) developed a habitat-based standardization method that uses the habitat at each hook and the habitat preference of the species to determine the effective effort of pelagic longlines. However, appropriately specifying habitat preferences from observations proved challenging and misspecification of the preference introduces bias into the abundance indices (Goodyear 2003). More recent applications of this standardization method to commercial data estimate the habitat preferences and abundance indices directly from the data, which improves the fit to the catch data (Maunder et al. 2006a, Bigelow and Maunder 2007). Hook-level habitat standardization of abundance indices has not been applied to bottom longline survey data despite the potential influence of fine-scale habitat on these indices.

Using bottom longlines to target Yelloweye and Quillback, I investigated the capture per hook of these strongly structure-associated species, and their competitors, relative to the habitat surrounding each longline hook. I used a Remotely Operated Vehicle (ROV) to directly observe
the hooks and surrounding habitat underwater. With the paired observations of the habitat underwater and the catch on the deck, I investigated whether: (1) habitat variables that influence the capture of Yelloweye and Quillback on a fine spatial scale, i.e., at the hook-level, could be identified; and (2) standardizing for the habitat variables that influence their capture improved the fit to the observed rockfish density and precision of the instantaneous rate of bait loss per species index ($\lambda_s$), which corrects for hook competition (Murphy 1960, Rothschild 1967, Somerton and Kikkawa 1995) and is currently used in the stock assessments for these species (Yamanaka et al. 2012a, Yamanaka et al. 2012b). The habitat-adjusted $\lambda_s$ index was estimated in a Bayesian framework that included a Generalized Linear Model to standardize for the effects of the habitat variation per hook. Finally, as correcting for hook-level habitat variation is data demanding and data may not always be available at a fine-scale, I investigated whether: (3) species, or groups of species, with fine-scale habitat distributions that were similar to, or contrasted with, those of Yelloweye and Quillback could be identified. These species, or groups of species, could indicate whether sections of the longline were fishing on, or off, the favourable habitat for the target species (e.g., Ovaskainen et al. 2010).

4.2 Methods

4.2.1 Data collection

To understand how hook-level habitat variation impacts the capture and abundance indices of inshore rockfish and their competitors, I compared the catch on each bottom longline hook to the habitat observed around the hook during a field experiment in March 2010. During this experiment, 13 longline sets were conducted in Nanoose Bay and Northwest Bay, in the Strait of Georgia, BC, Canada (Figure 2.1). The longline gear, with 225 hooks on each longline,
was deployed by a commercial fishing vessel. A government research vessel then deployed a ROV, after the last hook was released from the fishing vessel. The ROV passed along the entire length of the longline three times during the soak time (i.e., the time between the last hook leaving the deck of the fishing vessel and the first hook returning to the deck). This allowed for underwater observation of the hooks, as well as the surrounding habitat. As the hooks returned to the fishing vessel, I recorded the state of each hook as baited, having caught a species, bare (i.e., returning with neither bait nor catch) or unknown (i.e., the hook was missing). Both fish and invertebrate species were identified to the species level, if possible. Details of the fishing and ROV operations can be found in the Methods section of Chapter 2 (Sections 2.2.1.1 and 2.2.1.2) and Appendix A.

4.2.1.1 Habitat variables

The ROV video recorded during each longline set was reviewed to gather habitat information for each hook on the longline. Habitat observations were only made during the first ROV pass along the longline. To ensure the accuracy of the habitat variables recorded, three different reviewers watched the video for each set and categorized the habitat surrounding each hook: one reviewer in real-time, while the ROV was underwater, and two reviewers after the experiment. The habitat variables recorded for each hook included the depth measured at the ROV’s position (in m), and four categorical variables: the substrate type, bottom complexity, vertical relief and biota. These variables come from previous ROV, towed camera and submarine studies of inshore rockfish habitat (Martin et al. 2006, Pacunski and Palsson 2001, Yamanaka et al. 2012c, Haggarty 2015, Haggarty et al. 2016, Haggarty et al. 2017), and are known to influence the distribution of inshore rockfish species (Richards 1986, Richards 1987, Matthews
1990a, Matthews 1990b, O'Connell and Carlile 1993, Johnson et al. 2003, Cook et al. 2008, Marliave et al. 2009, Yamanaka et al. 2012c, Haggarty 2015). For the substrate type, I recorded only the main substrate type, defined as occupying 80% of the area in view around the hook. Substrate type was recorded as one of three categories: rock, mixed coarse or mixed fine. Rock included bedrock and boulders, mixed coarse included cobble and gravel-like substrates, and mixed fine included sand and mud. Complexity is a measure of the rugosity of the habitat, or the number of crevices, and was recorded as either low (smooth or less than 25% of the habitat with crevices) or high (greater than 25% of the habitat with crevices). Relief reflects the slope, or vertical change, in the habitat and was also recorded as either low (less than 2m of vertical relief) or high (more than 2m of vertical relief). Biota, or biocover, is a measure of the organisms that contribute to the structure of the habitat. Biota was scored as bare (e.g., bare, debris, detritus, unknown), encrusting organisms (e.g., scallops, barnacles, encrusting organism complex, ophiuroids, tube worms) or emergent (e.g., kelp, anemones, sea pens, sponges, sea whips, sea lilies). The categories for the habitat variables come from Pacunski and Palsson (2001), and were simplified by Haggarty (2015) and Haggarty et al. (2016). Further explanation of the habitat variables can be found in Haggarty et al. (2017).

4.2.2 Predicting capture of inshore rockfish from the hook-level habitat

During the March experiment, 2925 hooks were deployed over the 13 sets and sampled a variety of habitats. As the habitats sampled by each hook were not predetermined, nor the main focus of the experimental design, all habitat categories and depths ranges were sampled unequally (Table 4.1). In order to reduce the habitat categories with very few (<5% of the hooks) or zero observations, I combined the substrate and complexity habitat variables into a new
variable, substrate-complexity, with four categories: mixed fine-low complexity \((n = 1666)\); mixed coarse-low complexity \((n = 466)\); rock-low complexity \((n = 523)\); and rock-high complexity \((n = 270)\).

To identify which combination of the four habitat variables, depth (DEP), substrate-complexity (SC), biota (BIO) and relief (REL), best explained the capture of inshore rockfish at the hook-level, I initially applied a logistic regression (binomial Generalized Linear Model (GLM), Zuur et al. 2009), with a logit link, to the probability of capturing a (1) Yelloweye \((\kappa_Y)\); and (2) Quillback \((\kappa_Q)\), on each hook \(j\):

\[
\log\left(\frac{K_{Yj}}{1-K_{Yj}}\right) = a + B_{DEP}^Y \cdot DEP_j + B_{SC}^Y + B_{BIO}^Y + B_{REL}^Y + \varepsilon \\
\log\left(\frac{K_{Qj}}{1-K_{Qj}}\right) = a + B_{DEP}^Q \cdot DEP_j + B_{SC}^Q + B_{BIO}^Q + B_{REL}^Q + \varepsilon
\]

Eq. 4.1

Eq. 4.2

where the \(a\) parameter is the intercept for the logistic regression, and the \(B\) parameters are the coefficients for the effect of each habitat variable on the probability of capture. I fitted these logistic regressions using the "glm" function in the base stats package of the R statistical software (R Core Team 2017). A key assumption of the logistic regression is independence among the observations (Zuur et al. 2009). However, potential dependence exists between observations (hooks) that come from the same longline. Furthermore, hooks on the same longline may show autocorrelation, as the hooks were only spaced approximately 1.8m apart. Responses on adjacent hooks are probably more closely related than those further apart on the longline.

One method of dealing with the potential dependence among the hooks is to apply generalized estimation equations for regression modelling (GEE, Liang and Zeger 1986,
Dormann et al. 2007, Zuur et al. 2009). The GEE approach differs from GLMs in that a working correlation structure between the observations is specified and included in the estimation of the regression parameters, instead of assuming independence of the observations (reviewed in Ballinger 2004, Zuur et al. 2009). I applied the GEE approach to the models for the probability of capturing a Yelloweye and Quillback, κY and κQ respectively (Eqs. 4.1 - 4.2), using the “geeglm” function in the geepack package (Højsgaard et al. 2006) in R (R Core Team 2017). I assumed the working correlation structure was autoregressive (AR1) (see Zuur et al. 2009 for an example). With AR1, the correlation within each longline is a function of the distance between the hooks; the correlation between any two hooks is a baseline correlation value (value ≤ 1) raised to a power equal to the distance between the two hooks (i.e., the number of hooks between them). To find the best model with the GEE approach, I first used the “anova” function in the base R stats package (R Core Team 2017) to identify habitat variables that were not significant in the full model (Eqs. 4.1 - 4.2), and dropped the variable with the largest p-value. I then used the “anova” function again to compare the χ²-distributed difference in the residual deviance between the new model and the old model with a Wald test (Zuur et al. 2009). The old model was retained only if the Wald test returned a p-value less than 0.05. This continued until I arrived at a model where no more variables could be dropped without creating a significant difference in the residual deviance between the models.

The best fitting model for both Yelloweye and Quillback estimated the correlation between adjacent hooks as $0.11 \pm 0.03$ (± standard error) and $-0.01 \pm 0.01$, respectively. Additionally, when the number of subjects or groups is small and the number of observations within each group is high, the GEE approach tends to estimate biased robust standard errors for the coefficients (Prentice 1988, Horton and Lipsitz 1999), which results in more conservative
inferences about the statistical significance of the variables (Ballinger 2004). Due to the low estimated correlation between adjacent hooks and the possibility of biased standard errors for the coefficients, I decided to use the results of both the GEE approach and the GLM analysis to make inferences about the habitat variables that best predict the capture of Yelloweye and Quillback. I tested for the best GLM using the “drop1” function in the base stats package (R Core Team 2017). This function tests the $\chi^2$-distributed difference in the residual deviance between the models with a Likelihood Ratio test and returns the Akaike Information Criterion (AIC). I selected the best model by comparing the AIC values (Akaike 1992). I then used the “anova” function in the base stats package (R Core Team 2017) to test the significance of the habitat variables in the model with a Wald test (Zuur et al. 2009) and to identify the habitat variables that best explained the capture of Yelloweye and Quillback in the March 2010 experiment.

4.2.3 Habitat-adjusted abundance indices

To estimate an abundance index adjusted for habitat effects at the hook-level, I included habitat variables in the estimation of the instantaneous rate of bait loss per species ($s$) index ($\lambda^D_s$), for each set in the March 2010 experiment. The $D$ superscript in $\lambda^D_s$ indicates that the $\lambda_s$ index is estimated from catch observations made on the deck of the vessel. Further details on the $\lambda_s$ index can be found in Chapter 2 (Methods section 2.2.2.2). I included the habitat variables that best explained the capture of Yelloweye and Quillback at the hook-level from the GLM and GEE analyses. For Yelloweye, these hook-level habitat variables were the depth and substrate-complexity. For Quillback, these hook-level habitat variables were the depth, substrate-complexity, biota and relief. As substrate-complexity and depth were included for both
Yelloweye (Y) and Quillback (Q), I developed a model that corrected for depth and substrate-complexity when estimating the habitat-adjusted $\lambda'_s$ index ($\lambda'^{D-H}_s$) for each hook $j$ on set $i$:

$$\lambda'^{D-H}_{Yi,j} = \lambda'^{D-H}_{Yi} + \beta^Y_{DEP} \cdot DEP_{i,j} + \beta^Y_{SC}$$  

Eq. 4.3

$$\lambda'^{D-H}_{Qi,j} = \lambda'^{D-H}_{Qi} + \beta^Q_{DEP} \cdot DEP_{i,j} + \beta^Q_{SC}$$  

Eq. 4.4

where $\lambda'^{D-H}_{Y}$ and $\lambda'^{D-H}_{Q}$ are the set-level intercepts for the model, or the value of $\lambda'^{D-H}_s$ at the base level of each habitat variable. For example, $\lambda'^{D-H}_{Y}$ is $\lambda'^{D-H}_s$ on mixed fine-low complexity substrate at 0 m depth. To test the sensitivity of the $\lambda'^{D-H}_s$ estimates to the choice of habitat variables included in the model, I also tested three models with alternate structures: (1) depth only;

$$\lambda'^{D-H}_{Yi,j} = \lambda'^{D-H}_{Yi} + \beta^Y_{DEP} \cdot DEP_{i,j}$$  

Eq. 4.5

$$\lambda'^{D-H}_{Qi,j} = \lambda'^{D-H}_{Qi} + \beta^Q_{DEP} \cdot DEP_{i,j}$$  

Eq. 4.6

(2) substrate-complexity only;

$$\lambda'^{D-H}_{Yi,j} = \lambda'^{D-H}_{Yi} + \beta^Y_{SC}$$  

Eq. 4.7

$$\lambda'^{D-H}_{Qi,j} = \lambda'^{D-H}_{Qi} + \beta^Q_{SC}$$  

Eq. 4.8

and (3) depth and substrate-complexity for only Yelloweye (see Eq. 4.3), plus biota and relief for Quillback:

$$\lambda'^{D-H}_{Qi,j} = \lambda'^{D-H}_{Qi} + \beta^Q_{DEP} \cdot DEP_{i,j} + \beta^Q_{SC} + \beta^Q_{BIO} + \beta^Q_{REL}$$  

Eq. 4.9

In all four $\lambda'^{D-H}_s$ models, Yelloweye ($\lambda'^{D-H}_Y$), Quillback ($\lambda'^{D-H}_Q$), other species ($\lambda'^{D}_O$) and bare hooks ($\lambda'^{D}_E$) all contributed to the total instantaneous rate of bait loss ($\lambda^{D-H}$) for each longline set $i$, as:

$$\lambda^{D-H}_i = \sum_s \lambda'^{D-H}_{s,i} = \lambda'^{D-H}_{Yi} + \lambda'^{D-H}_{Qi} + \lambda'^{D}_O + \lambda'^{D}_E$$  

Eq. 4.10
4.2.3.1 Bayesian estimation

To estimate the hook-level \( \lambda^{D-H} \) values for Yelloweye and Quillback, I used a Bayesian methodology similar to Chapter 2 (Methods section 2.2.2.3). At the end of the soak time for the set (t), each hook j was recorded as being still baited (\( N_B \)) or having caught a Yelloweye (\( N_Y \)), Quillback (\( N_Q \)), another species (\( N_O \)) or was bare (\( N_E \)) (e.g., 0,1,0,0,0 for a Yelloweye on the hook) and followed a Multinomial distribution on set i:

\[
(N_{B_i,j}, N_{Y_i,j}, N_{O_i,j}, N_{E_i,j}) \sim M(1, p = (p_{B_i,j}, p_{Y_i,j}, p_{Q_i,j}, p_{O_i,j}, p_{E_i,j})
\]

Eq. 4.11

where \( p \) is the probability of a hook being baited (\( p_B \)) or in one of the four categories of catch (\( p_s \)). Each hook was treated as an individual trial. As habitat was measured at the hook-level, the probability of a hook having caught a Yelloweye (\( p_Y \)) or a Quillback (\( p_Q \)) for each hook \( j \) on set \( i \) was:

\[
p_{Y_i,j} = \frac{\lambda_{Y_i,j}^D}{\lambda_{D-H}^D} (1 - e^{-\lambda_{D-H}^D t})
\]

Eq. 4.12

\[
p_{Q_i,j} = \frac{\lambda_{Q_i,j}^D}{\lambda_{D-H}^D} (1 - e^{-\lambda_{D-H}^D t})
\]

Eq. 4.13

with hook-level \( \lambda_{Y_i}^{D-H} \), \( \lambda_{Q_i}^{D-H} \) (Eqs. 4.3 - 4.9) and \( \lambda_{D-H}^{D-H} \) (Eq. 4.10) specified as in Methods section 4.2.3. This meant \( p_B \) was specified as:

\[
p_{B_i,j} = e^{-\lambda_{D-H}^D t}
\]

Eq. 4.14

and the probability for the other categories of catch (\( p_O \) and \( p_E \)) were specified as:

\[
p_{s,i,j} = \frac{\lambda_{s,i,j}^D}{\lambda_{D-H}^D} (1 - e^{-\lambda_{D-H}^D t})
\]

Eq. 4.15
with

\[ p_{Bi,j} + p_{Yi,j} + p_{Qi,j} + p_{Oi,j} + p_{Ei,j} = 1 \]  

Eq. 4.16

Posterior median \( \lambda^D-H \) and posterior median \( \lambda^D-Ha \) were estimated at the set-level (i.e., one value for each set, constant across all the hooks in that set), while the posterior medians of the \( \beta \) parameters were estimated over all the sets (i.e., one value for each \( \beta \) parameter, constant across all the sets). As \( \lambda^D-H \) was estimated for each hook, the average \( \lambda^D-H \) for all hooks on the longline was calculated as the habitat-adjusted index of abundance for each set. For each set \( i \), the average \( \lambda^D-H (\bar{\lambda}^D-H_{Yi,t}) \) and the average \( \lambda^D-H (\bar{\lambda}^D-H_{Qi,t}) \) were calculated from the posterior median \( \lambda^D-Ha \), or \( \lambda^D-Ha \), for each set, and from the posterior medians of the \( \beta \) parameters included in the model (\( \beta_{DEP}, \beta_{SC}, \beta_{BIO}, \beta_{REL} \)) for the category of habitat observed under each hook \( j \), for all the hooks deployed on the set \( (N) \) as:

\[
\bar{\lambda}^D-H_{Yi,t} = \lambda^D-Ha_{Yi,t} + \frac{\sum_j^N \beta^Y_{DEP,i,j} \cdot DEP_{i,j} + \sum_j^N \beta^Y_{SC,i,j} \cdot DEP_{i,j}}{N_i} 
\]  

Eq. 4.17

\[
\bar{\lambda}^D-H_{Qi,t} = \lambda^D-Ha_{Qi,t} + \frac{\sum_j^N \beta^Q_{DEP,i,j} \cdot DEP_{i,j} + \sum_j^N \beta^Q_{SC,i,j} \cdot DEP_{i,j} + \sum_j^N \beta^Q_{BIO,i,j} + \sum_j^N \beta^Q_{REL,i,j}}{N_i} 
\]  

Eq. 4.18

These equations show the \( \bar{\lambda}^D-H_{Yi,t} \) and \( \bar{\lambda}^D-H_{Qi,t} \) when all the habitat effects that best described capture were included in the estimation of \( \lambda^D-H \) (Eq. 4.3) and \( \lambda^D-H \) (Eq. 4.9) per hook. Habitat \( \beta \) parameters were dropped from these equations depending on which habitat variables were included in the estimation of the \( \lambda^D-H \) and \( \lambda^D-Ha \) indices (Eqs. 4.3 - 4.9). Alternatively, \( \lambda^D-Ha \) and \( \lambda^D-Ha \) could be used as an index of abundance where the effect of habitat has been standardized.
I estimated the posterior medians of $\lambda_{D-Ha}^D$, $\lambda_{Q-Ha}^Q$ and the $\beta$ parameters using WinBUGS 1.4 (Lunn et al. 2000) called from within the R statistical software (R Core Team 2017) using the R2WinBUGS package (Sturtz et al. 2005). The prior distributions for $\lambda_s^D$ for other species and bare hooks were the same as in Chapter 2 (Methods section 2.2.2.3), while the prior distributions for the set-level indices, $\lambda_{D-Ha}^D$ and $\lambda_{Q-Ha}^Q$, and the habitat $\beta$ parameters were set independently for each model (Table 4.2) to ensure that the post-model pre-data distributions (McAllister 2014) of $p_B$ had a mean close to 0.4; this is similar to the average proportion of baited hooks on the British Columbia fisheries-independent longline survey for Yelloweye and Quillback (Lochead and Yamanaka 2007). I tested for sensitivity of the posterior distributions for $\lambda_{s-D-Ha}^s$ to: (1) altering the rate parameters for the exponential priors; and (2) changing the model structure, by adding/removing habitat variables. The prior rate parameters for each of the sensitivity tests can be found in Table 4.2. To sample the joint posterior distribution for the $\lambda_{s-D-Ha}^s$ parameters, I used Markov Chain Monte Carlo (MCMC) methods. After removing the first 15,000 samples from each of the two Markov chains, 200,000 samples were taken from the joint posterior distribution. For each MCMC run, the Gelman-Rubin convergence statistic (Gelman et al. 2004) was calculated using the R coda package (Plummer et al. 2006). As the Gelman-Rubin convergence statistic was less than 1.1 for all parameters, it was assumed that the chains had approached a stationary distribution. Autocorrelation plots, trace plots and the posterior distributions for each parameter (Appendix E, Figure E.1 - Figure E.5) were checked to ensure the chains were well-mixed and there were no signs of strong autocorrelation. MC error was calculated to determine if the posterior distributions were approximated with sufficient precision (Powers and Xie 2008). The MC error was less than 5% of the posterior standard deviation for all the distributions.
4.2.3.2 Model fits between the habitat-adjusted abundance indices and observed density

To test whether accounting for habitat effects at the hook-level improved the fit between the posterior medians of the $\lambda_s$ index, and the observed density of each rockfish species ($D_s$), I fit both linear:

$$\lambda_{s,l}^D = q_s \cdot D_{s,l} + v_s$$  \hspace{1cm} \text{Eq. 4.19}

$$\overline{\lambda_{s,l}^{D-H}} = q_{s,l} \cdot D_{s,l} + v_s$$  \hspace{1cm} \text{Eq. 4.20}

and non-linear asymptotic models:

$$\lambda_{s,l}^D = q_s \cdot D_{s,l}^h + v_s$$  \hspace{1cm} \text{Eq. 4.21}

$$\overline{\lambda_{s,l}^{D-H}} = q_{s,l} \cdot D_{s,l}^{h_s} + v_s$$  \hspace{1cm} \text{Eq. 4.22}

to the posterior medians of the original unadjusted index $\lambda_s^D$ and the average habitat-adjusted index ($\overline{\lambda_{s,l}^{D-H}}$) estimated for each longline set for each of the models with different habitat variables (Eqs. 4.3 - 4.9). The observed density of Yelloweye and Quillback for each longline set ($D_s$) was the number of individuals counted on the video divided by the total area surveyed by the ROV (m$^2$) and multiplied by 100 (density per 100 m$^2$). I included both free-swimming fish and fish caught on the hooks in the count and averaged the density from all three passes of the ROV over the longline gear. Detailed methods for calculating the observed density are in Chapter 2 (Methods section 2.2.2.1) and Appendix A. For each of the linear and non-linear models, I compared the parameter values and fits between the abundance indices and observed density, as in Chapter 2 (Methods section 2.2.2.4). $q$ is the slope of the relationship between the catch-based index and the observed density, $h$ is the shape parameter, to account for
hyperstability or hyperdepletion (Hilborn and Walters 1992), and \( v \) represents the capture of rockfish when zero rockfish are observed by the ROV. I estimated the parameters using maximum likelihood estimation (MLE), with \( q \), \( h \) and \( v \) constrained to be non-negative. In order to prevent the prediction of negative \( \lambda_s^D \) and \( \overline{\lambda_s^{D-H}} \) indices, \( v \) was constrained to be non-negative, and non-zero (\( v \geq 1 \times 10^{-18} \)) when necessary to converge on a stable solution. Due to heteroscedasticity in the variance of the residuals, I used a weighted-MLE, where the error in the predicted values of \( \lambda_s^D \) and \( \overline{\lambda_s^{D-H}} \) for each set \( i \) was treated as normally distributed with a variance (\( \sigma^2_{s,i} \)) of:

\[
\sigma^2_{s,i} = (c_s \cdot predicted{\lambda^D_{s,i}})^2 \quad \text{Eq. 4.23}
\]

\[
\sigma^2_{s,i} = (c_s \cdot predicted{\overline{\lambda^{D-H}_{s,i}}})^2 \quad \text{Eq. 4.24}
\]

where \( c_s \) is the coefficient of variation for all the observed values of the index and was estimated along with the other parameters (see McAllister et al. 1994). To quantitatively compare the model fits between \( \lambda_s^D \) and \( \overline{\lambda_s^{D-H}} \) and the observed density, I computed the coefficient of determination (\( R^2 \)) for the linear and non-linear models and compared them between the two indices. The \( R^2 \) values represent the variance in the indices that can be explained by the variance in the observed density. As the model fits were estimating using a weighted-MLE method, it was possible for \( R^2 \) to be negative, if the model fit had increased variance compared to the mean. I also searched for the best model by comparing the values of the Akaike Information Criterion (AIC) adjusted for small sample sizes (\( AIC_c \)) based on the number of parameters (\( k \)) and the number of samples (\( n \)) (Burnham and Anderson 2002):

\[
AIC_c = AIC + \frac{2k^2 + 2k}{n - k - 1} \quad \text{Eq. 4.25}
\]
4.2.4 Correspondence analysis

To identify species with fine-scale habitat distributions similar to, or contrasting with, those of Yelloweye and Quillback, I created contingency tables for the habitat variables that had greater than two categories. For depth, a continuous variable, I created four depth categories: 20-45 m, 46-70 m, 71-95 m and 96-120 m (Table 4.1). The 46-70 m and 71-95 m categories are similar to the depths surveyed by the annual inshore rockfish survey in British Columbia, which uses two depth strata: 40-70 m and 71-100 m (Lochead and Yamanaka 2007). In each contingency table, I examined the relative frequencies, or row profiles, for each species across the habitat categories. Row profiles are the number of the species caught (the rows) in each habitat category (the columns) relative to the total number of captures for that species. I used correspondence analysis to visualize the relatedness of the row profiles using the “ca” function in the ca package (Nenadić and Greenacre 2007) in R (R Core Team 2017). Correspondence analysis is a common tool for visualizing patterns of species distributions across habitat types (e.g., Friedlander and Parrish 1998, Yamanaka et al. 2012c) or sampling stations (e.g., Hunt and Hosie 2005). Correspondence analysis calculates the $\chi^2$ distance between each row profile and the average profile for all rows (Greenacre 2007). These $\chi^2$ distances are a weighted Euclidean distance, and can be mapped in a scatterplot, or asymmetric biplot, where the distances between the profile points are meaningful and the origin of the plot (0,0) is the average profile (Greenacre 2007). Here, profile points that are closer together indicate species that have similar distributions of catch over the different habitat categories. The multiple habitat categories mean that the points can be represented in multiple dimensions (i.e., the number of columns in the contingency table minus one), so the axes in the asymmetric biplot are those that explain the most inertia for the table (Greenacre 2007). Inertia is the weighted average of the squared $\chi^2$ distances, with the
relative number of samples in each row as the weights (Greenacre 2007). The two axes that explain the most inertia together represent the plane that is closest to the profile points in multidimensional space. If the inertia explained by the axes is high, then the biplot representation is close to the true position of the profile points in multidimensional space (Greenacre 2007). Spiny Dogfish (*Squalus acantbias*), Yelloweye, Quillback, Walleye Pollock (*Theragra chalcogramma*), Sunflower Stars (*Pycnopodia helianthoides*) and Copper Rockfish (*S. caurinus*), another inshore rockfish, were the six most commonly caught species during the 13 longline sets (Table 4.5). Their row profiles, plus those of Tiger Rockfish (*S. nigrocinctus*), the only other inshore rockfish species caught, were mapped relative to the habitat categories (column vertices).

### 4.3 Results

#### 4.3.1 Habitat variables that affect the capture of Yelloweye Rockfish and Quillback Rockfish

The habitat surveyed by the longline hooks during the March experiment was generally dominated by one category in each of the habitat variables. This included the depth range of 46-70 m (48% of all hooks), mixed fine substrate with low complexity (57%), bare biota (60%) and low relief (83%, Table 4.1). However, the GEE approach and GLM analyses still identified habitat variables that significantly altered the probability of capturing Yelloweye and Quillback at the hook-level. For the model that included all four of the habitat variables (Eq. 4.1 and 4.2), none of the habitat variables had a significant effect on the probability of capturing a Yelloweye in the GEE approach, whereas both substrate-complexity and depth had a significant effect on the probability of capture in the GLM analysis (Table 4.3). In contrast, all four habitat variables significantly affected the probability of capturing a Quillback in the GEE approach, while depth,
substrate-complexity and relief had a significant effect on the probability of capture in the GLM analysis (Table 4.3). For both Yelloweye and Quillback, increasing depth and harder substrates increased the probability of capture, while high relief reduced the probability of capturing a Quillback (Table 4.3). The estimates of the B parameters (Eq. 4.1 and 4.2) were very similar between the GEE approach and the GLM analysis, but for Yelloweye, the standard error for the depth and substrate-complexity variables decreased in the GLM analysis, compared to the GEE approach (Table 4.3). Searching for the model with the best fit by dropping habitat variables and testing the difference with a Wald test (GEE approach), or a Likelihood Ratio test plus the change in the AIC (ΔAIC, GLM analysis), returned similar results to testing for significant effects in the model with all four habitat variables (Table 4.4). In the GEE approach, all habitat variables were dropped from the model for predicting capture of Yelloweye without a significant difference between the models, whereas in the GLM analysis, the model that retained depth and substrate-complexity had the lowest AIC and dropping either depth or substrate-complexity from this model created a significant difference (Table 4.4). For Quillback, dropping the parameter with the lowest p-value from the model created a significant difference between the models in the first step with the GEE approach, whereas in the GLM analysis, the model that included all the habitat variables had the lowest AIC, but dropping biota from the model did not create a significant difference between the two models (Table 4.4). For Yelloweye, the model with depth and substrate-complexity was selected as the best model. For Quillback, the model with depth, substrate-complexity, biota and relief was selected as the best model.

To identify species whose fine-scale habitat distribution was similar, or contrasted, with those of Yelloweye and Quillback, I examined: (1) the relative frequency of the species caught in relation to the habitat observed at the hook-level (Table 4.5); and (2) the relative position of their
row profiles to the habitat variables (column vertices) mapped with correspondence analysis. The axes for all three asymmetric maps for the habitat variables accounted for a high level of the variation in the table (the inertia), with 92.8% explained for depth, 97.8% explained for substrate-complexity and 100% explained for biota (Figure 4.1). For depth, three of the four inshore rockfish species observed, Yelloweye, Quillback and Copper, were close to the origin (the average row profile), which differed from Tiger and Sunflower Stars, away from the origin and closer to the shallowest depth, and Spiny Dogfish and Walleye Pollock, away from the origin and closer to the deeper depths (Figure 4.1). For substrate-complexity, all the inshore rockfish species were towards the harder substrates (mixed coarse or rock) in the principal axis (Dimension 1), while Spiny Dogfish and Sunflower Stars were closer to the soft substrate (Figure 4.1). Quillback, Copper and Walleye Pollock were closest to the mixed coarse and Yelloweye and Tiger were closest to the rock substrates (Figure 4.1). For biota, the encrusting and emergent categories were in very similar positions along the principal axis and three of the four inshore rockfish species, Quillback, Yelloweye and Tiger, along with Walleye Pollock were closest to the habitats with biota, while Copper, Spiny Dogfish, Sunflower Stars were closest to the bare category (Figure 4.1). Overall, the positions of the Yelloweye and Quillback row profiles were more similar to each other across the habitat variables than to those of Spiny Dogfish, Sunflower Stars and Walleye Pollock (Figure 4.1). Both Spiny Dogfish and Sunflower Stars were consistently well separated from Yelloweye and Quillback on the principal axis in the maps for all three habitat variables (Figure 4.1)
4.3.2 Habitat-adjusted abundance indices compared to the unadjusted index

To test if adjusting the $\lambda_s$ index for hook-level habitat variation could improve the precision and the fit of the index to the observed density for Yelloweye and Quillback, the hook-level depth and substrate-complexity habitat variables were included in the estimation of $\lambda^{D-H}_s$ per hook. Depth and substrate-complexity were selected to be included in the base habitat-effects model because they significantly affected the probability of capturing both Yelloweye and Quillback (Table 4.3). As the Bayesian estimation incorporated hook-level variables, the $\lambda^{D-H}_s$ indices were estimated at the hook-level, and the posterior distributions for each hook could not feasibly be examined. Instead, the posterior distributions for $\lambda^{D-Ha}_s$ were examined, along with the posteriors for the habitat $\beta$ parameters. The data updated the priors for $\lambda^{D-Ha}_s$ and $\lambda^D_s$, across all the sets, and for all the species-specific habitat $\beta$ parameters (Figure E.1 -Figure E.5). The data were mildly to moderately informative for all the habitat parameters (Figure E.5). Across all the longline sets, the posterior distributions for the unadjusted $\lambda^D_s$ index were more precise than the posterior distributions for the habitat-adjusted $\lambda^{D-Ha}_s$, regardless of the habitat variables included in the estimation of $\lambda^{D-Ha}_s$ (Figure 4.2). The median coefficient of variation increased as the number of variables included in the estimation of $\lambda^{D-Ha}_s$ increased (Figure 4.2).

For both Yelloweye and Quillback, the shape of the marginal $\lambda^{D-Ha}_s$ posterior distributions was generally insensitive to the specification of the rate parameter for the exponential priors for $\beta_{DEP}$ and $\beta_{SC}$ (Figure E.6 - Figure E.7), except when the prior for $\beta_{SC}$ was very narrow (green line, Figure E.6 - Figure E.7). The $\beta_{DEP}$ and $\beta_{SC}$ parameters showed the greatest sensitivity to the shape of the prior for the $\beta_{SC}$ parameter (Figure E.8).
The shape of the marginal $\lambda_s^{D-ha}$ posterior distributions was generally insensitive to the removal of the depth variable from the Bayesian estimation, but was more sensitive to the removal of the substrate-complexity habitat variable, particularly for Yelloweye (Figure E.9 - Figure E.10). The $\beta_{DEP}$ and $\beta_{SC}$ parameters showed little sensitivity to the removal of the other habitat variable, except for removing depth for Yelloweye, which resulted in a larger median (Figure E.11). The $\beta$ parameters were also generally insensitive to the addition of the biota and relief variables (Figure E.11). The data was only mildly informative for the $\beta_{BIO}$ and $\beta_{REL}$ parameters (Figure E.12).

The linear and non-linear model fits, between the $\lambda_s^D$ index and the $\lambda_s^{D-H}$ indices and the observed rockfish density, varied by species. For Yelloweye, only the linear and non-linear model fits for the $\lambda_s^{D-H}$ index that included depth alone had higher $R^2$ values than the fits for the $\lambda_s^D$ index (Table 4.6, Figure 4.3). The non-linear models for all the $\lambda_s^{D-H}$ indices and the $\lambda_s^D$ index had higher $R^2$ values (Table 4.6) and smaller AIC values than the linear models. However, when the AIC was adjusted for the small sample size (AICc), the AICc values for the linear model were smaller for the $\lambda_s^D$ and the $\lambda_s^{D-H}$ index with only depth included (Table 4.6). For Quillback, both the linear and non-linear model fits for the $\lambda_s^D$ index had higher $R^2$ values than the fits for any of the $\lambda_s^{D-H}$ indices, except for the linear model for the $\lambda_s^{D-H}$ index that included all the habitat variables, which was marginally larger (Table 4.6, Figure 4.4). For the $\lambda_s^{D-H}$ indices, the non-linear model fits generally had slightly smaller AIC values and slightly smaller $R^2$ values than the linear model fits (Table 4.6). The reverse was true for the $\lambda_s^D$ index. However, when the AIC was adjusted for the small sample size (the AICc), the AICc values for the linear model were smaller than those for the non-linear model for all the indices. Overall, the $R^2$ values
supported the $\lambda_{D-H}^s$ index corrected for depth as the best index for the observed Yelloweye density (Table 4.6). For Quillback, the $\lambda_{s}^D$ index that was not adjusted for habitat was the best index for the observed density (Table 4.6).

The estimated parameters of the linear and non-linear model fits were very similar for all the $\lambda_{D-H}^s$ indices (Table 4.7). For Yelloweye, the parameters for the linear model fits appeared to be most affected by the inclusion of depth in the model (Table 4.7). Including depth tended to decrease $q$ (the slope). For Quillback, the parameters for the linear model fit for the $\lambda_{s}^D$ index with only depth showed the greatest difference, with an increased $q$ value (Table 4.7). The most consistent difference in the parameters for both the linear and non-linear fits for the $\lambda_{D-H}^s$ indices was the slight reduction in the estimated coefficient of variation ($\sigma$) compared with the $\lambda_{s}^D$ model fits (Table 4.7, Figure 4.3 - Figure 4.4). The estimates of $h$ (the shape parameter) in the non-linear model were all less than one for $\lambda_{s}^D$ and $\lambda_{D-H}^s$, indicating that the observed rockfish density declined faster than the indices (hyperstability) for both Yelloweye and Quillback.

### 4.4 Discussion

Habitat variation affects the spatial distribution of species (e.g., Day and Pearcy 1968, Carlson and Straty 1981, Friedlander and Parrish 1998, Laidig et al. 2009), creating spatial variability in their catches (e.g., Chester et al. 1984, Husebø et al. 2002, Wieland et al. 2009, Stobart et al. 2012) and introducing bias and uncertainty in abundance indices derived from catch (Rooper and Martin 2012, Stobart et al. 2012, Shelton et al. 2014). Failure to account for habitat variation can result in incorrectly interpreting the abundance trends (Cordue 2007, Bigelow and Maunder 2007) and could result in inappropriate management advice due to abundance indices that do not reflect true temporal patterns in population abundance. For species
with strong habitat associations, fine-scale habitat variation influences their distribution (Pacunski and Palsson 2001, Anderson and Yoklavich 2007), and may influence their capture at the hook-level on a longline set. Currently, no published studies have directly observed and corrected for hook-level habitat variation in bottom longline catches or the abundance indices derived from catch. I used observations from a ROV to test the relationship between hook-level habitat and catch for bottom longlines, and to create habitat-adjusted abundance indices for two highly structure-associated species, Yelloweye and Quillback (Richards 1986, O’Connell and Carlile 1993, Yamanaka et al. 2012c, Haggarty et al. 2016). During the experiment in March 2010, the relative capture frequencies of Yelloweye and Quillback across the categories of depth (in bins), substrate-complexity and biota were more similar to each other than to species like Spiny Dogfish and Sunflower Stars. For both Yelloweye and Quillback, depth and substrate-complexity of the habitat surrounding the hooks significantly affected their capture on the longline hooks. However, only Quillback capture was significantly affected by the biota and relief of the habitat surrounding the hooks. Abundance indices adjusted for these habitat effects ($\lambda_{\text{adj}}^D - H$) showed variable fits with the observed rockfish densities. For Yelloweye, the index with the best fit to the observed Yelloweye density was the $\lambda_{\text{adj}}^D - H$ index corrected for depth, whereas, for Quillback, the abundance index with the best fit to the observed density was the $\lambda_{\text{adj}}^D$ index, with no correction for the habitat. Additionally, the precision of the $\lambda_{\text{adj}}^D$ posteriors was generally higher and varied less than the precision of the posteriors for the $\lambda_{\text{adj}}^D - H$ indices.

Hook-level habitat effects on the catch and abundance indices differed between the two rockfish species. Depth and substrate-complexity affected the capture of both Yelloweye and Quillback, while biota (in the GLM analysis only) and relief affected only the capture of Quillback. The dependence of Yelloweye and Quillback distributions on depth (Richards 1986,
Richards 1987), substrate type and complexity (Richards 1986, O’Connell and Carlile 1993, Yamanaka et al. 2012c, Haggarty et al. 2016) is well-known from ROV and submersible observations made without baited longline gear present. Additionally, both Yelloweye and Quillback strongly associate with high relief habitat (Jagielo et al. 2003, Johnson et al. 2003), particularly if refuges, like crevices or holes, are present (O’Connell and Carlile 1993). However, the probability of capturing Quillback on the longline hooks was lower for high relief habitat than low relief habitat and relief did not have a significant effect on the probability of capturing Yelloweye. Both species also strongly associate with structure-forming biota (Haggarty et al. 2016), like sponges, both in reefs (Cook et al. 2008, Marliave et al. 2009) and with scattered sponges (Du Preez and Tunnicliffe 2011), but only the probability of capturing Quillback was affected by the biota around the hook. Additionally, only the habitat-adjusted $\lambda_s^{D-H}$ index with depth included for Yelloweye showed a better fit to the observed rockfish density than the $\lambda_s^D$ index with no corrections for habitat. The $\lambda_s^{D-H}$ indices for Quillback generally did not have a better fit to the observed rockfish density than the $\lambda_s^D$ index. These differences in capture and the resulting abundance indices between Yelloweye and Quillback, and between published observations and the observations in this study made when longline gear was present, may be due to: (1) the feeding behaviour of the rockfish species; (2) the modelling framework used to estimate the abundance indices; and (3) the design of the experiment.

The feeding behavior of Yelloweye and Quillback in response to the baited hooks may have influenced their pattern of capture, and the relationship between the abundance indices and the observed density. Unlike trawl nets, longlines rely on fish detecting the baited hooks, responding and successfully attacking the bait. The presence of baited hooks may have blurred the relationship between the fine-scale habitat variables and the capture of Yelloweye and
Quillback, depending on their willingness to move to the hooks. Atlantic Cod (*Gadus morhua*) will move hundreds of meters to attack baited longline hooks (Løkkeborg 1998). Variables including temperature, tides, current, light intensity, visibility, availability of natural prey, hunger, bait type, bait size, and the size of competitors also influence feeding behaviour and attraction to baited hooks (see reviews in Stoner 2004 and Løkkeborg et al. 2014). Yelloweye grow to a larger maximum size than Quillback (Love et al. 2002) and may search for food over a larger area, as habitat use and diet change with increasing size due to decreased predation risk (Mittelbach 1986, Love et al. 1991). Additionally, larger fish outcompete smaller fish and can prevent them from accessing hooks (Løkkeborg and Bjordal 1992, Stoner and Ottmar 2004). If interspecific competition is greater on higher quality habitat, Yelloweye may have outcompeted Quillback for the hooks, obscuring the relationship between the Quillback catch and the observed density. Additionally, a smaller proportion of the Quillback observed by the ROV may have been able to successful attack the baited hooks. Longline size selectivity is determined by the size of the hooks (Sousa et al. 1999, Gregalis et al. 2012, Leaman et al. 2012) and the size of the bait (Løkkeborg 1990, Johannessen et al. 1993, Løkkeborg and Bjordal 1995, Ingólfsson et al. 2017). More of the observed Yelloweye may have been vulnerable to the gear, improving the fit between the Yelloweye abundance indices and the observed density. In fitting these relationships, all the observed rockfish were included in the density, as in Rodgveller et al. 2011. However, Richards and Schnute (1986) found a significant relationship between hook and line CPUE and the observed density of Quillback, when fish below a minimum size were removed from the observed density. Haggarty and King (2006) also found a proportional relationship for Copper, but not for Quillback, which they attributed to the depth range of their study. Additionally, juvenile and adult rockfish show different habitat preferences (Carlson and Straty
1981, Matthews 1990a, Love et al. 1991, Rooper and Martin 2012) which may add further uncertainty into the relationship between the habitat-adjusted $\lambda_s^{D-H}$ indices and the observed density if juvenile and adult rockfish are not assessed separately.

The modelling framework may also have reduced the fit and precision of the relationship between the abundance indices and the observed density. The habitat effects on the Quillback and Yelloweye abundance indices were modelled with a Generalized Linear Model with fixed effects. Additionally, the habitat $\beta$ parameters were constrained to positive values by the exponential priors, to ensure the probabilities for all the hook states ($p_B$ and $p_{s,i}$) were positive. The linear model could be inappropriate if the habitat variables have a non-linear relationship with abundance (Murawski and Finn 1988), as seen with other rockfish species (Rooper and Martin 2012). Yelloweye and Quillback do exhibit depth preferences (Richards 1986) that could result in a non-linear relationship between abundance and depth. An alternate model, where the relationships between the habitat variables and the abundance indices are dome-shaped or exponential (Rooper and Martin 2009, Rooper and Martin 2012), might improve the fit and precision of the estimates. Additionally, several recent papers applied Generalized Linear Mixed Models (GLMMs) when attempting to account for spatial variation of demersal fishes, including rockfish (Thorson and Ward 2013, Shelton et al. 2014, Haggarty et al. 2016). GLMMs allow effects to be either fixed or random (Zuur et al. 2009), meaning that habitat effects can vary across grouping variables, such as regions (Haggarty et al. 2016) or strata (Thorson and Ward 2013, Shelton et al. 2014). Ignoring random effects from a grouping variable can negatively bias precision for abundance indices (Helser et al. 2004). During the March experiment, the longline sets occurred in a relatively small area, so the assumption of fixed habitat effects across the sets seems unlikely to influence the precision.
Alternatively, observation error due to the design of the March experiment may have influenced the pattern of capture, and the relationship between the abundance indices and the observed density for Yelloweye and Quillback. The ROV operations had several objectives during the longline sets. First, the ROV was to observe each hook on the longline to allow the state of each hook to be recorded three times during the two hour soak time. Second, the ROV was to observe the free-swimming fish around the longline so that density could be determined. Finally, the ROV was to observe the habitat to allow habitat variables to be recorded for each hook. Focusing on each hook meant sometimes zooming in the ROV camera or driving the ROV closer to the longline, both of which reduced the field of view. During the experiment, the average field of view for the ROV was 1.79 ± 1.30 m (Appendix A). The small field of view may have limited the observation of rockfish attracted to the baited hooks. A limited vertical field of view (Trenkel et al. 2004), along with hidden biomass (Willis 2001) and attraction or avoidance by fish outside the camera view (Trenkel et al. 2004, Stoner et al. 2008) can all introduce observation error into visual sampling methods. In addition, the classification of the habitat may have been affected by the limited field of view. For each hook, the substrate, complexity, biota and relief categories were all determined by qualitatively determining the category that described 80% of the habitat around the hook. However, when the field of view was small, the category may have been missed. For example, distinguishing between a sediment-covered rock ledge, or a sediment-filled valley between boulders, and a section of mud or sand bottom may have been difficult from the ROV video. A habitat variable like distance to rock, used in some studies of the influence of spatial distribution on rockfish catch (Shelton et al. 2014, Thorson et al. 2015, Carrasquilla-Henao et al. in prep.), may have been a better measure of habitat for Yelloweye and Quillback.
While behaviour of the rockfish, the modelling framework and the experimental design may all have obscured the effect of the habitat variables on the abundance indices, the relative frequency of capture across the different habitats represent real patterns of capture for longlines targeting Yelloweye and Quillback. Yelloweye and Quillback captures were more associated with hard substrates compared to other species, which is similar to the results of Yamanaka et al. (2012c), where fish were observed during ROV transects without longline gear present. However, Yamanaka et al. (2012c) saw closer correspondence between Yelloweye and Quillback and rock substrate. This may indicate that Yelloweye and Quillback were induced by the baited hooks to move from favourable habitat or that the habitat variables here were poorly measured. One benefit of the correspondence analysis for captures on different habitat is that the pattern of Spiny Dogfish captures could be examined in relation to fine-scale habitat. Spiny Dogfish typically avoid the ROV when they detect it (my observations, Matlock et al. 1991, Trenkel et al. 2004). Spiny Dogfish are considered to be a major source of interspecific competition for longline hooks during the annual longline survey for Yelloweye and Quillback in the waters of British Columbia. Spiny Dogfish can occupy greater than 50% of all the hooks deployed on the survey (Lochead and Yamanaka 2007). In the longline sets during this experiment, very few of the Spiny Dogfish captures occurred on rock substrate, regardless of the bottom complexity, and few were caught in habitat with encrusting or emergent biota. Interspecific competition on the annual longline survey for Yelloweye and Quillback may be less than previously suspected. Instead, Spiny Dogfish captures may indicate locations where the gear is not on rockfish habitat. Jaglieo et al. (2003) also observed a habitat-based separation of Spiny Dogfish and Yelloweye and Quillback, with Spiny Dogfish only found in trawlable areas and Yelloweye and Quillback only found in untrawlable areas. Captures of Sunflower Stars also
differed from those of Yelloweye and Quillback, with most Sunflower Stars caught at shallower depths, on mixed fine substrate and with bare biota. Captures of both Spiny Dogfish and Sunflower Stars could act as indicators of poor habitat for Yelloweye and Quillback. However, captures of other species also depend on their abundance. In recent years, populations of large predatory starfish have declined drastically due to a sea star wasting disease (Hewson et al. 2014, Eisenlord et al. 2016) and Spiny Dogfish can undertake extensive migrations, although Spiny Dogfish in the Strait of Georgia are generally resident (McFarlane and King 2003). Additionally, each hook in the correspondence analysis was treated as an independent observation, which may have overemphasized the associations. For example, many of the Sunflower Star captures came from one shallow set on mixed fine-low complexity substrate with no biota. Finally, the longline sets only occurred in March, in one small area in the Strait of Georgia. Feeding patterns and habitat use can vary by season. Matthews (1990a) found that Quillback use of high and low relief rocky reefs varied between the summer and winter, and Spiny Dogfish feeding is much higher in the summer than winter (Jones and Geen 1977), which could alter the level of interspecific competition for the longline hooks by season.

Including fine-scale habitat variables recorded at the hook-level did improve the non-linear fits of the $\lambda_s$ abundance indices to the observed density of Yelloweye, but caution needs to be taken when extrapolating the habitat-based relationships developed here to other bottom longline data. For pelagic longlines, applying habitat-based corrections, developed from survey data using GLMs, to other data can lead to misinterpretation of the trends in the abundance indices (Bigelow and Maunder 2007). Given the poor fits between the habitat-adjusted $\lambda_s^{D-H}$ indices and the observed Quillback density, the increased variance of the $\lambda_s^{D-Ha}$ posteriors compared with the unadjusted $\lambda_s^b$ posteriors and the time required to collect and process direct
measurements of hook-level habitat variables, this approach to incorporating fine-scale habitat variation appears to be impractical and inefficient and may provide little improvement over the habitat-stratification in the survey design. However, the results indicate that captures along a single bottom longline set can be influenced by fine-scale habitat variation, potentially resulting in patchy captures of non-target species like Spiny Dogfish and Sunflower Stars. Knowledge of the habitat along the longline could be useful in creating habitat-based weightings of longline sections when estimating the abundance indices. Determining habitat patches along the longline with digital bathymetry models and medium resolution remote sensing imagery, as used at the set-level (e.g., Haggarty 2015, Carrasquilla-Henao et al. in prep.), may provide a more practical approach. Future work would need to establish whether the habitat along a vessel’s GPS track, recorded as the longline gear is deployed or retrieved, accurately and consistently reflects the habitat where the longline settles. Additionally, a recent study with trawl survey data suggests that geostatistical models, which estimate smoothed surfaces for species densities and can incorporate habitat variables to explain the variance, outperform GLMs or GLMMs (Thorson et al. 2015) and may be the next step in the development of longline indices adjusted for habitat variation.
Table 4.1. Number of hooks observed in each habitat category during the March 2010 experiment, based on observation of the hooks and habitat underwater by the Remotely Operated Vehicle. The number of hooks in each habitat variable equals the total number of hooks deployed ($n = 2925$) on the longline sets ($n = 13$). Depth is a continuous variable, but is separated into bins here.

<table>
<thead>
<tr>
<th>Habitat Variable</th>
<th>Number of hooks</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Substrate-complexity</strong></td>
<td></td>
</tr>
<tr>
<td>Mixed fine - low complexity</td>
<td>1666</td>
</tr>
<tr>
<td>Mixed coarse - low complexity</td>
<td>466</td>
</tr>
<tr>
<td>Rock - low complexity</td>
<td>523</td>
</tr>
<tr>
<td>Rock - high complexity</td>
<td>270</td>
</tr>
<tr>
<td><strong>Relief (slope)</strong></td>
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</tr>
<tr>
<td>Low (vertical relief $&lt; 2$ m)</td>
<td>2440</td>
</tr>
<tr>
<td>High (vertical relief $&gt; 2$ m)</td>
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</tr>
<tr>
<td><strong>Biota</strong></td>
<td></td>
</tr>
<tr>
<td>Bare</td>
<td>1742</td>
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<tr>
<td>Encrusting</td>
<td>395</td>
</tr>
<tr>
<td>Emergent</td>
<td>788</td>
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<tr>
<td><strong>Depth</strong></td>
<td></td>
</tr>
<tr>
<td>21 - 45 m</td>
<td>336</td>
</tr>
<tr>
<td>46 - 70 m</td>
<td>1407</td>
</tr>
<tr>
<td>71 - 95 m</td>
<td>729</td>
</tr>
<tr>
<td>96 - 120 m</td>
<td>453</td>
</tr>
</tbody>
</table>
Table 4.2. Rate parameters (h⁻¹) for the exponential priors used in the Bayesian estimation of the habitat-adjusted abundance indices ($\lambda_{s-D-H}^{D-H}$) for Yelloweye Rockfish ($Y$) and Quillback Rockfish ($Q$). The base habitat model, along with the models used to test sensitivity to the model structure, included some or all of the habitat variables: depth (DEP), substrate-complexity (SC), biota (BIO) and relief (REL). The models used to test sensitivity to the prior rate parameters included the same habitat variables as the base habitat model.

<table>
<thead>
<tr>
<th>Habitat variables included</th>
<th>$\lambda_{s-D-H}^{D-H}$</th>
<th>$\lambda_{s-D}^{D}$</th>
<th>$\beta_{DEP}^{Y}$</th>
<th>$\beta_{SC}^{Y}$</th>
<th>$\beta_{BIO}^{Y}$</th>
<th>$\beta_{REL}^{Y}$</th>
<th>$\lambda_{s-D-H}^{Q}$</th>
<th>$\lambda_{s-D}^{D}$</th>
<th>$\beta_{DEP}^{Q}$</th>
<th>$\beta_{SC}^{Q}$</th>
<th>$\beta_{BIO}^{Q}$</th>
<th>$\beta_{REL}^{Q}$</th>
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</thead>
<tbody>
<tr>
<td><strong>Base Model</strong></td>
<td></td>
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<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>DEP, SC</td>
<td>22.5</td>
<td>7.5</td>
<td>1550</td>
<td>22.5</td>
<td>---</td>
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<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Prior Value Sensitivity</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>DEP-broad, SC-narrow</td>
<td>22.5</td>
<td>7.5</td>
<td>155</td>
<td>225</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>DEP-narrow, SC-broad</td>
<td>22.5</td>
<td>7.5</td>
<td>15500</td>
<td>2.5</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>All priors broad</td>
<td>0.51</td>
<td>0.17</td>
<td>34.7</td>
<td>0.51</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Structural Sensitivity</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>DEP</td>
<td>22.5</td>
<td>7.5</td>
<td>1550</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SC</td>
<td>22.5</td>
<td>7.5</td>
<td>---</td>
<td>22.5</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>DEP, SC, REL, BIO (Quillback only)</td>
<td>37.5</td>
<td>7.5</td>
<td>2569</td>
<td>37.5</td>
<td>37.5</td>
<td>37.5</td>
<td>---</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 4.3. $\chi^2$ statistics ($df =$ degrees of freedom), $p$-values and $B$ parameter estimates (Est.) with standard errors (S.E.) for the logistic regressions applied to predict the capture of Yelloweye Rockfish and Quillback Rockfish ($n = 2925$ hooks) based on habitat variables observed at the hook-level (Eqs. 4.1 - 4.2). The generalized estimation equations approach (GEE) assumes that the hooks on each longline are correlated with an autoregressive correlation structure and uses a Wald test for significance, while the generalized linear model (GLM) assumes that the hooks on each longline are independent and uses a Likelihood Ratio test. For the categorical variables, substrate-complexity (SC), biota (BIO) and relief (REL), the parameters were estimated relative to the base categories: mixed fine-low complexity, bare and low relief, respectively. Depth (DEP) is a continuous variable.

<table>
<thead>
<tr>
<th>Model Variables</th>
<th>GEE</th>
<th>GLM</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$df$</td>
<td>Est.</td>
</tr>
<tr>
<td><strong>Yelloweye Rockfish</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>DEP</td>
<td>1</td>
<td>0.01</td>
</tr>
<tr>
<td>SC</td>
<td>3</td>
<td>---</td>
</tr>
<tr>
<td>Mixed Coarse-Low</td>
<td></td>
<td>0.75</td>
</tr>
<tr>
<td>Rock-Low</td>
<td></td>
<td>1.09</td>
</tr>
<tr>
<td>Rock-High</td>
<td></td>
<td>1.01</td>
</tr>
<tr>
<td>BIO</td>
<td>2</td>
<td>---</td>
</tr>
<tr>
<td>Encrusting</td>
<td></td>
<td>-0.24</td>
</tr>
<tr>
<td>Emergent</td>
<td></td>
<td>0.13</td>
</tr>
<tr>
<td>REL</td>
<td>1</td>
<td>---</td>
</tr>
<tr>
<td>High</td>
<td></td>
<td>0.30</td>
</tr>
<tr>
<td><strong>Quillback Rockfish</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>DEP</td>
<td>1</td>
<td>0.02</td>
</tr>
<tr>
<td>SC</td>
<td>3</td>
<td>---</td>
</tr>
<tr>
<td>Mixed Coarse-Low</td>
<td></td>
<td>0.85</td>
</tr>
<tr>
<td>Rock-Low</td>
<td></td>
<td>0.76</td>
</tr>
<tr>
<td>Rock-High</td>
<td></td>
<td>1.63</td>
</tr>
<tr>
<td>BIO</td>
<td>2</td>
<td>---</td>
</tr>
<tr>
<td>Encrusting</td>
<td></td>
<td>0.18</td>
</tr>
<tr>
<td>Emergent</td>
<td></td>
<td>0.50</td>
</tr>
<tr>
<td>REL</td>
<td>1</td>
<td>---</td>
</tr>
<tr>
<td>High</td>
<td></td>
<td>-1.02</td>
</tr>
</tbody>
</table>
Table 4.4. The best logistic regression model to explain the capture of Yelloweye Rockfish and Quillback Rockfish based on habitat variables was determined by dropping the variable with the lowest $p$-value until removing a variable created a significant difference between the old and new models. The generalized estimation equations approach (GEE) assumes that the hooks on each longline are correlated with an autoregressive correlation structure and uses a Wald test for significance, while the generalized linear model (GLM) assumes that the hooks on each longline are independent and uses a Likelihood Ratio test. In the GLM, all variables were dropped one at a time and Akaike Information Criterion (AIC) was reported with the test, while the GEE approach only dropped the variable with smallest $p$-value in each test. $df$ is the difference in degrees of freedom between the two models. The habitat variables included depth (DEP), substrate-complexity (SC), biota (BIO) and relief (REL) and were observed underwater at the hook-level by a ROV ($n = 2925$ hooks).

<table>
<thead>
<tr>
<th>Model variables</th>
<th>Yelloweye Rockfish</th>
<th>Quillback Rockfish</th>
</tr>
</thead>
<tbody>
<tr>
<td>Original</td>
<td>Dropped</td>
<td>$\chi^2$</td>
</tr>
<tr>
<td>GEE</td>
<td>DEP, SC, REL, BIO</td>
<td>BIO</td>
</tr>
<tr>
<td>GEE</td>
<td>DEP, SC, REL</td>
<td>REL</td>
</tr>
<tr>
<td>GEE</td>
<td>DEP, SC</td>
<td>SC</td>
</tr>
<tr>
<td>GEE</td>
<td>DEP</td>
<td>DEP</td>
</tr>
<tr>
<td>GLM</td>
<td>DEP, SC, REL, BIO</td>
<td>BIO</td>
</tr>
<tr>
<td>GLM</td>
<td>DEP, SC, REL, BIO</td>
<td>REL</td>
</tr>
<tr>
<td>GLM</td>
<td>DEP, SC, REL, BIO</td>
<td>DEP</td>
</tr>
<tr>
<td>GLM</td>
<td>DEP, SC, REL, BIO</td>
<td>SC</td>
</tr>
<tr>
<td>GLM</td>
<td>DEP, SC, REL</td>
<td>REL</td>
</tr>
<tr>
<td>GLM</td>
<td>DEP, SC, REL</td>
<td>DEP</td>
</tr>
<tr>
<td>GLM</td>
<td>DEP, SC, REL</td>
<td>SC</td>
</tr>
<tr>
<td>GLM</td>
<td>DEP, SC</td>
<td>DEP</td>
</tr>
<tr>
<td>GLM</td>
<td>DEP, SC</td>
<td>SC</td>
</tr>
</tbody>
</table>
Table 4.5. Relative frequency of capture of all fish and large invertebrate species caught on each habitat, for habitat variables with more than two categories. All hooks \((n = 2925)\) are treated as independent and frequency is relative to the total number caught for each species and sums to one for each habitat variable. Habitat categories include depth, a continuous variable grouped in 25 m bins, substrate complexity with mixed fine-low complexity (Fine Low), mixed coarse-low complexity (Coarse Low), rock-low complexity (Rock Low) and rock-high complexity (Rock High) categories, and biota with bare, encrusting (Encr) and emergent (Emrg) categories. Rockfish species are listed first, followed by other fish species and finally, large invertebrate species.

<table>
<thead>
<tr>
<th>Species</th>
<th>Depth (m)</th>
<th>Substrate-Complexity</th>
<th>Biota</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>21-45</td>
<td>46-70</td>
<td>71-95</td>
</tr>
<tr>
<td>Copper Rockfish ((Sebastes caurinus))</td>
<td>0.00</td>
<td>0.74</td>
<td>0.26</td>
</tr>
<tr>
<td>Quillback Rockfish ((S. maliger))</td>
<td>0.05</td>
<td>0.48</td>
<td>0.25</td>
</tr>
<tr>
<td>Tiger Rockfish ((S. nigrocinctus))</td>
<td>0.50</td>
<td>0.50</td>
<td>0.00</td>
</tr>
<tr>
<td>Yelloweye Rockfish ((S. ruberrimus))</td>
<td>0.06</td>
<td>0.42</td>
<td>0.42</td>
</tr>
<tr>
<td>Canary Rockfish ((S. pinniger))</td>
<td>0.00</td>
<td>0.00</td>
<td>0.67</td>
</tr>
<tr>
<td>Greenstriped Rockfish ((S. elongatus))</td>
<td>0.00</td>
<td>0.20</td>
<td>0.00</td>
</tr>
<tr>
<td>Cabezon ((Scorpaenichthys marmoratus))</td>
<td>0.33</td>
<td>0.67</td>
<td>0.00</td>
</tr>
<tr>
<td>Kelp Greenling ((Hexagrammos decagrammus))</td>
<td>1.00</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Lingcod ((Ophiodon elongatus))</td>
<td>0.00</td>
<td>1.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Longnose Skate ((Raja binoculata))</td>
<td>0.00</td>
<td>0.00</td>
<td>0.25</td>
</tr>
<tr>
<td>Species</td>
<td>Depth (m)</td>
<td>Substrate-Complexity</td>
<td>Biota</td>
</tr>
<tr>
<td>-------------------------------</td>
<td>-----------</td>
<td>----------------------</td>
<td>-------</td>
</tr>
<tr>
<td></td>
<td>21-45</td>
<td>46-70</td>
<td>71-95</td>
</tr>
<tr>
<td>Pacific Sanddab (<em>Citharichthys sordidus</em>)</td>
<td>0.00</td>
<td>0.50</td>
<td>0.50</td>
</tr>
<tr>
<td>Rock Sole (<em>Lepidopsetta bilineata</em>)</td>
<td>0.00</td>
<td>1.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Spiny Dogfish (<em>Squalus acanthias</em>)</td>
<td>0.00</td>
<td>0.13</td>
<td>0.66</td>
</tr>
<tr>
<td>Spotted Ratfish (<em>Hydrolagus colliei</em>)</td>
<td>0.00</td>
<td>0.67</td>
<td>0.00</td>
</tr>
<tr>
<td>Walleye Pollock (<em>Theragra chalcogramma</em>)</td>
<td>0.00</td>
<td>0.10</td>
<td>0.53</td>
</tr>
<tr>
<td>Fish-eating Star (<em>Stylasterias forreri</em>)</td>
<td>0.25</td>
<td>0.50</td>
<td>0.25</td>
</tr>
<tr>
<td>Mud Star (<em>Luidia foliolata</em>)</td>
<td>0.33</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Sunflower Star (<em>Pycnopodia helianthoides</em>)</td>
<td>0.51</td>
<td>0.49</td>
<td>0.00</td>
</tr>
<tr>
<td>Giant Pacific Octopus (<em>Enteroctopus dofleini</em>)</td>
<td>1.00</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>37</td>
<td>176</td>
<td>239</td>
</tr>
</tbody>
</table>
Table 4.6. Coefficient of determination ($R^2$) and the difference in the Akaike Information Criterion corrected for small sample size ($\text{AIC}_c$) for the linear (Eqs. 4.19 - 4.20) and non-linear (Eqs. 4.21 - 4.22) model fits between observed rockfish density and the abundance indices estimated with ($\lambda^D_{s-H}$) and without ($\lambda^D_s$) correction for the habitat variables, depth (DEP), substrate-complexity (SC), biota (BIO) and relief (REL). The $\text{AIC}_c$ differences are shown as the linear model $\text{AIC}_c$ minus the non-linear model $\text{AIC}_c$ (L-NL).

<table>
<thead>
<tr>
<th>Species</th>
<th>Habitat variables</th>
<th>Linear model</th>
<th>Non-linear model</th>
<th>$\text{AIC}_c$ (L-NL)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Yelloweye Rockfish</td>
<td>$\lambda^D_s$: None</td>
<td>0.06</td>
<td>0.57</td>
<td>-1.47</td>
</tr>
<tr>
<td></td>
<td>$\lambda_{s-D-H}$: DEP</td>
<td>0.26</td>
<td>0.65</td>
<td>-2.08</td>
</tr>
<tr>
<td></td>
<td>$\lambda_{s-D-H}$: SC</td>
<td>-0.42</td>
<td>0.44</td>
<td>1.23</td>
</tr>
<tr>
<td></td>
<td>$\lambda_{s-D-H}$: DEP, SC</td>
<td>-0.10</td>
<td>0.56</td>
<td>0.54</td>
</tr>
<tr>
<td>Quillback Rockfish</td>
<td>$\lambda^D_s$: None</td>
<td>0.23</td>
<td>0.24</td>
<td>-2.64</td>
</tr>
<tr>
<td></td>
<td>$\lambda_{s-D-H}$: DEP</td>
<td>-0.26</td>
<td>0.20</td>
<td>-2.06</td>
</tr>
<tr>
<td></td>
<td>$\lambda_{s-D-H}$: SC</td>
<td>0.21</td>
<td>0.19</td>
<td>-2.33</td>
</tr>
<tr>
<td></td>
<td>$\lambda_{s-D-H}$: DEP, SC</td>
<td>0.21</td>
<td>0.18</td>
<td>-1.92</td>
</tr>
<tr>
<td></td>
<td>$\lambda_{s-D-H}$: DEP, SC, BIO, REL</td>
<td>0.24</td>
<td>0.22</td>
<td>-1.66</td>
</tr>
</tbody>
</table>
Table 4.7. Parameter estimates for the linear (Eqs. 4.19 - 4.20) and non-linear (Eqs. 4.21 - 4.22) model fits between observed rockfish density and the abundance indices estimated with \( \lambda_{s-H} \) or without \( \lambda_s \) correction for the habitat variables: depth (DEP), substrate-complexity (SC), biota (BIO) and relief (REL).

<table>
<thead>
<tr>
<th>Species</th>
<th>Habitat variables</th>
<th>Parameters</th>
<th>Linear model</th>
<th>Non-linear model</th>
</tr>
</thead>
<tbody>
<tr>
<td>Yelloweye</td>
<td>( \lambda_s^D ): None</td>
<td>( q )</td>
<td>0.019</td>
<td>0.021</td>
</tr>
<tr>
<td></td>
<td></td>
<td>( v )</td>
<td>1.01 x 10^{-3}</td>
<td>1.80 x 10^{-3}</td>
</tr>
<tr>
<td></td>
<td></td>
<td>( c )</td>
<td>0.36</td>
<td>0.57</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.30</td>
</tr>
<tr>
<td>Rockfish</td>
<td>( \lambda_{s-H} ): DEP</td>
<td>( q )</td>
<td>0.016</td>
<td>0.020</td>
</tr>
<tr>
<td></td>
<td></td>
<td>( v )</td>
<td>4.13 x 10^{-3}</td>
<td>1.67 x 10^{-3}</td>
</tr>
<tr>
<td></td>
<td></td>
<td>( c )</td>
<td>0.33</td>
<td>0.39</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.0</td>
</tr>
<tr>
<td></td>
<td>( \lambda_{s-H} ): SC</td>
<td>( q )</td>
<td>0.019</td>
<td>0.021</td>
</tr>
<tr>
<td></td>
<td></td>
<td>( v )</td>
<td>1.67 x 10^{-3}</td>
<td>4.09 x 10^{-3}</td>
</tr>
<tr>
<td></td>
<td></td>
<td>( h )</td>
<td>0.34</td>
<td>0.48</td>
</tr>
<tr>
<td></td>
<td></td>
<td>( c )</td>
<td>0.36</td>
<td>0.57</td>
</tr>
<tr>
<td></td>
<td>( \lambda_{s-H} ): DEP, SC</td>
<td>( q )</td>
<td>0.016</td>
<td>0.022</td>
</tr>
<tr>
<td></td>
<td></td>
<td>( v )</td>
<td>4.09 x 10^{-3}</td>
<td>0.48</td>
</tr>
<tr>
<td></td>
<td></td>
<td>( h )</td>
<td>0.34</td>
<td>0.57</td>
</tr>
<tr>
<td></td>
<td>Quillback</td>
<td>( \lambda_s^D ): None</td>
<td>( q )</td>
<td>0.003</td>
</tr>
<tr>
<td></td>
<td></td>
<td>( v )</td>
<td>1.32 x 10^{-2}</td>
<td>1.23 x 10^{-2}</td>
</tr>
<tr>
<td></td>
<td></td>
<td>( h )</td>
<td>0.54</td>
<td>0.50</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.62</td>
</tr>
<tr>
<td></td>
<td>Rockfish</td>
<td>( \lambda_{s-H} ): DEP</td>
<td>( q )</td>
<td>0.008</td>
</tr>
<tr>
<td></td>
<td></td>
<td>( v )</td>
<td>1.54 x 10^{-3}</td>
<td>1.33 x 10^{-2}</td>
</tr>
<tr>
<td></td>
<td></td>
<td>( h )</td>
<td>0.51</td>
<td>0.52</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.63</td>
</tr>
<tr>
<td></td>
<td>( \lambda_{s-H} ): SC</td>
<td>( q )</td>
<td>0.003</td>
<td>0.012</td>
</tr>
<tr>
<td></td>
<td></td>
<td>( v )</td>
<td>1.33 x 10^{-2}</td>
<td>1.23 x 10^{-2}</td>
</tr>
<tr>
<td></td>
<td></td>
<td>( h )</td>
<td>0.52</td>
<td>0.50</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.63</td>
</tr>
<tr>
<td></td>
<td>( \lambda_{s-H} ): DEP, SC</td>
<td>( q )</td>
<td>0.004</td>
<td>0.012</td>
</tr>
<tr>
<td></td>
<td></td>
<td>( v )</td>
<td>1.23 x 10^{-2}</td>
<td>1.21 x 10^{-2}</td>
</tr>
<tr>
<td></td>
<td></td>
<td>( h )</td>
<td>0.50</td>
<td>0.47</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.62</td>
</tr>
<tr>
<td></td>
<td>( \lambda_{s-H} ): DEP, SC, BIO, REL</td>
<td>( q )</td>
<td>0.003</td>
<td>0.012</td>
</tr>
<tr>
<td></td>
<td></td>
<td>( v )</td>
<td>1.21 x 10^{-2}</td>
<td>1.23 x 10^{-2}</td>
</tr>
<tr>
<td></td>
<td></td>
<td>( h )</td>
<td>0.47</td>
<td>0.47</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.60</td>
</tr>
</tbody>
</table>
Figure 4.1. Asymmetric correspondence analysis map for species catch (in principal coordinates, row profiles) across different habitat categories (in standard coordinates, column vertices). Habitat variables include depth (DEP, upper left panel), substrate-complexity (SC, upper right panel) and biota (BIO, lower left panel). Habitat was directly observed at the hook-level with a ROV during the March experiment ($n = 2925$). The percentage of the inertia explained by each dimension is labelled in grey. Sea Star refers to the Sunflower Star in Table 4.5.
Figure 4.2. Coefficient of variation (%) for the precision of the posterior distribution of the abundance indices, with ($\alpha_{D-Ha}$) and without ($\alpha_i$) correction for the habitat variables included in the Bayesian estimation for Yelloweye Rockfish (left panel) and Quillback Rockfish (right panel). $\alpha_{D-Ha}$ is the intercept of the models for the habitat correction, i.e., the value of the per hook $\lambda_{D-H}$ indices at the base level of each habitat variable. Habitat variables included the depth (DEP), substrate-complexity (SC), biota (BIO) and relief (REL). The abundance indices were estimated from catch observed on the deck of the vessel, across all longline sets in the March experiment ($n = 13$).
Figure 4.3. Linear (solid lines) and non-linear (dashed lines) model fits for the relationship between the mean observed density of Yelloweye Rockfish and the abundance indices, with (Avg $\lambda_s$ or $\lambda^D_s$ or $\lambda^{D-H}_{s}$, right column) and without ($\lambda_s$, left column) correction for hook-level habitat variables. The average $\lambda^{D-H}_{s}$ values were calculated from the posterior median $\lambda^{D-H}_{s}$ for each set, and from the posterior medians of the $\beta$ parameters included in the model ($\beta_{DEP}, \beta_{SC}, \beta_{BIO}, \beta_{REL}$) for the category of habitat observed under each hook. The abundance indices were estimated from catch data observed on the deck of the vessel. Density was observed by the ROV during the March experiment ($n = 13$ longline sets).
Figure 4.4. Linear (solid lines) and non-linear (dashed lines) model fits for the relationship between the mean observed density of Quillback Rockfish and the abundance indices, with (Avg $\lambda^{D-H}$ or $\overline{\lambda}_{s}^{D-H}$, right column) and without ($\lambda^{D}$, left column) correction for hook-level habitat variables. The average $\lambda^{D-H}$ values were calculated from the posterior median $\lambda^{D-H}$ for each set, and from the posterior medians of the $\beta$ parameters included in the model ($\beta_{DEP}, \beta_{SC}, \beta_{BIO}, \beta_{REL}$) for the category of habitat observed under each hook. The abundance indices were estimated from catch data observed on the deck of the vessel. Density was observed by the ROV during the March experiment ($n = 13$ longline sets).
Chapter 5: Conclusion

Fisheries stock assessments generally rely on the observed trends in abundance indices to fit the predicted abundance trends generated by a stock assessment model (e.g., Beverton and Holt 1957, Hilborn and Walters 1992, Kimura and Somerton 2006). The dangers of relying on abundance indices generated from commercial catch data are well-known and contributed to the collapse of the Atlantic Cod (Gadus morhua) on the northern Grand Banks (e.g., Rose and Kulka 1999). Abundance indices generated from fisheries-independent surveys are preferred, as the survey design is expected to correct many of the issues with commercial catches (e.g., Gunderson 1993). However, issues specific to the catching process of the fishing gear won’t necessarily be corrected in survey design. For longline gear, catch is dependent on activity of the fish, and issues like interspecific competition and gear saturation may lead to abundance indices that no longer reflect the true abundance trends (Gulland 1955, Beverton and Holt 1957, Murphy 1960, Rothschild 1967, Ricker 1975). The species-specific instantaneous rate of bait loss parameter (λs) is expected to be a robust relative abundance index, uninfluenced by gear saturation and interspecific competition, as it accounts for all the hooks on the longline (Somerton and Kikkawa 1995). However, many of the assumptions of the λs index have not been empirically tested, including the assumption that the index has a proportional relationship with abundance (i.e., a linear relationship with an intercept of zero). The main aims of this thesis were to empirically evaluate the assumptions of the λs index using fishery-independent bottom longline catches of Yelloweye Rockfish (Sebastes ruberrimus) and Quillback Rockfish (S. maliger) as a case study. Yelloweye and Quillback are an appropriate case study as their annual multispecies survey appears to suffer from high levels of interspecific competition from Spiny Dogfish (Squalus acanthias, Lochead and Yamanaka 2007), and the strong habitat associations
of Yelloweye and Quillback likely create patchy fine-scale distributions. Additionally, the $\lambda_s$ index is currently used in their stock assessment.

In this thesis, I found neither strong nor consistent evidence that would support a linear over a non-linear relationship between the $\lambda_s$ index and the observed densities of Yelloweye and Quillback, in the March or August experiments. For Yelloweye, better fitting non-linear relationships (i.e., higher values of $R^2$) were found between the $\lambda_s$ index and abundance than for the linear model, and results from the August experiment lead to the rejection of a linear model in favour of a non-linear relationship between the $\lambda_s$ index and the observed density of Yelloweye. However, for the March experiment, the hypothesis of a linear relationship could not be rejected in favour of a non-linear relationship. In contrast, the results led to the rejection of a non-linear relationship in favour of a linear relationship in the March and August experiments for Quillback. Both these results were largely due to the heavier penalty imposed by the AICc for small sample sizes for the extra parameter in the non-linear model, rather than due to a difference in the log likelihood between the linear and non-linear model. The lack of strong evidence for a linear model is consistent with the results in Rodgveller et al. (2011), who did not find a significant proportional relationship between longline catch per unit effort (CPUE) and the observed density of deeper water rockfish in their experiments. Additionally, my results did not support that the $\lambda_s$ index was an improvement over CPUE for Quillback, but the $\lambda_s$ index showed better fits than CPUE with the observed density for Yelloweye. Haimovici and Ávila-da-Silva (2007) also observed little difference between commercial longline CPUE and the $\lambda_s$ index for two of the three most abundant species caught in the commercial fishery. Taken together these results caution against the common assumption that the $\lambda_s$ index from survey catches has a linear relationship with abundance and that simply accounting for the catch on all the hooks or
correcting for the number of baited hooks that return (e.g., Webster and Stewart 2015) creates a robust abundance index that improves upon the survey CPUE.

Rodgveller et al. (2011) is the only other study I am aware of that has empirically tested the relationship between a longline abundance index and the observed underwater abundance through underwater observation of the density along a longline. Rodgveller et al. (2011) used a submarine to make underwater observations, whereas I used a Remotely Operated Vehicle (ROV) in my experiments. The benefit of using a ROV was that the state of each hook could be observed on each pass, as the ROV could navigate close to the longline. Marking the longline allowed me to compare the state of each hook underwater to the state of the same hook when it was retrieved on the deck. Grimes et al. (1982) is the only other study I am aware that matched underwater observations of longline hooks to observations on the deck of the fishing vessel at the end of the longline soak time. They used a similar protocol on two sets to observe the loss of bait from the longline and to observe predation by benthic invertebrate predators, while they focused on estimating the optimal soak time. With underwater and on-deck observation of the hooks, I was able to construct underwater $\lambda_s$ indices from capture times based on the ROV’s camera times. However, the additional information gave very similar results to the on-deck $\lambda_s$ index, except that the fit of the underwater $\lambda_s$ indices were better for Yelloweye, suggesting that the effort of collecting underwater video for the $\lambda_s$ index only had some benefit for Yelloweye, and not for Quillback.

Direct observation of the hooks underwater also allowed me to evaluate some of the key assumptions of the $\lambda_s$ index. As predicted, $\lambda_s$ was not constant during the soak time. Somerton and Kikkawa (1995) found the same result when estimating the $\lambda_s$ index from hook timers instead of direct observations. As the model for $\lambda_s$ assumes that the amount of bait loss from the
gear decreases exponentially with time, this could create problems when applying the index to commercial fisheries where soak times vary.

Additionally, the repeated passes over the longline with the ROV, along with observation of the hooks on deck allowed me to determine probable sources of bare hooks. As with previous studies (High 1980, Grimes et al. 1982, He 1996), large invertebrates were observed to attack baited hooks underwater. However, unlike other studies, comparing my underwater observations of the hooks to the observation of the same hook on the deck showed that these large invertebrate species were rarely brought to the deck, and their contribution to bare hooks would be underestimated based on the catch. Additionally, large sea stars were observed on the hooks underwater, but many of these sea stars were lost during the retrieval of the longline and none of these large sea stars removed the bait. During the longer soak time of their observations, Grimes et al. (1982) found that sea stars (Astropectin sp.) and crabs (Cancer sp. and Acanthocarpus alexanderi) removed 50% of the bait in four hours. Although only some of the bare hooks observed underwater in the March experiment were due to Spiny Dogfish, Spiny Dogfish catches observed on the deck best explained the proportion of available hooks that were bare on sets during the annual inshore rockfish longline survey. These observations provided evidence for the choice of assumptions about bare hooks in the $\lambda_s$ model applied to the data from the annual inshore rockfish longline survey. However, temporal trends in the $\lambda_s$ index were robust to the different assumptions about bare hooks and to corrections for sea star loss from the hooks, indicating that erroneous assumptions about the source of bare hooks may only minimally affect the temporal trends in the $\lambda_s$ index.

The underwater observations of the behaviours and interactions among Yelloweye and Quillback and their competitors in relation to the longline are novel in themselves. Most studies
of behaviour and longlines have focused on more mobile demersal species like Pacific Halibut (*Hippoglossus stenolepis*, High 1980, Kaimmer 1999), Atlantic Cod (*Fernø et al.* 1986, Løkkeborg *et al.* 1989, He 1996, Godø *et al.* 1997), Whiting (*Gadus merlangus*, *Fernø et al.* 1986) and Haddock (*Melanogrammus aeglefinus*, *Fernø et al.* 1986, Løkkeborg *et al.* 1989, Godø *et al.* 1997) and not on highly structure-associated and more sedentary species. Additionally, the use of the ROV allowed observation of the hooks along the entire length of the longline, allowing for the observation of behaviours over a range of fine-scale habitats. The other studies of demersal species, except High (1980), used an underwater camera in a fixed frame with only a few baited hooks in the camera frame. Rodgveller *et al.* (2011) also looked at the behaviour of deeper water rockfish, Shortraker Rockfish (*S. borealis*) and Roughey Rockfish (*S. aleutianus*), in relation to the longline, but did not mention any other bait competitors or the interaction of other species with the baited longline hooks.

The hook by hook underwater observations in this thesis allowed for fine-scale identification of habitat variables and correction for the habitat under every hook. As far as I know, this is the first study that has attempted to correct abundance indices for bottom longlines based on directly observed hook-level habitat. However, Stobart *et al.* (2012) removed hooks on unfavourable habitat when estimating commercial longline CPUE, based on hook-level habitat from multibeam-sonar maps. Based on the hook-level habitat observed with the ROV, the probability of capture of Yelloweye and Quillback depended on different habitat variables, although the substrate-complexity and depth variables were common to both species. However, the abundance indices adjusted for the habitat effects $\lambda_s^{D-H}$ showed variable fits with the observed rockfish densities, similar to the results for the different indices when no habitat variables were included. While adding depth to the estimation of the $\lambda_s$ index improved the fits
for Yelloweye, the unadjusted $\lambda$ index fit best for Quillback. A bonus of viewing the hook-level habitat was the opportunity to define habitat associations for the capture of Spiny Dogfish. Spiny Dogfish tend to avoid the ROV (my observations, Matlock et al. 1991, Trenkel et al. 2004), so they are rarely observed on ROV transects. Simple correspondence analysis of the deck catch with the habitat under each hook showed that the relative capture frequencies of Yelloweye and Quillback across the categories of depth, substrate-complexity and biota were more similar to each other than to Spiny Dogfish and Sunflower Stars. This suggests that spatial overlap along the longline between inshore rockfish and Spiny Dogfish may be lower than suspected. This differs greatly from the general perception of the annual inshore rockfish longline survey, where interspecific competition was assumed to be very high due to large catches of Spiny Dogfish (Lohead and Yamanaka 2007).

Care needs to be taken when extrapolating the results of this thesis to other situations. The field experiments conducted for this thesis required two vessels, one to deploy the longline gear and one to deploy the ROV, and five days of preliminary experiments were conducted in order to establish a protocol where the two vessels could work together efficiently. Since such experiments are expensive and vessel time is limited, only a few paired sets could be undertaken. The paired sets in the March experiment, which provided the underwater observations of species interactions with the longline gear, only occurred in a limited geographic area in one season of the year, when the resident population of Spiny Dogfish in the Strait of Georgia (McFarlane and King 2003) were likely at deeper depths (Fargo et al. 1990). Co-occurrence of species varies by season, in relation to temperature and depth and annual abundance (Murawski and Finn 1988). It seems unlikely that the extent of the variation in the abiotic and biotic habitat of Yelloweye and Quillback is adequately represented by the sets in the March experiment. For example, many of
the sea star catches came from one shallower set in the experiment. Additionally, the experiment did not refute a linear relationship between the $\lambda_s$ index and the observed Quillback density and the fit was very similar for most of the indices for Quillback. This may be a real result or it may be a product of the observed density poorly representing the true abundance available to the longline. This reinforces why absolute abundance cannot be derived from longlines. Even with a ROV present at the longline, it was difficult to assess whether we observed the spatial extent of the individuals that could detect the baited hooks and whether the fish we observed were actually vulnerable to the longline gear based on size.

5.1 Overall conclusions and recommendations

Generally, the results of this thesis cast doubt on the assumption that the survey $\lambda_s$ index is always linearly related to abundance, and imply that caution needs to be taken in applying the index to commercial catches. This is similar to the situation recognized for commercial CPUE, since the 1950s (e.g., Gulland 1955, Beverton and Holt 1957). Additionally, the $\lambda_s$ index performed no better than CPUE for Quillback, and the performance of the $\lambda_s$ index did not improve with the inclusion of hook-level habitat variables. However, there was marginal improvement for Yelloweye, when the $\lambda_s$ index came from underwater observations and when depth was included as a fixed effect in the estimation of the habitat-adjusted $\lambda_s$ index. For the habitat-adjusted $\lambda_s$ index, the marginal increase in fit came at the expense of knowing the habitat under each hook, which was expensive and time-demanding to obtain. However, depth at the hooks may be gathered from charts matched with the vessel track when the survey vessel releases or retrieves the longline gear, which may make including the habitat per hook more feasible.
The most interesting applications for the research in this thesis come from the behaviours and species interactions observed underwater. First, assumptions about bare hooks should consider that a large proportion of bare hooks may be due to sources that are not observed on the deck of the fishing vessel. Partitioning a large portion of the bare hooks to non-target species would be consistent with my results, but not all bare hooks were due to non-target species. Additionally, the interspecific competition for baited hooks between Spiny Dogfish, Sunflower Star, and Yelloweye and Quillback may be less than assumed, particularly in the winter months. One option to consider is that surveys for inshore rockfish may be better served in March, rather than in August when interspecific competition may be higher, as Spiny Dogfish are at shallower depths. Additionally, as Richards and Schnute (1986) established a proportional relationship between angling CPUE and density for Quillback, perhaps this gear is more useful for this inshore rockfish species, when in the appropriate depth range. Angling moves the bait more frequently than on a longline and Quillback might be more attracted to moving bait, particularly as Quillback were often observed near the bait, but were not caught. Visual surveys may also be an option for surveying Yelloweye and Quillback, instead of longline gear. Visual surveys are employed in Alaska for these species (Olson et al. 2016). However, during the August experiment, larger Yelloweye were caught on the longline gear than were observed by the ROV.

Due to the expense of paired vessel experiments, future work should first focus on simulation testing the model and assumptions that were empirically tested in this thesis. Greater variability could be incorporated into a simulation study than in the empirical study here. Simulation studies that investigate the potential impact of hidden sources of bare hooks and hook competition on the relative abundance indices, the management parameters and the resulting management advice would improve understanding of the necessity of correcting for hidden
processes. Additionally, as there appears to be some benefit in incorporating habitat variables into the $\lambda_s$ index for Yelloweye, determining habitat patches along the longline with digital bathymetry models and medium resolution remote sensing imagery, as has been applied at the set-level (e.g., Haggarty 2015, Carrasquilla-Henao et al. in prep.), may provide a more practical approach. Finally, alternative approaches, such as catch-effort standardization (Maunder and Punt 2004), which could include variables for interspecific competition and gear saturation, should be tested against the current practice of using the $\lambda_s$ index in stock assessments. A recent study with trawl survey data suggests that geostatistical models, which estimate smoothed surfaces for species densities and can incorporate habitat variables to explain the variance, outperform GLMs or GLMMs (Thorson et al. 2015) and may be the next step in the development of longline indices adjusted for habitat variation.
References


Løkkeborg, S., Bjordal, Å., and Fernö, A. 1989. Responses of cod (Gadus morhua) and haddock (Melanogrammus aeglefinus) to baited hooks in the natural environment. Canadian Journal of Fisheries and Aquatic Sciences, 46:1478-1483.


Appendices

Appendix A  Estimating rockfish density from Remotely Operated Vehicle observations

In both the March and August experiments, Yelloweye Rockfish and Quillback Rockfish were observed using DFO's Deep Ocean Engineering Phantom HD2+2 Remotely Operate Vehicle (ROV). In order to turn these observations into fish density, the total number of fish seen was recorded and divided by the total area observed by the ROV. I used a strip transect method for estimating density, instead of a line transect method, because the line transect method assumes that fish are uniformly distributed (Buckland et al. 2001). This assumption was violated in the March experiment as a baited longline was present, which likely attracted fish to the observation area. The strip size surveyed was calculated from the position (UTM coordinates) and field of view (FOV) of the ROV, measured with two green lasers mounted 10 cm apart on the ROV.

A.1  ROV position

The ROV was tethered to the survey vessel with a 335 m umbilical. The umbilical is a cable that supplies electrical power to the ROV and allows transmission of video and data signals between the ROV and the vessel. The position (in UTM) of the ROV was recorded every second (in GMT), as the transponder on the ROV communicated with the hydrophone pole held underneath the vessel. Determining the position of the ROV depended on the bottom features of the area traversed and whether the ROV was inside or outside a 45° cone down from the hydrophone. Bottom features like steep rock walls cause reflection and scattering of acoustic energy, which can give erroneous trackpoints. Additionally, if the ROV was outside of the 45° cone, the trackpoints, while correct relative to each other, could be recorded up to 20 m away.
from the hydrophone. Occasionally the ROV was pulled off track when the vessel drifted or the ROV exceeded the extent of the umbilical cord, but these events did not change ROV position by more than a few meters. Position changes greater than this were likely errors and were corrected. Technicians at DFO processed the raw position data. DFO used ArcGIS and ArcEditor PAEK (Polynomial Approximation with Exponential Kernel, Bodansky et al. 2002) to map the raw trackpoints, remove the outliers and obvious tracking errors, and generate a smoothed track, approximating track curves by piecewise polylines. They corrected suspect trackpoints based on the distance to the vessel's GPS position, ROV heading, and typical ROV speed. Haggarty et al. (2017) detail the standard operations of this ROV for rockfish surveys.

A.2 ROV video review

During the March experiment, corrugated plastic line markers were attached to the groundline as the hooks were deployed. Markers indicated the first hook, the last hook and every 10 hooks, which aided the ROV pilot in finding the start of the groundline and allowed numbering of the hooks during video review. DFO digitally stored the ROV video on hard drives and on Mini DV tapes. For each pass over the longline gear, two people independently reviewed the ROV video. On each pass, we recorded the state of each hook, as baited, bare or with a species caught, along with the time the hook was observed (in GMT). For both the March and August experiments, we counted, and identified to species, the free-swimming rockfish and other species commonly caught on the annual longline survey (Lochead and Yamanaka 2007) and recorded the time of each observation. The time of observation was the time when the fish or hook was in the same plane as the paired lasers. Additionally, every 30 s the FOV was measured,
as the distance across the video screen; I assumed that the FOV did not change significantly in 30 s.

A.3 Calculating rockfish density

In both the March and August experiments, for each pass along the transect, I calculated the density of Yelloweye and Quillback from the number of individuals in the strip area and multiplied by 100 (individuals / 100 m²). I treated the FOV as the width of the strip and the sum of the distance between adjacent FOV measurements as the length of the transect. For the March experiment, where the longline was visible, I included both free-swimming fish and those caught on hooks in the density. I also restricted the transect to the area between the start and end markers on the longline, as the behaviour of the ROV was consistent between these points. For the August experiment, the transect was restricted to the areas where the ROV was on-bottom (i.e., on-transect).

I assumed 100% detection of inshore rockfish in the strip. Rockfish are generally known to show little to no avoidance during visual survey methods (Richards and Schnute 1986, Adams et al. 1995, Yoklavich et al. 2007, Stoner et al. 2008). Line transect detection functions for rockfish species show ≥90% probability of detection with a 2.5 - 4 m FOV on submersible surveys (O'Connell et al. 2003; Yoklavich et al. 2007; Rodgveller et al. 2011). In the March experiment, the average FOV was 1.79 ± 1.30 m, across all passes on all sets, and 1.44 ± 1.34 m, across all sets of the August experiment.

As the position of the ROV was transmitted every second, I determined the UTM coordinates of the FOV measurements using the ROV position nearest in time. When the ROV was pulled off course or back along the transect by the ship, or had poor visibility of the
surrounding area due to disturbed sediment or navigating complex terrain, I removed that area from the density calculation. Using the UTM coordinates of the ROV (X and Y), I calculated the distance (d, in m) between adjacent FOV measurements (k and k+1) using Pythagoras’ theorem:

$$d_{k,k+1} = \sqrt{(X_{k+1} - X_k)^2 + (Y_{k+1} - Y_k)^2}$$  \hspace{1cm} \text{Eq. A.1}$$

Since the sea floor is not flat, particularly in rockfish habitat, I calculated a corrected distance (dd) for the difference in depth (de) between adjacent FOV measurements, as:

$$dd_{k,k+1} = \sqrt{(de_{k+1} - de_k)^2 + (d_{k,k+1})^2}$$  \hspace{1cm} \text{Eq. A.2}$$

The average distance between adjacent FOV measurements was very small (<12 m). Thus, I assumed that the curvature of the earth produced minimal error in the distance calculated from UTM coordinates. I calculated the total area of the transect (A) for each pass (j) as:

$$A_j = \sum_{k=1}^{m-1} 0.5 \cdot fov_k \cdot dd_{k,k+1} + 0.5 \cdot fov_{k+1} \cdot dd_{k,k+1}$$  \hspace{1cm} \text{Eq. A.3}$$

where m is the total number of strip width (fov) measurements. In the March experiment, when the ROV passed over the longline three times, I had three measurements for the total strip area. In the August experiment, there was only one measurement for the total strip area. Prior to calculating the total area of the transect, I checked the largest 1% of the areas calculated between adjacent FOV measurements against the ROV video. I removed areas where errors were created due to ROV navigation, along with the corresponding hook and free-swimming fish observations. Density was calculated as the number of fish observed divided by the average total area of the strip transect and multiplied by 100 (individuals / 100 m$^2$).
Appendix B  Relative abundance index parameter estimates from the March and August longline experiments

This Appendix shows posterior outputs for the relative abundance indices in Chapter 2, with output for each longline set of the March and August experiments. The Appendix includes:

1. a comparison of the Bayesian (BEM) and maximum likelihood estimates (MLE) for each $\lambda^D_i$ with a relative difference ($R_{diff}$) calculated as $(\text{MLE} - \text{BEM})/\text{BEM}$;
2. the marginal posterior distributions for the species-specific instantaneous rate of bait loss indices, estimated from deck ($\lambda^D_i$) or underwater ($\lambda^D_i$) observations; and
3. the results of sensitivity analyses that examined the effect on $\lambda^D_i$ and $\lambda^U_i$ of altering the rate parameter for the exponential prior.
Table B.1. Maximum likelihood estimates (MLE), Bayesian posterior modes (BEM), and their relative difference (Rdiff) for the Yelloweye Rockfish, Quillback Rockfish, other species and bare hooks, relative abundance indices ($\lambda_s^D$). The indices were estimated from catch observed on the deck of the vessel for in the March ($n = 13$) and August experiments ($n = 12$). For the BEM estimates, the prior rate parameter was 7.5 h$^{-1}$.

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Table B.2. Maximum likelihood estimates (MLE), Bayesian posterior modes (BEM), and their relative difference (Rdiff) for the Yelloweye Rockfish, Quillback Rockfish, other species and bare hooks, relative abundance indices ($\lambda_i^D$). The indices were estimated from catch observed on the deck of the vessel for in the March ($n = 13$) and August experiments ($n = 12$). For the BEM estimates, the prior rate parameter was $0.17 \, \text{h}^{-1}$.

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Table B.3. Maximum likelihood estimates (MLE), Bayesian posterior modes (BEM), and their relative difference (Rdiff) for the Yelloweye Rockfish, Quillback Rockfish, other species and bare hooks, relative abundance indices ($\lambda^D_s$). The indices were estimated from catch observed on the deck of the vessel for in the March ($n = 13$) and August experiments ($n = 12$). For the BEM estimates, the prior rate parameter was 25 h$^{-1}$.

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Figure B.1. Sensitivity of the marginal posterior for the Yelloweye Rockfish relative abundance index, $\lambda^D_s$, to the specification of the rate parameter of the exponential prior. $\lambda^D_s$ was estimated from catch observed on the deck of the vessel for each longline set in the March experiment ($n = 13$).
Figure B.2. Sensitivity of the marginal posterior for the Yelloweye Rockfish relative abundance index, $\lambda_s^W$, to the specification of the rate parameter of the exponential prior. $\lambda_s^W$ was estimated from multiple observations of the hooks underwater during three passes (Pass 1, Pass 2, and Pass 3) over the longline for each longline set in the March experiment ($n = 13$).
Figure B.3. Sensitivity of the marginal posterior for the Quillback Rockfish relative abundance index, $\lambda^D_s$, to the specification of the rate parameter of the exponential prior. $\lambda^D_s$ was estimated from catch observed on the deck of the vessel for each longline set in the March experiment ($n = 13$).
Figure B.4. Sensitivity of the marginal posterior for the Quillback Rockfish relative abundance index, $\lambda_s^W$, to the specification of the rate parameter of the exponential prior. $\lambda_s^W$ was estimated from multiple observations of the hooks underwater during three passes (Pass 1, Pass 2, and Pass 3) over the longline for each longline set in the March experiment ($n = 13$).
Figure B.5. Sensitivity of the marginal posterior for the other species relative abundance index, $\lambda^D_s$, to the specification of the rate parameter of the exponential prior. $\lambda^D_s$ was estimated from catch observed on the deck of the vessel for each longline set in the March experiment ($n = 13$).
Figure B.6. Sensitivity of the marginal posterior for the other species relative abundance index, $\lambda_s^W$, to the specification of the rate parameter of the exponential prior. $\lambda_s^W$ was estimated from multiple observations of the hooks underwater during three passes (Pass 1, Pass 2, and Pass 3) over the longline for each longline set in the March experiment ($n = 13$).
Figure B.7. Sensitivity of the marginal posterior for the bare hooks relative abundance index, $\lambda_s^D$, to the specification of the rate parameter of the exponential prior. $\lambda_s^D$ was estimated from catch observed on the deck of the vessel for each longline set in the March experiment ($n = 13$).
Figure B.8. Sensitivity of the marginal posterior for the bare hooks relative abundance index, \( \lambda^w_s \), to the specification of the rate parameter of the exponential prior. \( \lambda^w_s \) was estimated from multiple observations of the hooks underwater during three passes (Pass 1, Pass 2, and Pass 3) over the longline for each longline set in the March experiment (\( n = 13 \)).
Figure B.9. Sensitivity of the marginal posterior for the Yelloweye Rockfish relative abundance index, $\lambda_s^D$, to the specification of the rate parameter of the exponential prior. $\lambda_s^D$ was estimated from catch observed on the deck of the vessel for each longline set in the August experiment ($n = 12$).
Figure B.10. Sensitivity of the marginal posterior for the Quillback Rockfish relative abundance index, $\lambda^D_s$, to the specification of the rate parameter of the exponential prior. $\lambda^D_s$ was estimated from catch observed on the deck of the vessel for each longline set in the August experiment ($n = 12$).
Figure B.11. Sensitivity of the marginal posterior for the other species relative abundance index, $\lambda^D$, to the specification of the rate parameter of the exponential prior. $\lambda^D$ was estimated from catch observed on the deck of the vessel for each longline set in the August experiment ($n = 12$).
Figure B.12. Sensitivity of the marginal posterior for the bare hooks relative abundance index, $\lambda_s^D$, to the specification of the rate parameter of the exponential prior. $\lambda_s^D$ was estimated from catch observed on the deck of the vessel for each longline set in the August experiment ($n = 12$).
Figure B.13. Exponential prior (rate = 7.5 h$^{-1}$) and marginal posteriors for the Yelloweye Rockfish relative abundance index, $\lambda_s^D$, for each longline set in the March experiment ($n = 13$). $\lambda_s^D$ was estimated from catch observed on the deck of the vessel.
Figure B.14. Exponential prior (rate = $7.5 \text{ h}^{-1}$) and marginal posteriors for the Yelloweye Rockfish relative abundance index, $\lambda^W_s$, for each longline set in the March experiment ($n = 13$). $\lambda^W_s$ was estimated from multiple observations of the hooks underwater during three passes (Pass 1, Pass 2, and Pass 3) over the longline.
Figure B.15. Exponential prior (rate = 7.5 h$^{-1}$) and marginal posteriors for the Quillback Rockfish relative abundance index, \( \lambda^D_s \), for each longline set in the March experiment \((n = 13)\). \( \lambda^D_s \) was estimated from catch observed on the deck of the vessel.
Figure B.16. Exponential prior (rate = 7.5 h\(^{-1}\)) and marginal posteriors for the Quillback Rockfish relative abundance index, \(\lambda_s^W\), for each longline set in the March experiment (\(n = 13\)). \(\lambda_s^W\) was estimated from multiple observations of the hooks underwater during three passes (Pass 1, Pass 2, and Pass 3) over the longline.
Figure B.17. Exponential prior (rate = 7.5 h\(^{-1}\)) and marginal posteriors for the other species relative abundance index, \(\lambda_s^D\), for each longline set in the March experiment \((n = 13)\). \(\lambda_s^D\) was estimated from catch observed on the deck of the vessel.
Figure B.18. Exponential prior (rate = 7.5 h$^{-1}$) and marginal posteriors for the other species relative abundance index, $\lambda_s^W$, for each longline set in the March experiment ($n = 13$). $\lambda_s^W$ was estimated from multiple observations of the hooks underwater during three passes (Pass 1, Pass 2, and Pass 3) over the longline.
Figure B.19. Exponential prior (rate $= 7.5 \text{ h}^{-1}$) and marginal posteriors for the bare hooks relative abundance index, $\lambda^D_s$, for each longline set in the March experiment ($n = 13$). $\lambda^D_s$ was estimated from catch observed on the deck of the vessel.
Figure B.20. Exponential prior (rate = 7.5 h$^{-1}$) and marginal posteriors for the bare hooks relative abundance index, $\lambda_s^W$, for each longline set in the March experiment ($n = 13$). $\lambda_s^W$ was estimated from multiple observations of the hooks underwater during three passes (Pass 1, Pass 2, and Pass 3) over the longline.
Figure B.21. Exponential prior (rate = 7.5 h$^{-1}$) and marginal posteriors for the Yelloweye Rockfish relative abundance index, $\lambda^D_s$, for each longline set in the August experiment ($n = 12$). $\lambda^D_s$ was estimated from catch observed on the deck of the vessel.
Figure B.22. Exponential prior (rate = 7.5 h\(^{-1}\)) and marginal posteriors for the Quillback Rockfish relative abundance index, \(\lambda_s^D\), for each longline set in the August experiment (\(n = 12\)). \(\lambda_s^D\) was estimated from catch observed on the deck of the vessel.
Figure B.23. Exponential prior (rate = 7.5 h$^{-1}$) and marginal posteriors for the other species relative abundance index, $\lambda^D$, for each longline set in the August experiment ($n = 12$). $\lambda^D$ was estimated from catch observed on the deck of the vessel.
Figure B.24. Exponential prior (rate = 7.5 h\(^{-1}\)) and marginal posteriors for the bare hooks relative abundance index, \(\lambda^D_s\), for each longline set in the August experiment \((n = 12)\). \(\lambda^D_s\) was estimated from catch observed on the deck of the vessel.
Appendix C  Supplementary results from Chapter 2: An empirical evaluation of key assumptions of a relative abundance index, the instantaneous rate of bait loss

This Appendix includes additional comparisons of the relative abundance indices for other species and bare hooks in Chapter 2.
Figure C.1. Estimates of the relative abundance index $\lambda_s$ (posterior medians) from catch data observed on the deck of the vessel ($\lambda_s^D$) and from multiple observations of the hooks underwater ($\lambda_s^W$) for other species (left panel) and bare hooks (right panel). The solid line is the best fitting linear model and the dashed line is the 1:1 line. Observations from the March experiment (three passes along the longline, $n = 13$).
Figure C.2. Coefficient of variation (%) for the precision of the posterior distribution of $\lambda_s$ across all longline sets in the March ($n = 13$) and August ($n = 12$) experiments for other species (top row) and bare hooks (bottom row). $\lambda_s^D$ was estimated from catch observed on the deck of the vessel, $\lambda_s^W$ from multiple observations of the hooks underwater during three passes (Pass 1, Pass 2, and Pass 3) over the longline. $\lambda_s^{W-PI}$ used all the hooks viewed in each pass over the longline, while $\lambda_s^{W-PC}$ used a reduced number based on catch in the previous pass.
Appendix D Supplementary results from Chapter 3: Evaluating assumptions about species behaviours and competitive interactions and their influence on a relative abundance index, the instantaneous rate of bait loss

This Appendix includes the marginal posterior distributions for the $\lambda_r^D$ relative abundance indices (Yelloweye Rockfish and Quillback Rockfish) estimated in Chapter 3 from catch data adjusted for: (1) different assumptions about the source of bare hooks (Figure D.1-Figure D.14); and (2) sea star loss during gear retrieval (Figure D.15-Figure D.28). Longline sets included in the catch data are from the annual inshore rockfish longline survey (2003-2005, 2007-2015) in the Pacific fishery management areas (PFMAs) frequently sampled over the survey years ($n = 701$ sets).
Figure D.1. Exponential prior (rate = 5.4 h^{-1}) and marginal posteriors for the Yelloweye Rockfish relative abundance index, $\lambda_N^D$, under different assumptions about the source of bare hooks. $\lambda_N^D$ was estimated from catch observed on the deck of the vessel for all longline sets in PFMA 12 (Area 12) ($n = 256$ sets).
Figure D.2. Exponential prior (rate = 5.4 h$^{-1}$) and marginal posteriors for the Yelloweye Rockfish relative abundance index, $\lambda_n^D$, under different assumptions about the source of bare hooks. $\lambda_n^D$ was estimated from catch observed on the deck of the vessel for all longline sets in PFMA 13 (Area 13) ($n = 167$ sets).
Figure D.3. Exponential prior (rate = 5.4 h$^{-1}$) and marginal posteriors for the Yelloweye Rockfish relative abundance index, $\lambda_s^D$, under different assumptions about the source of bare hooks. $\lambda_s^D$ was estimated from catch observed on the deck of the vessel for all longline sets in PFMA 14 (Area 14) ($n = 43$ sets).
Figure D.4. Exponential prior (rate = 5.4 h\(^{-1}\)) and marginal posteriors for the Yelloweye Rockfish relative abundance index, \(\lambda_D\), under different assumptions about the source of bare hooks. \(\lambda_D\) was estimated from catch observed on the deck of the vessel for all longline sets in PFMA 15 (Area 15) \((n = 65\) sets).
Figure D.5. Exponential prior (rate = 5.4 h\(^{-1}\)) and marginal posteriors for the Yelloweye Rockfish relative abundance index, \(\lambda_s^D\), under different assumptions about the source of bare hooks. \(\lambda_s^D\) was estimated from catch observed on the deck of the vessel for all longline sets in PFMA 16 (Area 16) \((n = 76\) sets).
Figure D.6. Exponential prior (rate = 5.4 h\(^{-1}\)) and marginal posteriors for the Yelloweye Rockfish relative abundance index, \(\lambda_s^D\), under different assumptions about the source of bare hooks. \(\lambda_s^D\) was estimated from catch observed on the deck of the vessel for all longline sets in PFMA 17 (Area 17) \((n = 62\) sets).
Figure D.7. Exponential prior (rate = 5.4 h\(^{-1}\)) and marginal posteriors for the Yelloweye Rockfish relative abundance index, \(\lambda^D_s\), under different assumptions about the source of bare hooks. \(\lambda^D_s\) was estimated from catch observed on the deck of the vessel for all longline sets in PFMA 28 (Area 28) \((n = 32\) sets).
Figure D.8. Exponential prior (rate = 5.4 h⁻¹) and marginal posteriors for the Quillback Rockfish relative abundance index, $\lambda_s^D$, under different assumptions about the source of bare hooks. $\lambda_s^D$ was estimated from catch observed on the deck of the vessel for all longline sets in PFMA 12 (Area 12) ($n = 256$ sets).
Figure D.9. Exponential prior (rate = 5.4 h\(^{-1}\)) and marginal posteriors for the Quillback Rockfish relative abundance index, \(\lambda^D_s\), under different assumptions about the source of bare hooks. \(\lambda^D_s\) was estimated from catch observed on the deck of the vessel for all longline sets in PFMA 13 (Area 13) \((n = 167\) sets).
Figure D.10. Exponential prior (rate = 5.4 h\(^{-1}\)) and marginal posteriors for the Quillback Rockfish relative abundance index, \(\lambda^D_s\), under different assumptions about the source of bare hooks. \(\lambda^D_s\) was estimated from catch observed on the deck of the vessel for all longline sets in PFMA 14 (Area 14) \((n = 43\) sets).
Figure D.11. Exponential prior (rate = 5.4 h\(^{-1}\)) and marginal posteriors for the Quillback Rockfish relative abundance index, \(\lambda_s^D\), under different assumptions about the source of bare hooks. \(\lambda_s^D\) was estimated from catch observed on the deck of the vessel for all longline sets in PFMA 15 (Area 15) \((n = 65\) sets).
Figure D.12. Exponential prior (rate = 5.4 h\(^{-1}\)) and marginal posteriors for the Quillback Rockfish relative abundance index, \(\lambda_s^D\), under different assumptions about the source of bare hooks. \(\lambda_s^D\) was estimated from catch observed on the deck of the vessel for all longline sets in PFMA 16 (Area 16) (\(n = 76\) sets).
Figure D.13. Exponential prior (rate = 5.4 h\(^{-1}\)) and marginal posteriors for the Quillback Rockfish relative abundance index, \(\lambda^D_s\), under different assumptions about the source of bare hooks. \(\lambda^D_s\) was estimated from catch observed on the deck of the vessel for all longline sets in PFMA 17 (Area 17) \((n = 62\) sets).
Figure D.14. Exponential prior (rate $= 5.4 \text{ h}^{-1}$) and marginal posteriors for the Quillback Rockfish relative abundance index, $\lambda^D_s$, under different assumptions about the source of bare hooks. $\lambda^D_s$ was estimated from catch observed on the deck of the vessel for all longline sets in PFMA 28 (Area 28) ($n = 32$ sets).
Figure D.15. Exponential prior (rate = 7.5 h\(^{-1}\)) and marginal posteriors for the Yelloweye Rockfish relative abundance index, \(\lambda^D_s\), when catch is adjusted for different levels of sea star loss during gear retrieval. \(\lambda^D_s\) was estimated from catch observed on the deck of the vessel for all longline sets in PFMA 12 (Area 12) \((n = 256 \text{ sets})\).
Figure D.16. Exponential prior (rate = 7.5 h⁻¹) and marginal posteriors for the Yelloweye Rockfish relative abundance index, $\lambda_n^D$, when catch is adjusted for different levels of sea star loss during gear retrieval. $\lambda_n^D$ was estimated from catch observed on the deck of the vessel for all longline sets in PFMA 13 (Area 13) ($n = 167$ sets).
Figure D.17. Exponential prior (rate = 7.5 h⁻¹) and marginal posteriors for the Yelloweye Rockfish relative abundance index, $\lambda_s^D$, when catch is adjusted for different levels of sea star loss during gear retrieval. $\lambda_s^D$ was estimated from catch observed on the deck of the vessel for all longline sets in PFMA 14 (Area 14) ($n = 43$ sets).
Figure D.18. Exponential prior (rate = 7.5 h$^{-1}$) and marginal posteriors for the Yelloweye Rockfish relative abundance index, $\lambda^D$, when catch is adjusted for different levels of sea star loss during gear retrieval. $\lambda^D$ was estimated from catch observed on the deck of the vessel for all longline sets in PFMA 15 (Area 15) ($n = 65$ sets).
Figure D.19. Exponential prior (rate = 7.5 h\(^{-1}\)) and marginal posteriors for the Yelloweye Rockfish relative abundance index, \(\lambda^D_s\), when catch is adjusted for different levels of sea star loss during gear retrieval. \(\lambda^D_s\) was estimated from catch observed on the deck of the vessel for all longline sets in PFMA 16 (Area 16) (\(n = 76\) sets).
Figure D.20. Exponential prior (rate = 7.5 h\(^{-1}\)) and marginal posteriors for the Yelloweye Rockfish relative abundance index, \(\lambda_\text{D}^s\), when catch is adjusted for different levels of sea star loss during gear retrieval. \(\lambda_\text{D}^n\) was estimated from catch observed on the deck of the vessel for all longline sets in PFMA 17 (Area 17) \((n = 62\) sets).
Figure D.21. Exponential prior (rate = 7.5 h\(^{-1}\)) and marginal posteriors for the Yelloweye Rockfish relative abundance index, \(\lambda_s^D\), when catch is adjusted for different levels of sea star loss during gear retrieval. \(\lambda_s^D\) was estimated from catch observed on the deck of the vessel for all longline sets in PFMA 28 (Area 28) (\(n = 32\) sets).
Figure D.22. Exponential prior (rate = 7.5 h$^{-1}$) and marginal posteriors for the Quillback Rockfish relative abundance index, $\lambda_s$, when catch is adjusted for different levels of sea star loss during gear retrieval. $\lambda_s$ was estimated from catch observed on the deck of the vessel for all longline sets in PFMA 12 (Area 12) ($n = 256$ sets).
Figure D.23. Exponential prior (rate = 7.5 h⁻¹) and marginal posteriors for the Quillback Rockfish relative abundance index, $\lambda^D_s$, when catch is adjusted for different levels of sea star loss during gear retrieval. $\lambda^D_s$ was estimated from catch observed on the deck of the vessel for all longline sets in PFMA 13 (Area 13) ($n = 167$ sets).
Figure D.24. Exponential prior (rate = 7.5 h$^{-1}$) and marginal posteriors for the Quillback Rockfish relative abundance index, $\lambda_{s}^{D}$, when catch is adjusted for different levels of sea star loss during gear retrieval. $\lambda_{s}^{D}$ was estimated from catch observed on the deck of the vessel for all longline sets in PFMA 14 (Area 14) ($n = 43$ sets).
Figure D.25. Exponential prior (rate = 7.5 h\(^{-1}\)) and marginal posteriors for the Quillback Rockfish relative abundance index, \(\lambda^D\), when catch is adjusted for different levels of sea star loss during gear retrieval. \(\lambda^D\) was estimated from catch observed on the deck of the vessel for all longline sets in PFMA 15 (Area 15) \((n = 65\) sets).
Figure D.26. Exponential prior (rate = 7.5 h$^{-1}$) and marginal posteriors for the Quillback Rockfish relative abundance index, $\lambda^{D}_{s}$, when catch is adjusted for different levels of sea star loss during gear retrieval. $\lambda^{D}_{s}$ was estimated from catch observed on the deck of the vessel for all longline sets in PFMA 16 (Area 16) ($n = 76$ sets).
Figure D.27. Exponential prior (rate = 7.5 h\(^{-1}\)) and marginal posteriors for the Quillback Rockfish relative abundance index, \(\lambda^D_s\), when catch is adjusted for different levels of sea star loss during gear retrieval. \(\lambda^D_s\) was estimated from catch observed on the deck of the vessel for all longline sets in PFMA 17 (Area 17) \((n = 62\) sets).
Figure D.28. Exponential prior (rate = 7.5 h\(^{-1}\)) and marginal posteriors for the Quillback Rockfish relative abundance index, \(\lambda^D_s\), when catch is adjusted for different levels of sea star loss during gear retrieval. \(\lambda^D_s\) was estimated from catch observed on the deck of the vessel for all longline sets in PFMA 28 (Area 28) \((n = 32\) sets).
Appendix E  Supplementary results from Chapter 4: Evaluating the impact of fine-scale habitat variation on a hook-based abundance index developed from bottom longline catches

This Appendix includes the marginal posterior distributions and post-model pre-data distributions for: (1) the set-level intercepts ($\lambda_i^{D-Ha}$) for the habitat-adjusted models for Yelloweye Rockfish and Quillback Rockfish; and (2) the species-specific habitat $\beta$ parameters for depth ($\beta_{DEP}$), substrate-complexity ($\beta_{SC}$), biota ($\beta_{BIO}$) and relief ($\beta_{REL}$), estimated in Chapter 4 from the catch data and underwater observations of hook-level habitat. Also included are the results of sensitivity analyses that examine the effect on the $\lambda_i^{D-Ha}$ parameters and the habitat $\beta$ parameters of: (1) the rate parameters for the exponential priors; and (2) the inclusion of different habitat variables. Longline sets included in the catch data are from the March experiment ($n = 13$ sets).
Figure E.1. Exponential prior (rate = 22.5 h\(^{-1}\)), post-model pre-data distribution and marginal posteriors for the set-level intercept \(\lambda_s^{D-Ha}\) in the habitat-adjusted Yelloweye Rockfish model corrected for the effect of depth and substrate-complexity. \(\lambda_s^{D-Ha}\) is \(\lambda_s^{D-H}\) for mixed fine substrate with low complexity at 0 m depth, or the intercept for the habitat-effects model, and was estimated from catch observed on the deck of the vessel for each longline set \((n = 13)\) in the March experiment. The solid light blue line is the \(\lambda_s^D\) index, which is not corrected for habitat effects.
Figure E.2. Exponential prior (rate = 22.5 h\(^{-1}\)), post-model pre-data distribution and marginal posteriors for the set-level intercept (\(\lambda^{s-Ha}_D\)) in the habitat-adjusted Quillback Rockfish model corrected for the effect of depth and substrate-complexity. \(\lambda^{s-Ha}_D\) is \(\lambda^{s-H}_s\) for mixed fine substrate with low complexity at 0 m depth, or the intercept for the habitat-effects model, and was estimated from catch observed on the deck of the vessel for each longline set (\(n = 13\)) in the March experiment. The solid light blue line is the \(\lambda^D_s\) index, which is not corrected for habitat effects.
Figure E.3. Exponential prior (rate = 7.5 h\(^{-1}\)), post-model pre-data distribution and marginal posterior for the other species abundance index (\(\lambda_s^{D}\)) estimated in the Bayesian model with correction for habitat effects. The \(\lambda_s^{D}\) index was estimated from catch observed on the deck of the vessel for each longline set (\(n = 13\)) in the March experiment.
Figure E.4. Exponential prior (rate = 7.5 h\(^{-1}\)), post-model pre-data distribution and marginal posterior for the bare hooks abundance index (\(\lambda_s^D\)) estimated in the Bayesian model with correction for habitat effects. The \(\lambda_s^D\) index was estimated from catch observed on the deck of the vessel for each longline set (\(n = 13\)) in the March experiment.
Figure E.5. Exponential prior, post-model pre-data distribution and marginal posterior for the species-specific habitat $\beta$ parameters for depth ($\beta_{\text{DEP}}$) and substrate-complexity ($\beta_{\text{SC}}$). The exponential prior rate parameter was $1550 \text{ h}^{-1}$ for the $\beta_{\text{DEP}}$ parameters and $22.5 \text{ h}^{-1}$ for the $\beta_{\text{SC}}$ parameters. All parameters were estimated from catch observed on the deck of the vessel and habitat variables recorded per hook ($n = 2925$) from underwater observation of each longline set in the March experiment.
Figure E.6. Sensitivity of the marginal posterior of the set-level intercept ($\lambda_s^{D-Ha}$) in the habitat-adjusted Yelloweye Rockfish model to the specification of the exponential priors for the habitat $\beta$ parameters for depth ($\beta_{DEP}^Y$) and each category of substrate-complexity ($\beta_{SC}^Y$). For $\lambda_s^{D-Ha}$, the exponential prior rate parameter was 22.5 h$^{-1}$, except in the green line scenario, where all priors had broader distributions, and the rate was 0.51 h$^{-1}$. $\lambda_s^{D-Ha}$ is $\lambda_s^{D-H}$ for mixed fine substrate with low complexity at 0 m depth, and was estimated from catch observed on the deck of the vessel for each longline set ($n = 13$) in the March experiment. The solid light blue line is the $\lambda_s^D$ index, which is not corrected for habitat effects.
Figure E.7. Sensitivity of the marginal posterior of the set-level intercept \( \lambda_{s-Ha} \) in the habitat-adjusted Quillback Rockfish model to the specification of the exponential priors for the habitat \( \beta \) parameters for depth \( \beta_{DEP} \) and each category of substrate-complexity \( \beta_{SC} \). For \( \lambda_{s-Ha} \), the exponential prior rate parameter was 22.5 h\(^{-1}\), except in the green line scenario, where all priors had broader distributions, and the rate was 0.51 h\(^{-1}\). \( \lambda_{s-Ha} \) is \( \lambda_{s-H} \) for mixed fine substrate with low complexity at 0 m depth, and was estimated from catch observed on the deck of the vessel for each longline set \( (n = 13) \) in the March experiment. The solid light blue line is the \( \lambda_{s-D} \) index, which is not corrected for habitat effects.
Figure E.8. Sensitivity of the marginal posterior of the species-specific habitat $\beta$ parameters ($\beta_{DEP}$ and $\beta_{SC}$) to the specification of the exponential priors for depth ($\beta^0_{DEP}$) and each category of substrate-complexity ($\beta^0_{SC}$). All parameters were estimated from catch observed on the deck of the vessel and habitat variables recorded per hook ($n = 2925$) from underwater observation in the March experiment.
Figure E.9. Sensitivity of the marginal posterior of the set-level intercept (\( \lambda_s^{D-Ha} \)) in the habitat-adjusted Yelloweye Rockfish model to changing model structure by adding/removing the habitat variables depth (DEP), substrate-complexity (SC), biota (BIO) and relief (REL). \( \lambda_s^{D-Ha} \) is \( \lambda_s^{D-H} \) for mixed fine substrate with low complexity at 0 m depth, and was estimated from catch observed on the deck of the vessel for each longline set \( (n = 13) \) in the March experiment. The solid light blue line is the \( \lambda_s^D \) index, which is not corrected for habitat effects. The rate parameters for the exponential priors for \( \lambda_s^{D-Ha} \) and the habitat \( \beta \) parameters in each model can be found in Table 4.2.
Figure E.10. Sensitivity of the marginal posterior of the set-level intercept ($\lambda_i^{D-Ha}$) in the habitat-adjusted Quillback Rockfish model to changing model structure by adding/removing the habitat variables depth (DEP), substrate-complexity (SC), biota (BIO) and relief (REL). $\lambda_i^{D-Ha}$ is $\lambda_i^{D-H}$ for mixed fine substrate with low complexity at 0 m depth, and was estimated from catch observed on the deck of the vessel for each longline set ($n = 13$) in the March experiment. The solid light blue line is the $\lambda_i^D$ index, which is not corrected for habitat effects. The rate parameters for the exponential priors for $\lambda_i^{D-Ha}$ and the habitat $\beta$ parameters in each model can be found in Table 4.2.
Figure E.11. Sensitivity of the marginal posterior of the species-specific habitat $\beta$ parameters ($\beta_{\text{DEP}}$ and $\beta_{\text{SC}}$) to changing model structure by adding/removing the habitat variables depth (DEP), substrate-complexity (SC), biota (BIO) and relief (REL). The rate parameters for the exponential priors for $\lambda_{jH}^{D-HA}$ and the habitat $\beta$ parameters in each model can be found in Table 4.2. All parameters were estimated from catch observed on the deck of the vessel and habitat variables recorded per hook ($n = 2925$) from underwater observation of each longline set in the March experiment.
Figure E.12. Exponential prior, post-model pre-data distribution and marginal posterior of the habitat $\beta$ parameters for biota ($\beta_{BIO}$) and relief ($\beta_{REL}$) for Quillback Rockfish (Eq. 4.9). The rate parameters for the exponential priors for $\alpha_{D-Ha}$ and the habitat $\beta$ parameters in each model can be found in Table 4.2. All parameters were estimated from catch observed on the deck of the vessel and habitat variables recorded per hook ($n = 2925$) from underwater observation of each longline set in the March experiment.