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# Updated Reference Points and Harvest Options for the Giant Red Sea Cucumber *(Apostichopus californicus)* Fishery in British Columbia using data from Experimental Fishing Areas

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**Foreword**

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

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## ABSTRACT

The Giant Red Sea Cucumber, *Apostichopus californicus*, is the subject of a lucrative commercial dive fishery in British Columbia (BC), Canada. Despite considerable research, the life history of this species is poorly understood and many biological parameters cannot be estimated, preventing the use of typical fisheries models. As a result, Four Experimental Fishing Areas (EFAs) were established in BC in 1998 to study the effects of harvest on sea cucumber densities. After 10 years, EFA data were analyzed, a latent productivity model was developed, and recommendations were made regarding harvest rates and provisional reference points (Hand et al. 2009). The EFAs continued until 2015, generating another 8 years of data. This document updates harvest advice based on the original latent productivity model (with some updates) and the full time series of EFA data. Maximum sustainable harvests are presented for various harvest strategies, combining harvest intervals of 1 to 5 years with different minimum equilibrium stock level thresholds (minimum observed, 0.50 $B_0$, 0.60 $B_0$, and 0.80 $B_0$) and estimates of either current or virgin biomass. Recommendations include implementing harvests that do not exceed the range of the lower 0.01 quantile for equilibrium stock outcomes above 0.60 $B_0$. For example, for annual harvest rates, the range not to be exceeded is 2.0 to 8.0% of estimated pre-harvest biomass, whereas for triennial harvest it is 5.7 to 18.8% of estimated pre-harvest biomass, with the caveat that the upper ranges may only be appropriate for highly productive areas. Furthermore, the adoption of empirical reference points is recommended: a conservative Limit Reference Point of 0.029 sea cucumbers $m^{-2}$ on sea cucumber habitat, and an Upper Stock Reference Point of 0.038 sea cucumbers $m^{-2}$ on sea cucumber habitat.

# 1. INTRODUCTION

The Giant Red Sea Cucumber, *Apostichopus californicus* (formerly *Parastichopus*) (Stimpson 1857), is a valued marine resource, like many other members of the Phylum Echinodermata. Although there are 47 species of sea cucumbers (Class Holothuroidea) in British Columbia (BC) waters (Lambert 1997; Lambert and Boutillier 2011), *A. californicus* is the only one subject to a commercial fishery. Its history of commercial exploitation dates to 1971, when landings were first recorded, however its use as a traditional food by coastal First Nations dates back countless generations (Stephenson et al. 1995). Regulation of the fishery, in the form of commercial licenses, was introduced in 1980 on an experimental basis. The commercial fishery for *A. californicus* initially followed the boom and bust pattern typical of emerging fisheries targeting poorly understood species, which triggered conservation concerns, a series of arbitrary quota reductions and additional management measures (DFO 2022; Hand et al. 2009; Hand and Rogers 1999). A history of management measures for the commercial sea cucumber fishery is provided in the Integrated Fisheries Management Plan (IFMP Table 1, Appendix 5 of DFO 2022).

*A. californicus* is the largest species of sea cucumber in BC and is distributed from the intertidal to ~250 m depth. It is targeted by commercial SCUBA dive harvesters within diveable depths (< 20 m). Much of the species' depth distribution is therefore not accessible to the commercial fishery, creating a de facto reserve, however abundance at deeper than diveable depths is largely unknown (Duprey et al. 2011). While the fishery (IFMP) is managed on an annual basis (commercial license year from October 1 - September 30), harvest is rapid, with the majority of removals occurring in October and November (DFO 2022).

Numerous biological knowledge gaps complicate the assessment and management of this species. Notably, there is no practical method to age A. californicus, as the composition and metabolic activity of the buccal ring, one of the sea cucumber's only hard structures, is unknown at this time. Ebert (1978) suggests that the buccal ring is directly intertwined to somatic growth, indicating that during periods of no or little growth that the buccal ring also demonstrated the same growth projections. Structures targeted for age estimation must comply with several postulates (Campana and Thorrold 2001), the most import being the structure must undergo continual growth as demonstrated within teleost otoliths (Maillet and Checkley 1990). Structures that do not demonstrate continual growth should be avoided for the purpose of age estimation as this will lead to an underestimation of age (Stephen Wischniowski, Fisheries and Oceans Canada (DFO) Sclerochronology Lab Program Head, Pacific Biological Station, Nanaimo, BC, February 2022, pers. comm.). Furthermore, A. californicus is a soft-bodied organism that can change body dimensions by absorbing or expelling water and contracting muscles in the body wall. This species also reabsorbs and regenerates viscera and changes body wall thickness seasonally (Fankboner and Cameron 1985). Spatial and temporal variation in size and growth make this species difficult to size consistently and preclude the use of size-based proxies for age. Adults are relatively sedentary, moving less than 4 m $day^{-1}$, although some sources suggest that they undertake seasonal depth migrations (Hand and Rogers 1999; Lambert 1997). A long larval duration (51 to 125 days) (Cameron and Fankboner 1989; Strathmann 1978) likely plays a more important role in genetic mixing and migration, but source/sink dynamics are currently largely unknown (Xuereb et al. 2018). Finally, juveniles are rarely observed during surveys[1], suggesting an unknown ontogenetic shift in crypsis or habitat. All of these features limit the collection of typical fisheries biology parameters and the inclusion of life-history data in fisheries models.

In 1995, the first stock assessment and quota options paper for the *A. californicus* fishery was produced (Phillips and Boutillier 1998), and the process highlighted a number of knowledge gaps and data deficiencies. The authors of the first assessment, Phillips and Boutillier (1998), accordingly recommended a change in approach for the BC *A. californicus* fishery and alignment with Perry et al. (1999)'s recommended framework for managing new and developing invertebrate fisheries. The framework for emerging invertebrate fisheries involves a phased approach, wherein Phase 0 collects existing information, Phase 1 collects new information, and Phase 2 involves fishing for commerce (Perry et al. 1999). The 1998 assessment (Phillips and Boutillier 1998) synthesized much of the information on the *A. californicus* fishery in BC and was quickly followed by a more comprehensive Phase 0 review (Boutillier et al. 1998). The latter concluded that the *A. californicus* fishery was not providing sufficient information to conduct stock assessments nor assess fishery impacts. Boutillier et al. (1998) therefore recommended that Phase 1 of the commercial fishery be conducted in such a way as to facilitate the collection of fishery-dependent and -independent data and the testing of management assumptions. More specifically, recommendations included restricting the commercial fishery to 25% of the coast, using the most conservative density and exploitation estimates available, establishing experimental management areas (now referred to as Experimental Fishery Areas or EFAs), and establishing closed control areas. Many of these recommendations were implemented with Phase 1 and an Adaptive Management Plan (AMP) in 1997 (DFO 2022; Hand and Rogers 1999). Indeed, commercial harvest was restricted to a static 25% of the BC coast, 50% of the coast was closed to harvest as a control, and 25% of the coast was set aside for experimental fishery research. The research piece was a collaborative project between the Kitasoo/Xai'Xais Nations, the Pacific Sea Cucumber Harvesters Association and Fisheries and Oceans Canada (DFO). At this stage, commercial fishery quotas were based on a population density estimate from Alaskan surveys (2.5 sea cucumbers per metre of shoreline) and a sustainable annual harvest of 4.2% of virgin biomass as estimated from analyses of data collected in Washington State (Hand et al. 2009; Larson et al. 1995). Harvests generally ranging from 2% to 16% (but up to 50% in 2014 and 2015) were applied to the EFAs.

Phase 1 lasted 10 years, with the data from fisheries-dependent and -independent research, such as harvest data, open surveys (i.e. surveys conducted in areas of the coast that remained open), EFAs and biological sampling, culminating in fishery recommendations that were presented to and accepted by the Pacific Invertebrate Subcommittee of the Canadian Science Advisory Secretariat (CSAS) in 2007 (Hand et al. 2009). Hand et al. (2009) developed a latent productivity model based on experimental fisheries data, and the recommendation to re-open the commercial fishery beyond the formerly geographically restricted 25% of the coastline, using a harvest rate of 3.5 - 10.3% (based on the lower one percentile of maximum sustainable harvest rates calculated in the latent productivity model for EFAs) was approved. The approved recommendations also necessitated surveying areas prior to re-opening for commercial harvesting (Duprey et al. 2011; Hand et al. 2009). Furthermore, Hand et al. (2009) recommended adopting a Limit Reference Point (LRP) of 50% of virgin biomass ($B_0$), consideration of an Upper Stock Reference (USR) between 0.60 and 0.80 $B_0$, and continuation

[1] Bazinet, A.C., Garner, G.D., and Hansen, S.C. *In prep*. Biomass estimates for sea cucumber *(Apostichopus californicus)* as determined through surveys conducted from 2014 to 2020. *Can. Manuscr. Rep. Fish. Aquat. Sci.*

of the EFAs. While the updated harvest rates were implemented, there was no system in place to measure sea cucumber populations against the proposed reference points. Reference points are intended to be implemented on a different scale than the fishery, which is managed on a quota management area (QMA) basis. Since *A. californicus* is currently considered to be a coast wide stock, reference points are implemented on a coast wide scale.

The *A. californicus* commercial fishery entered Phase 2 in 2008. Since that time, large portions of the coast have been re-opened following targeted opening surveys. Indeed, the fishery has expanded from 25% of the coast during the AMP/Phase 1 to 49% in 2020, corresponding to an addition of ~6300 km of shoreline and a total of 211 Pacific Fisheries Management Area (PFMA) subareas open to fishing (DFO 2022; P. Ridings, Fisheries Manager, Fisheries and Oceans Canada, Nanaimo, BC, 2021, pers. comm.). It is important to note concurrent changes in the decision-making framework at DFO, with the Precautionary Approach developing from an accepted concept to a legislated requirement under the new Fish Stocks provisions in the revised *Fisheries Act*[2]. The Precautionary Approach Framework and current sea cucumber fishery management measures are well described elsewhere (DFO 2009; 2022). The EFAs continued for a few years in Phase 2. However, several changes compromised the integrity of the EFA experimental design, ultimately necessitating the conclusion of the EFA project by DFO Science in 2017: namely, inconsistent data collection between 2008 and 2015; opening of one EFA to commercial harvest; recolonization of one EFA by Sea Otters *(Enhydra lutris)*; and installation of two fin fish farms near one EFA. Nevertheless, there are currently an additional 8 years of unpublished EFA data collected as part of DFO stock assessment.

This report was produced on the request of DFO Resource Management, with the overall goals of updating estimates of harvest rates, Limit Reference Point and Upper Stock Reference using the full 1998-2015 time series of EFA data. This report will accordingly support management of the commercial sea cucumber fishery, and bring it further into alignment with the Precautionary Approach Framework.

# 2. METHODS

This paper provides a summary of EFA design and EFA survey protocol, as well as an overview of the previously peer reviewed and published latent productivity model. Full details of the survey protocol are documented in Campagna and Hand (2004) and Duprey et al. (2011) and a full description of the EFA methods and the model can be found in Hand et al. (2009) and Hajas et al. (2011). The error corrections and incremental improvements that were made to the model since the 2007 version (Hand et al. 2009; Hajas et al. 2011) are outlined in Appendix B.

## 2.1. THE EXPERIMENTAL FISHING AREAS

Four long-term Experimental Fishing Areas (EFAs; Jervis Inlet, Laredo Inlet, Tolmie Channel and Zeballos) were established along the BC coast (Figure 1) to study the impact of different harvest rates on sea cucumber stocks. The four EFAs were established in 1998 and 1999 in Pacific Fisheries Management (PFM) subareas that had not been fished for at least five years. The EFAs were accordingly assumed to be in a virgin state at the beginning of the experiment, prior to the first experimental harvest. The four EFAs were chosen to represent a variety of sea cucumber habitats, from a low density inlet to a high density channel. Existing data collected in Tolmie Channel and Laredo Inlet by Kitasoo Fisheries Program (1996-97), and in Jervis Inlet by DFO (Campagna and Hand 1999), were used to help design the EFAs.

[2] *Fisheries Act*, RSC, 1985, c. F-14

Five sites were identified within each EFA. Each site had a shoreline length of 10 km. Due to the low mobility of adult sea cucumbers (~4 m/day) (da Silva et al. 1986), each of the 20 sites approximates an independent population. Sites were randomly assigned one of five different harvest treatments. The target treatments were annual harvests of 0, 2, 4, 8 and 16% of preliminary estimates of virgin abundance, and these targeted annual harvest amounts provided a range of harvest intensities within each EFA. Sites were harvested annually, with the exception of Tolmie Channel and Laredo Inlet, which following 2011 and 2012 respectively, switched to triennial harvests to mimic the move to triennial harvest by the commercial fishery in most areas in BC. Target harvest amounts increased to 0, 4, 10, 25, and 50% in Tolmie Channel in 2014 and in Laredo Inlet in 2015. While the sites are referred to by the initial planned fraction of virgin biomass to harvest every year (e.g. Sites 0, 2, 4, 8 and 16), the actual fraction of virgin biomass harvested differed from the targeted fraction. Current analyses provide better estimates of the harvest rates that sites were actually subjected to (Figure 2). Note that all analyses consider the actual harvest amounts and site names are simply retained as consistent labels.

None of the EFAs are still in operation as several events compromised the integrity of the experimental design. Notably, Jervis Inlet was opened to commercial harvest, Laredo Inlet had low densities and was not considered representative of a commercially harvestable area, Tolmie Channel was subject to the installation and operation of two fin fish farms and Zeballos was recolonized by Sea Otters in 2008 (Nichol et al. 2015) The impact of Sea Otters is discussed in Section 4.3).

The EFA start and end dates are:

- Jervis Inlet – January 1999[3] to February 2007
- Laredo Inlet – September 1998 to September 2015
- Tolmie Channel – September 1998 to November 2014
- Zeballos – July 1999 to July 2012

## 2.2. EFA SURVEY PROTOCOL

Transect locations were randomly selected at the beginning of the experiment for each site, in each EFA, and the transect locations remained static for the duration of the experiment. There were 15 to 26 transects per site. Sites 0, 8 and 16 were surveyed every second year while Sites 2 and 4 were surveyed every fourth year (Figure 3 and Figure 4). Transects consisted of 4 m wide swaths extending perpendicularly from 18 m gauge depth to the shoreline. The transect lines were marked at 5 m intervals to define 20 $m^2$ quadrats. Most data were recorded at the quadrat level, however, transects are the primary sampling unit. SCUBA divers surveyed quadrats from deep to shallow and recorded counts of sea cucumbers, gauge depth, and habitat data such as the dominant substrate and algae. Tide height was used to convert gauge depth to chart datum.

In order to determine the size distribution of the population, samples of sea cucumbers were collected from each site within each EFA every year that the sites were visited, whether for a density survey and/or a harvest event. The samples were collected after the transect was surveyed or before the site was harvested. For each site within each EFA, two transects were

[3] Jervis was initially surveyed in 1998 as a trial to help determine the appropriate sample size for surveys associated with experimental fishing (Campagna and Hand 1999).

randomly selected each time it was visited, and the first 50 animals encountered on each of those transects were collected (sample size was reduced to 25 animals per transect in Laredo Inlet beginning in 2008). Each animal was longitudinally split, drained, any internal viscera removed, and individually weighed to the nearest gram to obtain ‘split weight’.

Data are archived in the sea cucumber biological database and maintained by the Shellfish Data Unit at the Pacific Biological Station.

## 2.3. ANALYTICAL METHODS

### 2.3.1. Measurements of density

Densities were calculated in the same way as in Hand et al. (2009) and Hajas et al. (2011).

Abundance was measured in two ways:

1. Population (number of sea cucumbers)
2. Biomass (grams of sea cucumbers)

The amount of habitat was measured in two ways:

a. Linearly (metres of shoreline)
b. Spatially (square metres of sea floor)

As a result, there can be four different ways that sea cucumber density is reported for each combination of transect and unit of area, of which, this paper presents the three in bold:

**1a. Linear Population Density**

**1b. Spatial Population Density**

2a. Linear Biomass Density

**2b. Spatial Biomass Density**

Linear population density is the number of sea cucumbers divided by the associated length of shoreline and is in units of numbers of sea cucumbers per metre of shoreline. Linear density is the density estimate used in quota calculations for the fishery because estimates of sea cucumber ‘bed’ area are not available whereas shoreline lengths are known (Duprey et al. 2011).

Spatial population density is the number of sea cucumbers divided by the associated area of sea floor and is in units of numbers of sea cucumbers per metre$^2$. The area of sea floor is believed to be a better measure of the amount of habitat than the length of shoreline. Furthermore, spatial population densities are used for reference points in other benthic invertebrate dive fisheries such as Red Sea Urchin (*Mesocentrotus franciscanus)* and Green Sea Urchin (*Strongylocentrotus droebachiensis*). In order to align the approach for echinoderms, the spatial population density unit is also considered for Giant Red Sea Cucumber reference points in this paper.

Spatial biomass density is the spatial population density multiplied by mean split weight. For every survey of every site, mean weight was estimated with a standard error. Estimates were made from biosamples collected from randomly selected transects as part of the density surveys or from the harvested sea cucumbers (described in Section 2.2).

The density over a given area was treated as a ratio estimator (Cochran 1977). Transects were the primary sampling unit but they were weighted according to their size. Bootstrapping and bias-corrected accelerated percentile intervals (Efron and Tibshirani 1994) were used to generate confidence bounds around density estimates.

### 2.3.2. Trimming transect lengths

Divers made best efforts to return to the same transect location from year to year, however the exact location of a transect will change every time it is surveyed. This error is due to differing winds and currents affecting the position of the boat while laying transect lines, the coarse resolution of Global Positioning Systems (GPS) especially at the onset of the EFAs, and the tide height at the time of the survey. In order to make a transect location as consistent as possible from year to year for the implementation of the productivity model, data was trimmed from the tips so that it had the same length and a similar depth profile for every survey year. Note that transects were not trimmed for calculating empirical reference points (Sections 2.3.5 and 2.3.6) because year to year changes were not being considered, rather all data from all depths were used.

Transect length was determined in a similar way as in Hand et al. (2009) and Hajas et al. (2011). The trimming process was improved and made more repeatable by using a best-agreement criterion for the depth profiles (see Appendix A for details on transect trimming methods).

### 2.3.3. The Bayesian model

The Bayesian model is similar to the one published in Hajas et al. (2011) and Hand et al. (2009). A description of the model is given in Appendix B as well as a list of changes made since 2009. The model was fit to data from a single EFA at a time. The model was applied to the full time-series of data and to the subset available in Hand et al. (2009). For Jervis Inlet, there was no data collected after 2007 so the two datasets are the same.

When posterior distributions were estimated for the model and associated datasets, the primary product was a probabilistic estimate of the productivity curve for the EFA. Appendix B provides a mathematical description of the model and a discussion of its implementation.

In the context of the EFAs, pre-harvest biomass refers to the biomass estimated on the survey that took place just prior to the harvest. In the context of managing a fishery, pre-harvest biomass would refer to the most recent biomass estimate for a location before a planned harvest at that location. Productivity, or more precisely “latent productivity”, is the rate at which biomass increases in the absence of harvest. A pervasive (Ricker 1975; Hilborn and Walters 1992) and simplifying assumption is that productivity can be determined from the current stock level, i.e. pre-harvest biomass.

Harvest data from the EFAs was represented as a series of instantaneous harvest events in the model. The more traditional approach is to approximate harvest as a continuous process, however that approach was not used in these analyses because in the case of the EFAs and BC’s sea cucumber fishery in general, harvest at any location is very brief. Harvest of all sites at any one EFA took 13 days or less. The fishery is executed in 4 to 6 weeks and fishing vessels stay at individual locations generally for a few days, and the time between harvests is at least a year. Therefore modelling harvest as an instantaneous process is more appropriate. Productivity is therefore approximated as a process that stops momentarily prior to harvest and resumes immediately after. Figure 5 illustrates a hypothetical succession of harvests and periods of productivity.

Since productivity is assumed to be a function of pre-harvest biomass, it is most easily expressed as an ordinary differential equation: $\frac{dB}{d\tau} = P(B|\theta)$ where $B$ is the pre-harvest biomass, $\tau$ is time, and $\theta$ is the set of parameters for the productivity function.

The following simplifying constraints were applied to the productivity model:

- Productivity is greater than or equal to zero. Stock levels never decrease except when there is harvest;
- Productivity is zero when biomass is zero; i.e., the stock will never recover after it has been completely depleted;
- Productivity is zero when biomass is at its virgin value; i.e., the virgin state represents the largest possible amount of biomass;
- There is a single maximum on the productivity curve; and
- Relative biomass can be reduced to any non-zero value and it will return to its virgin state in a finite amount of time.

#### 2.3.3.1. Generating Markov chains from the model

The model was implemented independently for each EFA. Four to six Markov Chains were generated for each EFA. For each chain, there was a burn-in of 10,000 iterations. After the burn-in, every 100$^{th}$ iteration was saved to file. The recorded chains were used as a representation of the estimated posterior distribution.

Convergence of the estimated posterior distributions was assessed on the basis of the Gelman-Rubin statistic (Gelman and Rubin 1992). The Gelman-Rubin test was applied to every model-parameter as well as relative biomass at the time of every harvest and survey. We considered the estimated posterior distribution for individual model-parameters to be converged if the corresponding scale reduction factor was less than 1.1. When there was convergence for all the model parameters, the software producing the chains was stopped. It took three to five days of computer time to reach convergence for each EFA.

### 2.3.4. Biomass

#### 2.3.4.1. Biomass estimated directly from the survey data

For some of the analyses, site biomass estimates were made directly from survey data (Figure 3 and Figure 4). Untrimmed transects were used in the calculations. Estimated biomass is the linear biomass density multiplied by the shoreline length and the estimated mean split weight. Bootstrapping (Davison and Hinkley 1997) was used to account for uncertainty in the estimate. This estimate is based upon the site-boundaries as observed by the divers carrying out the surveys and harvests. The impact of the experimental harvests may have extended beyond those bounds. In many instances, the estimated biomass the first time a site was surveyed was used as a proxy for virgin biomass.

#### 2.3.4.2. Virgin biomass estimated from the Bayesian analyses

The Bayesian analyses provide estimates of the posterior distribution for virgin biomass for each site (Appendix B). The same data and calculations used to estimate virgin biomass directly from survey data (see above) were incorporated into the Bayesian analyses - essentially serving as a prior distribution.

The Bayesian analyses look for virgin biomass values that are coherent not only with the survey data (see above), but also the harvest data and other parameter values in the model. For example, if two sites are subjected to similar harvests, and one site experiences a larger decline in biomass density, that site is assumed to have a smaller virgin biomass.

The advantages of the Bayesian estimates of virgin biomass are: they take into account the impact of harvest beyond the site boundaries, and there is no assumption that the site is in a virgin state during the first survey.

### 2.3.5. Harvest as a constant fraction of pre-harvest biomass

The harvest amounts can be calculated as a fraction of pre-harvest biomass. The advantage to this approach is that an appropriate harvest amount can be estimated directly from the most recent survey data, as is done currently in the sea cucumber fishery (DFO 2022; Duprey et al. 2011).

The maximum sustainable harvest amount, as a fraction of pre-harvest biomass, is estimated according to the interval between harvests (1, 2, 3, 4 or 5 years) and the desired equilibrium biomass for the post-harvest stock level expressed as a fraction of virgin biomass. In the hypothetical example shown in Figure 6, if the desired equilibrium post-harvest biomass is 0.60 $B_0$, then one year later (just prior to the next harvest) biomass is 0.6875 $B_0$ (post-harvest biomass plus estimated productivity). In order to return the stock to the equilibrium, a harvest of 0.0875 is taken. As a fraction of the pre-harvest biomass, the harvest amount is 0.0857/0.6875 = 0.125, or 12.5% and the post-harvest biomass is once again 0.60 $B_0$.

### 2.3.6. Defining a minimum density from multiple surveys

Based upon the first decade of EFA data, Hand et al. (2009) recommended a limit reference point of 0.50 $B_0$ and suggested an upper stock reference of 0.60 - 0.80 $B_0$, pending further studies. However, reference points measured relative to virgin biomass ($B_0$) are difficult to measure and implement. Another common limit reference point, especially useful for data poor stocks, is the lowest historical estimated stock-level from which recovery has been observed. The most common measure of stock-level for this type of reference point is biomass ($B_{recover}$). Density (D) is an alternate indicator of abundance that is measured directly from surveys and that is especially important for successful reproduction of broadcast spawning invertebrates (Read et al. 2012; Uthicke et al. 2009). Low population densities may induce an Allee effect of reduced fertilization efficiency, which could result in serious harm to the stock (Allee 1938; Courchamp et al. 1999; Uthicke et al. 2009). Here we explore the approach of using the lowest estimated density in a time series from which the stock recovered without intervention, as the LRP, an approach that has been applied in several Canadian fisheries (Marentette et al. 2021). Such a LRP is likely above the Allee effect threshold as demonstrated by the recovery, and is therefore a conservative choice. $D_{recover}$ can therefore be defined as the lowest density observed in the EFA time series, from which recovery was observed, a threshold intended to avoid serious harm to the stock. For selecting the LRP, recovery was defined as when the 95% confidence intervals of a subsequent density in the timeline was within the range of the first survey estimate (i.e. the proxy for the unfished density) and was above, and not overlapping, the 95% confidence intervals of the lowest density in the timeline. It is important to note that this is the definition of recovery for choosing the LRP, not for defining recovery of a stock, as would be part of a recovery plan.

The first step to identifying $D_{recover}$, is finding the lowest mean densities observed in the EFA time series. Since the mean densities are estimated with bootstrapping (Davison and Hinkley 1997), the estimated means are represented by a random sample of values. The minimum of all these estimates is a candidate for an LRP, however it is not always intuitive to define a minimum when all the values are represented by random samples.

The following hypothetical example is provided to illustrate the method used to define samples of $D_{recover}$ for each of the EFAs. If you had three hypothetical mean density distributions (e.g., Figure 7), the smallest value could come from one sample, the smallest mode could come from another sample, and the smallest sample average could come from yet another sample (Figure 7a). None of the three samples explicitly represents a smaller value than the other two. Rather than choosing one of the three samples to be the smallest, a new sample of 100 values can be generated to represent the smallest of the three original samples (Figure 7b). The first member of the new sample represents the 0.005 quantile. The 0.005 quantile of the three original samples are generated and the smallest becomes the 0.005 quantile of the new sample. Similarly, the 0.015 quantile of the new sample is the smallest 0.015 quantile of the original three samples. The process is continued until the 0.995 quantile of the new sample is generated.

This method was used to generate a sample of 100 values to represent the minima linear population densities and minima spatial population densities at each of the five EFAs.

Once the lowest mean densities observed in each EFA time series had been identified, survey data from later years were reviewed to determine whether densities recovered from these minima on any subsequent surveys. Minima that met the definition of recovery were averaged across EFAs to incorporate more spatial variability and determine a more conservative coast wide LRP.

### 2.3.7. Calculating an average of estimated mean densities

As described in Section 2.3.6, the minimum density from each EFA was represented by a sample of values. The values were regularly spaced quantiles:

$\frac{0+.5}{n}, \frac{1+.5}{n}, \frac{2+.5}{n}, \ldots, (n-1+.5)/n$; n=100 is usually a suitable value.

There are four EFAs and therefore 4 samples of minimum density to average. The $i^{th}$ quantile from the kth sample is $q_{i,k}$ where k = 0, 1, 2, 3.

The $k^{th}$ sample was assigned a weight of $w_k$.

There were minima values to represent each EFA minimum. Every one of the $n^m$ combinations was generated and the weighted average:

$$\frac{\sum w_k * x_k}{\sum w_k}$$

was calculated, with each EFA equally weighted.

The sample of weighted averages will be very, very large. For convenience, the sample of averages was thinned to the following quantiles:

$\frac{0+.5}{n}, \frac{1+.5}{n}, \frac{2+.5}{n}, \ldots, (n-1+.5)/n$; where n is 100.

## 3. RESULTS

While the harvest amounts are generally ordered, with greatest exploitation in Sites 8 and 16, low exploitation in Site 2, and negligible exploitation in Site 0, some variability is apparent between treatments and EFAs over time (Figure 2). The 95% credible intervals on the estimated harvest amounts used in the EFAs ranged from near-zero to 0.538 of the virgin biomass.

Fluctuations in the estimated population densities of sea cucumbers at sites in the EFAs over time are depicted in Figure 3 and Figure 4 (linear and spatial densities, respectively). In general, densities were highest at Tolmie Channel, intermediate at Jervis Inlet and Zeballos, and lowest at Laredo Inlet. Declines in population density over the time series are most evident at high exploitation sites (e.g. Site 16 at Jervis Inlet and Tolmie Channel; Figure 3 and Figure 4). Also of note is the persistence at or apparent recovery from low population densities at several sites (e.g. Tolmie Channel Site 8 and Laredo Inlet multiple sites). Note that although variable transect lengths lead to some discrepancy between the linear and spatial results (Hand et al. 2009), trends are similar.

## 3.1. PRODUCTIVITY

Sea cucumber productivity differed between EFAs and the variability around productivity estimates was heterogeneous (Figure 8; Table 1). Table 1 gives 95% credible-intervals for the productivity parameters but not covariance between the parameter values (discussed in Appendix D). In general, the greatest productivity was observed at Jervis Inlet. Inclusion of post 2008 data led to small alterations in the productivity curves of Tolmie Channel, Laredo Inlet and Jervis Inlet, with a larger effect observed at Zeballos. Notably, the inclusion of the post-2008 data at Zeballos reduced the maximum observed productivity over three fold and lowered the truncation point by approximately one half. The vertical portion of the curves occurs at the truncation point. Truncating productivity curves at the lowest observed relative biomass in the EFAs (on an iteration by iteration basis) provides a more conservative option, however, both truncated and untruncated curves were generated (see Figure 8).

## 3.2. VIRGIN BIOMASS

The estimated virgin biomass varied between EFAs and between sites within the same EFA (Table 2). The virgin biomass estimated through the Bayesian analyses, coheres to the model, the prior distributions and data. The largest estimated biomass occurred in Tolmie Channel, Site 2 and the smallest in Laredo Inlet Site 2.

## 3.3. HARVEST AMOUNTS

Hand et al. (2009) provides a range of annual harvest rates. Some of these rates are currently in use in the sea cucumber fishery. A rotational harvest strategy and a triennial harvest of approximately 10 percent is used on some QMAs, other QMAs are harvested annually with a harvest of between 2.2 and 4.2 percent (DFO 2022).

Setting harvest amounts for rotational harvests requires more sophisticated calculations than have been done in the past. For example, if harvesting Jervis Inlet on a triennial basis, the 0.01 quantile on maximum sustainable harvest is 24.9% of virgin biomass (Table 3) which corresponds to a maximum harvest rate of 8.3% of virgin biomass per year. For an annual harvest, the 0.01 quantile on maximum sustainable harvest at Jervis is 8.8% of virgin biomass (Table 3). The sustainable harvest amount is more complicated than multiplying a rate by the amount of time between harvests. To maintain a post-harvest stock level, as the harvest interval gets longer, the pre-harvest stock-level increases and pre-harvest productivity is smaller, the average productivity for the harvest interval becomes smaller, and the sustainable harvest rate also becomes smaller.

Updated maximum sustainable harvest amounts (as a fraction of virgin biomass) are provided in Table 3 and shown in Figure 9, using both the full (1998-2015) and early (to 2007) EFA data. Values obtained using only the early data are included to facilitate comparison with results in (Hand et al. 2009; see Table 12 in that report), which illustrates the effect of model updates. Conversely, comparing the results from the subset and full data herein (Table 3 and Figure 9) illustrates the effect of the additional data (collected since Hand et al. 2009). Using the entire available datasets the updated 0.01 quantiles on maximum sustainable annual harvest range from 2.0 to 8.8% of virgin biomass (Table 3). The 0.01 quantiles on maximum sustainable annual harvest (truncated productivity curves) at each of the EFAs are: 8.8% at Jervis Inlet, 3.7% at Laredo Inlet, 5.4% at Tolmie Channel, and 2.0% at Zeballos. These estimates of maximum sustainable harvest rates differ from those generated by Hand et al. (2009) by approximately -8 to +2%, with the largest difference at Zeballos. If we consider only the early data in the new model, the maximum sustainable harvest rates are estimated to be 8.3%, 5.1%, 4.6% and 13.5%, for Jervis, Laredo, Tolmie and Zeballos, respectively (Table 3). This demonstrates that the additional years of data result in slight adjustments to harvest rates for Jervis, Laredo and Tolmie (both increases and decreases), and a large difference for Zeballos.

Similarly, the 0.01 quantiles on maximum sustainable triennial harvests range from 6.0 to 24.9% of virgin biomass (Table 3). The 0.01 quantiles on maximum sustainable triennial harvest (relative to virgin biomass) at each of the EFAs are: 24.9% at Jervis Inlet, 11.2% at Laredo Inlet, 15.9% at Tolmie Channel, and 6.0% at Zeballos.

By selecting the 0.01 quantiles we can be 99% confident that the true maximum sustainable harvest amounts (whether for annual or rotational harvest strategies) are greater than the modeled maximum sustainable harvest amounts. For example, we are 99% confident that the maximum sustainable triennial harvest amount is greater than 6.0% of virgin biomass at Zeballos. Below the range of the data, the model conservatively assumes that latent productivity is zero, which would lead to stock collapse. While this is also the approach adopted in Hand et al. (2009), we include additional years of data, resulting in different data ranges and therefore lower minimum thresholds. Notably, the median minimum relative biomass in this study ranged from 0.114 to 0.341 (fraction of virgin biomass; Table 4), whereas it ranged from 0.280 to 0.462 in Hand et al. (2009). The maximum sustainable harvest rates from this study would therefore permit sea cucumber populations to drop to lower levels.

For ease of use, maximum sustainable harvest amounts are also provided as a fraction of pre-harvest biomass (see Table 5 and Figure 10), since virgin biomass estimates can be difficult to obtain. The 0.01 quantiles on maximum sustainable annual harvest range from 5.1 to 29.5% of pre-harvest biomass, while the 0.01 quantiles on maximum sustainable triennial harvests range from 14.7 to 55.8% of pre-harvest biomass (Table 5).

Finally, given that the minimum thresholds (based on the lower range of data) are less conservative than those used previously, this study also estimated maximum sustainable harvest amounts that would maintain sea cucumber populations above other thresholds, namely the 0.5, 0.6 and 0.8 $B_0$ reference points from Hand et al. (2009; see Table 6 and Table 7). For example, the range of annual harvest rates that would maintain stocks above 0.6 $B_0$ is 1.2 to 5.2% of the virgin biomass or 2.0 to 8.0% of the pre-harvest biomass (0.01 quantiles, Table 6 and Table 7). The range represents the different EFAs, with 8.0%, 5.1%, 4.4% and 2.0% of pre-harvest biomass at Jervis Inlet, Laredo Inlet, Tolmie Channel and Zeballos, respectively. The range of maximum sustainable triennial harvest amounts that would maintain stocks above 0.6 $B_0$ is 3.6 to 13.9% of virgin biomass or 5.7 to 18.8% of pre-harvest biomass (0.01 quantiles; Table 6 and Table 7). Again, the range represents the different EFAs, with 18.8%, 13.5%, 11.5% and 5.7% of pre-harvest biomass at Jervis Inlet, Laredo Inlet, Tolmie Channel and Zeballos, respectively. As such, it is important to note that upper ranges may only be appropriate for highly productive areas.

## 3.4. REFERENCE POINTS

Sea cucumbers in British Columbia are managed as one coast wide stock with many subunits (Quota Management Areas) and will accordingly be subject to one LRP. In the 18 year EFA time series, the sea cucumber population at several sites and several EFAs was observed persisting at low densities, occasionally even increasing from low levels under continued fishing pressure (Figures 2-4). For example, increases from low densities were observed at Tolmie Channel (Site 8) and Zeballos (Sites 4, 8 and 16). Densities at Laredo Inlet were generally low (the median ranges from 0.40 to 4.73 sea cucumbers $m^{-1}$ or 0.009 to 0.140 sea cucumbers $m^{-2}$) throughout the time series. In fact, the lowest estimated population density in any of the EFAs over the time series was observed at Site 8 in Laredo Inlet in 2005: 0.40 sea cucumbers $m^{-1}$ or 0.009 $m^{-2}$ (95% CI: 0.12 to 0.83 $m^{-1}$ and 0.003 to 0.018 $m^{-2}$). Statistically significant recovery from this low density to within the range of the first survey estimate occurred by 2015 when the median density reached 2.05 sea cucumbers $m^{-1}$ or 0.050 $m^{-2}$ (95% CIs: 1.02 to 3.42 $m^{-1}$; 0.024 to 0.083 $m^{-2}$), despite an additional harvest event in 2007. The second lowest population density that showed statistically significant recovery back to within the range of the first survey estimate was observed at Site 8 in Zeballos, where densities dropped to a minimum of 0.90 sea cucumbers $m^{-1}$ or 0.02 $m^{-2}$ (95% CIs: 0.43 to 1.4 $m^{-1}$; 0.01 to 0.04 $m^{-2}$) in 2008 and recovered to 3.43 sea cucumbers $m^{-1}$ or 0.09 $m^{-2}$ (2.31 to 4.86 $m^{-1}$; 0.06 to 0.13 $m^{-2}$) in 2010. The upper 99% CI of the minima are 0.92 $m^{-1}$ or 0.019 $m^{-2}$ at Laredo Inlet and 1.49 $m^{-1}$ or 0.039 $m^{-2}$ at Zeballos. Hence, $D_{recover}$, as defined in Section 2.3.5, is 0.92 sea cucumbers $m^{-1}$ or 0.019 sea cucumbers $m^{-2}$. Using the upper limit of the 99% CI provides a high degree of confidence of being above the true minima. We recommend using the mean of the Laredo Inlet and Zeballos upper 99% CI of the minimum spatial estimates as the LRP for sea cucumbers 0.029 $m^{-2}$, as this incorporates additional spatial variability and is more conservative. This equates to 1.20 sea cucumbers $m^{-1}$ (linear), a value we provide here for context, however we recommend that the spatial density be used as the LRP because it is independent of transect length and therefore more biologically meaningful and comparable among areas.

The EFAs show considerable differences in productivity and density. In order to incorporate some of this spatial variability into the reference points, we recommend setting the USR equal to the upper 99% CI on the minimum population density averaged across EFAs. The distribution of estimated minimum linear and spatial population densities for the EFAs are shown in Figure 11 and Figure 12, with the estimated mean minimum population density (across EFAs). Note that these minima exclude the final survey year, to ensure that stocks persisted following observed minima. The recommended minima-derived USR is accordingly 0.038 sea cucumbers $m^{-2}$ (spatial). In linear units this value is 1.95 sea cucumbers $m^{-1}$ (linear), and as stated above, we recommend the spatial density be used as the USR).

# 4. UNCERTAINTIES

## 4.1. MODEL UNCERTAINTY

The results in this document are based upon assumptions that are expressed through mathematical models and it is important to keep in mind ‘All models are wrong but some are useful’ (Box 1979).

As predominantly occurs with mathematical models, the model used to describe the biological system within the EFAs is a simplistic approximation. Most significantly, the model assumes the system is stationary; the joint distribution of the parameter values does not change with time. Implicitly, this means that changes to the stock levels are entirely attributable to harvest, productivity and random year effects. There is no allowance for declines in stock levels that are not related to the commercial fishery, such as climate change.

## 4.2. CLIMATE CHANGE

Climate change is impacting the oceans and marine organisms in a variety of ways. For example, increased atmospheric $CO_2$ is causing increased concentrations of $CO_2$ in the ocean, thereby lowering ocean pH, an effect called ocean acidification (OA). Although more research is required to better understand the effects of ocean acidification, the existing evidence is showing potential negative direct and indirect effects to echinoderms (Haigh et al. 2015). There are no known specific studies on OA effects for the Giant Red Sea Cucumber, however a study on a reef-dwelling sea cucumber species (*Holothuria* sp.) found impaired sperm motility at low pH values (Morita et al. 2010). Declines in sea cucumbers could have a detrimental effect on the nutrient cycling function they provide to ecosystems, however ecosystem-level effects remain unknown. Other aspects of climate change may also impact sea cucumbers. Warming temperatures and heat stress are associated with disease in echinoderms (Aalto et al. 2020; Harvell et al. 2019; Lester et al. 2007; Scheibling 1984; Scheibling and Stephenson 1984; Smale et al. 2019), and changing current regimes may have significant impacts on larval dispersal and population connectivity (Bashevkin et al. 2020; Kendall et al. 2016). Climate change impacts could be introduced into the modeling through further research.

The strategy of harvesting a fixed fraction of current stock-levels (Table 7 and Figure 10) provides a degree of protection of stocks from changes to the dynamics of the ocean. If the impact of a phenomenon such as climate change can be approximated as a change to virgin biomass, then harvests will increase or decrease with these changes. As a fraction of virgin stock-levels, the pre- and post-harvest stock-levels will remain approximately the same. Contrarily, as a fraction of pre-harvest biomass or population, the harvests and stock-levels will change in-step with the changing estimates of virgin stock-level. Since climate change may be more complicated than a change to equilibrium virgin stock-levels, it is unknown whether a strategy of harvesting a fixed fraction of current stock-levels will protect the viability of the stock.

## 4.3. SEA OTTERS

Sea Otter predation is expected to have increasing impacts on sea cucumber populations, as populations of the mammals continue to grow and expand following their re-introduction to BC in 1969 (Nichol et al. 2015). Although Sea Otters demonstrate strong prey preferences and tend to target high energy food sources such as sea urchins when they first arrive in an area, once these prey items become depleted, Sea Otters target other species including sea cucumbers (Ostfeld 1982). Sea Otter presence is accordingly associated with a decline in sea cucumber density, with the extent of the decline depending on the duration and magnitude of Sea Otter presence (Larson et al. 2013). In Lochead et al. (2019), the ability of a benthic echinoderm to persist at low densities despite the presence of Sea Otters was used to establish the LRP.

The Zeballos EFA was occupied by Sea Otters as of 2008 (Nichol et al. 2015). Although including the full EFA dataset resulted in a considerable reduction in recommended harvest rates at Zeballos, post-2008 sea cucumber densities fluctuated without a clear trend (Figure 3 and Figure 4). The lowest sea cucumber population densities observed throughout the EFAs were in Laredo Inlet, which has not yet been occupied by Sea Otters. The recommended reference points in this paper are therefore not related to Sea Otter presence. Nevertheless, the limited impacts noted to date may be due to the recent nature of the Sea Otter occupation in Zeballos and their preference for other prey species when initially recolonizing an area (Ostfeld 1982; Laidre and Jameson 2006). Future studies should consider Sea Otter impacts on sea cucumbers, particularly after longer occupancy times, and examine whether LRPs need to be adjusted in the presence of Sea Otters.

## 4.4. $D_{RECOVER}$ REFERENCE POINT

The use of $D_{recover}$, the lowest historical density from which recovery has been observed ($D_{recover}$), or its derivations, as a limit reference point comes with some uncertainty. Foremost, the assumption of recovery in the future depends on the prevailing conditions at the time. If the future drivers of productivity (e.g. recruitment success, natural mortality) are as good as, or better than, the past drivers of productivity then it is reasonable to expect a similar recovery. However, if productivity decreases, then recovery becomes more uncertain. Here, $D_{recover}$ is partially derived from the EFA with the lowest overall densities (Laredo Channel and Zeballos), while under ongoing fishing pressure and at a point in time when predation by *Pycnopodia* sea stars would have been occurring (i.e. before the onset of sea star wasting disease, which occurred in 2014-2015 on the central and north coast of BC. Although documentation of *Pycnopodia* predation on sea cucumbers is limited, *A. californicus* elicits a strong avoidance reaction when touched by the Sunflower Star, indicating a prey-predator relationship (Lambert 1997). Since recovery occurred during ongoing harvest and predation it is not unreasonable to expect recovery to be possible in commercially fished populations that generally have higher densities than a location like Laredo Channel, particularly since predation by sea stars is now low and intervention such as the cessation of fishing pressure is possible.

Knowledge gaps surrounding source/sink dynamics and recruitment introduce further uncertainty in $D_{recover}$. A stock-recruitment relationship cannot be defined in the traditional sense for sea cucumbers because planktonic larval duration is long, and recruitment to one location may not be linked to the reproductive capacity at the same location. Without information on larval movement in BC, it is not possible to determine which populations acts of sources of recruitment for others. Therefore, we do not know to what extent recovery from low densities may have been facilitated by immigration (adults or settling larvae arriving from elsewhere). Hence, while we can reasonably expect a site to recover from $D_{recover}$ if recruitment has not been altered or impaired (i.e. if it is an isolated incident and other areas are unaffected), we do not know what would happen if multiple areas were driven to $D_{recover}$ levels. However, given the broad depth distributions of sea cucumbers and the physical limitations imposed by SCUBA harvest, commercially fished areas have a de facto depth reserve that provides some buffer.

# 5. DISCUSSION

The *Apostichopus californicus* fishery in BC is managed using an Adaptive Rotational Fishery Strategy, whereby most areas are subject to a triennial harvest, but some areas have been assigned a different harvest interval (1-4 years). Furthermore, some areas have estimates of virgin biomass, while others do not. To facilitate the implementation of updated advice on harvest, we have provided advice in several forms to satisfy multiple strategies. Indeed, harvest amounts are presented as fractions of virgin biomass and pre-harvest biomass, for various harvest intervals (1-5 years), and to maintain sea cucumber populations above different thresholds: the lowest observed biomass in the EFA data, 0.50 $B_0$, 0.60 $B_0$, and 0.80 $B_0$. Combinations of all of these strategies are presented in tabular format, to be considered and implemented at the fishery managers' discretion (see Tables 3-7).

Given that the EFAs were chosen to represent different habitats and productivities (Figure 8), harvest advice is presented separately for each EFA. Combining the EFAs for these analyses would result in masking of trends and an increase in variability. Moreover, the fishery uses small scale QMAs and managers can exercise discretion in determining which EFA's harvest rates (low to high densities and different productivities) are most relevant to a given QMA.

Overall, results are similar to those obtained from the first 10 years of the EFA project (Hand et al. 2009), although recommended harvest amounts are slightly lower. To be precautionary and take into account the uncertainty in the data, models and environment, we recommend consideration of the 0.01 quantiles for harvest amounts and those calculated to maintain biomass above 0.60 $B_0$. This yields a recommended harvest range of 2.0 to 8.0% of pre-harvest biomass in an annual style fishery or 5.7 to 18.8% of pre-harvest biomass in a triennial fishery. Given that the range represents variability across EFAs, the higher percentages would only be suitable for very productive areas and therefore should be considered carefully. Further caution is incorporated by continuing to use conservative estimates of biomass (lower 90% confidence interval of estimated mean density) during survey assessments, and implementing reference points. While harvest amounts are provided relative to both pre-harvest and virgin biomass (Tables 3-7), the recommendations based on these tables are now provided solely relative to pre-harvest biomass (see Section 7). Recommended harvest rates in Hand et al. (2009) were expressed as a fraction of virgin biomass, yet harvest rates in the fishery are generally applied based on the best available information, namely the most recent survey results for a given area. Hence, by providing recommendations relative to pre-harvest biomass we are not proposing a change in approach, rather we are aligning advice to the current approach to facilitate improved implementation.

The recommended harvest advice that would maintain the stock at 0.60 $B_0$ is conservative given examples from other jurisdictions. In Australia, directed fisheries are closed for stocks that are estimated to be below 0.50 $B_{MSY}$ or 0.20 $B_0$ (Smith et al. 2009). In New Zealand, fisheries closures are considered when stocks are estimated to be below 0.25 $B_{MSY}$ or 0.10 $B_0$, whichever is higher (Anderton 2008). However, given the aforementioned uncertainties and gaps in knowledge about basic life history parameters for Giant Red Sea Cucumbers, caution is merited.

Reference points are important components of harvest strategies because they function as quantitative conservation thresholds that trigger management actions. In the identification of reference points for sea cucumbers in BC, this study explores the concept of serious harm defined by DFO's Precautionary Approach (PA) as the point at which there is "a high probability that productivity will be so impaired that serious harm will occur" (DFO 2009). This study also considers the four candidate guidance criteria for LRPs brought forward during the December 2021 Technical Expertise in Stock Assessment (TESA) workshop on Limit Reference Points in the selection of a LRP:

1. Consistent with objective to avoid serious harm;
2. Based on best available information;
3. Operationally useful; and
4. Reliably estimable (Marentette et al. 2021).

An objective to avoid serious harm to stocks is fundamental to Canada's Precautionary Approach strategy (DFO 2009). For broadcast spawners, low population densities may induce an Allee effect of reduced fertilization efficiency because gamete encounters decrease (Allee 1938; Courchamp et al. 1999; Uthicke et al. 2009). Studies have shown that the decline in fertilization rates with decreasing densities of benthic invertebrates is exponential (Levitan 1991; Babcock et al. 1994; Wahle and Peckham 1999). Serious harm could occur should populations go below a threshold density that could cause an Allee effect and inhibit recovery. Since density is an important metric for fertilization success of broadcast spawners, it is a metric that is considered here for sea cucumber reference points.

Reference points that define, or avoid, states of reproductive impairment are used worldwide (Sainsbury 2008). For example, the LRP that corresponds to the lowest value of biomass observed before recovery of the population is used in the international policy-making organization ‘The International Council for the Exploration of the Sea’ (ICES 2019). In Canada, the lowest biomass or density observed historically, from which recovery has been observed ($B_{recover;}$ $D_{recover}$) has been used as a limit reference point for Green Sea Urchin (*Strongylocentrotus droebachiensis*) (DFO 2018a), Atlantic Cod (*Gadus morhua*) (DFO 2011), southern Gulf of St. Lawrence cod (*Gadus morhua*) (DFO 2003), southern Gulf of St. Lawrence herring (DFO 2005), Haddock (DFO 2017) and Walleye Pollock (*Theragra chalcogramma*) (DFO 2018b; Marentette et al. 2021). For sea cucumbers, the Allee effect occurs with decreasing densities, and so the lowest density from which recovery was observed ($D_{recover}$) in the EFA datasets was chosen as a candidate limit reference point. This is not necessarily the point at which there is “a high probability that productivity will be so impaired that serious harm will occur” (DFO 2009), but it is easy to rationalize that the Allee threshold is likely lower that $D_{recover}$ because of the historic proof of concept in observed recovery. This inherently makes $D_{recover}$ a conservative choice for a LRP. Some advantages of $B_{recover}$ or $D_{recover}$ as a reference point are that it’s useful for data-poorer stocks, it’s independent of the stock-recruitment relationship, it’s not influenced as strongly by model assumptions, and it is easy to understand and communicate. An obvious disadvantage, as mentioned in Section 4.4, is that the assumption of possible recovery in the future depends on the prevailing conditions at the time.

The limit reference point should be established based on the best available scientific information (DFO 2009). Although there continues to be a paucity of data and gaps in the knowledge of the biology and ecology of *Apostichopus californicus*, the EFA project produced a rich, multi-year index of abundance in four different coastal environments. The current study draws upon this dataset, as the best available scientific information, in the establishment of reference points.

Hand et al. (2009) recommended a conservative limit reference point of 50% $B_0$. Although scientifically sound, this reference point was not operationally useful. This is due to the inability to estimate virgin biomass on the 25% of the coast that was open throughout Phase 1 of the fishery. In these locations, harvest often occurred for many years and sometimes occurred for multiple decades prior to the first survey. Therefore the biomass estimate from the first survey would not provide a reasonable estimate of virgin biomass.

The fourth criteria for a limit reference point is that it is can be estimated reliably. In this study, $D_{recover}$ is provided in units of sea cucumbers per metre of shoreline as well as units of sea cucumbers per metre squared. There are well-established sea cucumber survey methods in BC to reliably estimate densities per metre shoreline (Campagna and Hand 2004; Duprey et al. 2011). Furthermore, a multispecies benthic invertebrate monitoring survey has been under development since 2016, which estimates densities per metre squared (Lochead et al. In press) As such, the proposed reference points can be considered immediately in areas where surveys have already been completed, and continue to be implemented as sea cucumber assessments shift to a multispecies approach.

The sea cucumber and multispecies surveys employ randomized transect placement (Campagna and Hand 2004; Duprey et al. 2011; Lochead et al. In press), which suitable sea cucumber habitat will not always be targeted. Sea cucumbers are found on a variety of habitats, but generally do not prefer mud substrates, very exposed habitats, and the head of inlets (Duprey et al. 2016; 2011). In order for the reference points to be relevant with random survey designs, it is further recommended that the density estimates used for assessing stock status against the reference points be calculated only using data that includes sea cucumber habitat.

When the stock gets small, the most directly relevant serious harm is a management system that is too slow to respond. Therefore, operational control points (OCP) can be helpful in avoiding serious harm, in addition to reference points. An OCP is defined as a value of an indicator or other input variable that acts as a trigger for a change in management actions, as for example in a Harvest Control Rule (Marentette et al. 2021). The role of OCPs should be clearly defined as points for management action that function differently from (but can be set equal to) reference points. In BC's sea cucumber fishery, areas that are considered for reopening to the fishery as part of Phase 2 are surveyed and evaluated against a threshold of 2.5 sea cucumbers per metre of shoreline. This OCP threshold is a Science recommendation in the published Assessment Framework and part of the reopening plan (Duprey et al. 2011). Areas are generally not considered for opening to commercial harvest if the lower 90% confidence interval of the population density estimate is below this threshold. This ensures that lower density areas are avoided altogether and adds an additional layer of caution in the fishery's management framework. Reference points have a complementary role in ensuring that the stock does not decline to levels below which serious harm may be expected.

In addition to reference points, BC's sea cucumber fishery has additional aspects that promote conservation. For instance, only a portion of the stock is vulnerable to harvest. A natural reserve of sea cucumbers exists at deeper than depths of about 20 m, the maximum feasible depth for commercial harvest by SCUBA. Furthermore, only approximately 50% of the BC coast is open to commercial harvest and the reopening process is nearing completion. There are currently also 18 Commercial No Take Reserves totaling 930 km of shoreline (~6% of current total harvestable shoreline) and other processes are underway that may protect approximately 10% of areas open to sea cucumber harvest. Given that sea cucumber populations are connected by larval dispersal pathways, and the uncertainties around source/sink dynamics, no-harvest reserves will continue to be important components of BC's sea cucumber management strategy.

## 6. FUTURE DIRECTIONS

The next steps for the Pacific Region's Giant Red Sea Cucumber program are consistent with the DFO Science-wide initiative of Strategic Stock Assessment Planning currently being undertaken within the Department. The goals of this initiative are to:

- bring Pacific Region fisheries into compliance with the Precautionary Approach and DFO's Sustainable Fisheries Framework, now embedded in the new Fish Stocks Provisions in the revised *Fisheries Act;*
- balance legal obligations of conservation and needs for sustainable fisheries, including First Nations, industry and recreational interests;
- move from single species to multispecies approaches so as to incorporate ecosystem interactions and maximize efficiencies;
- take into account the biology of the species and environmental conditions affecting the stock; and
- identify and communicate to stakeholders and other interested parties, the process for prioritizing Science activities and adjusting them in response to emerging issues.

With updated reference points, next steps will be to evaluate stock status of the Giant Red Sea Cucumber in the Pacific Region. DFO is currently developing a new multispecies benthic invertebrate monitoring program, designed specifically to generate coast wide, time-series data for use in marine invertebrate stock status monitoring and assessment. This new monitoring approach was peer reviewed through the Canadian Science Advice Secretariat Regional Peer Review process (Lochead et al. In press). Once the monitoring approach is implemented, DFO Science will be able to assess and report on Giant Red Sea Cucumber stock status relative to reference points using the data generated by the multispecies monitoring program. Trigger points for reevaluation of the reference points may include any notable changes to sea cucumber populations, whether through disease, predation (Sea Otter expansion), recruitment, or another cause. The development of relevant reference points will benefit from an iterative and adaptive process. Future work could also compare the recommended empirical reference points to $B_{MSY}$ or $B_0$ based reference points developed through data-rich methods.

It is vital to continue researching *A. californicus*, filling knowledge gaps as new methodologies and studies permit, and incorporating such information into assessments and management. For example, despite the long pelagic larval stage and potential for long-distance dispersal of *A. californicus*, recent evidence suggests broadscale genetic differentiation between northern and southern regional groups in BC (Xuereb et al. 2018). Key sites may support dispersal pathways and population connectivity between these regions (e.g. Calvert Island, south central coast; Sunday et al. 2014; Xuereb et al. 2018). Future studies could investigate source/sink dynamics and migration, and explore the application of marine protected areas to protect dispersal pathways. Finally, regional reference points could be explored, as could the incorporation of environmental phenomena such as climate change and Sea Otter range expansion.

## 7. RECOMMENDATIONS

1. Implement annual harvest amounts that do not exceed the range of 2.0 to 8.0% of estimated pre-harvest biomass, with the caveat that the upper ranges may only be appropriate for highly productive areas,
2. Implement triennial harvest amounts that do not exceed the range of 5.7 to 18.8% of estimated pre-harvest biomass, with the caveat that the upper ranges may only be appropriate for highly productive areas,
3. For other rotational harvest strategies, consider the 0.01 quantiles of the sustaining harvest amounts on pre-harvest biomass in Table 7 and equilibrium stock outcomes of 0.60 $B_0$ or 0.80 $B_0$,
4. Adopt a conservative Limit Reference Point of 0.029 sea cucumbers $m^{-2}$ on sea cucumber habitat and an Upper Stock Reference Point of 0.038 sea cucumbers $m^{-2}$ on sea cucumber habitat, and
5. It is recommended that an independent scientific survey be used to assess the sea cucumber stock status against the LRP and USR. A coast wide multispecies benthic invertebrate survey is under development in a separate CSAS process.

## 8. SUPPLEMENTARY INFORMATION

The code used to implement the mathematical model is available on GitHub.

## 9. ACKNOWLEDGEMENTS

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# 11. TABLES

*Table 1. Estimated values for the productivity parameters. Three values are provided for each parameter: the 95% credible interval and the median of the estimated posterior distribution (lower, median, upper). 'a' controls the slope of the productivity curve at low stock abundance. 'b' controls the slope of the productivity curve at near virgin stock abundance. '$B_{max}$' is the value of $B$ where the untruncated productivity curve predicts maximum productivity. '$f_{max}$' is the maximum productivity under the untruncated productivity curve. 'Min(Relative Biomass)' is the minimum value of relative biomass to occur during the EFA (truncated curve). 'Max(Productivity)' is the maximum value of productivity to occur during the EFA (truncated curve). See Hand et al. (2009) for more details.*

| Data Set | EFA | Parameter Values: a | | | b | | | $B_{max}$ | | | $f_{max}$ | | | Min (Relative Biomass) | | | Max (Productivity) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Full | Jervis Inlet | 0.004 | 0.065 | 0.331 | 0.627 | 0.906 | 0.995 | 0.004 | 0.070 | 0.272 | 0.103 | 0.177 | 0.240 | 0.067 | 0.133 | 0.209 | 0.100 | 0.171 | 0.234 |
| | Laredo Inlet | 0.004 | 0.173 | 0.909 | 0.011 | 0.421 | 0.964 | 0.015 | 0.318 | 0.935 | 0.042 | 0.075 | 0.126 | 0.246 | 0.341 | 0.434 | 0.042 | 0.073 | 0.114 |
| | Tolmie Channel | 0.003 | 0.047 | 0.228 | 0.698 | 0.928 | 0.996 | 0.003 | 0.050 | 0.198 | 0.056 | 0.068 | 0.083 | 0.089 | 0.114 | 0.139 | 0.056 | 0.066 | 0.077 |
| | Zeballos | 0.002 | 0.043 | 0.273 | 0.709 | 0.947 | 0.997 | 0.003 | 0.042 | 0.224 | 0.022 | 0.062 | 0.143 | 0.132 | 0.191 | 0.265 | 0.022 | 0.057 | 0.119 |
| to 2007 | Jervis Inlet | 0.004 | 0.067 | 0.324 | 0.633 | 0.906 | 0.995 | 0.004 | 0.071 | 0.268 | 0.098 | 0.171 | 0.240 | 0.069 | 0.135 | 0.210 | 0.095 | 0.165 | 0.233 |
| | Laredo Inlet | 0.008 | 0.278 | 0.940 | 0.027 | 0.511 | 0.965 | 0.027 | 0.374 | 0.877 | 0.057 | 0.095 | 0.151 | 0.161 | 0.258 | 0.382 | 0.057 | 0.094 | 0.144 |
| | Tolmie Channel | 0.003 | 0.073 | 0.424 | 0.686 | 0.932 | 0.997 | 0.004 | 0.075 | 0.319 | 0.050 | 0.074 | 0.104 | 0.220 | 0.257 | 0.295 | 0.049 | 0.066 | 0.083 |
| | Zeballos | 0.005 | 0.160 | 0.757 | 0.039 | 0.613 | 0.986 | 0.002 | 0.032 | 0.708 | 0.153 | 0.211 | 0.248 | 0.259 | 0.348 | 0.454 | 0.150 | 0.200 | 0.240 |
| Prior Distribution | | 0.005 | 0.270 | 0.951 | 0.004 | 0.272 | 0.952 | 0.028 | 0.499 | 0.975 | 0.016 | 0.131 | 0.244 | - | - | - | - | - | - |

*Table 2. Estimated virgin biomass (kg split weight) for Experimental Fishing Area sites.*

| EFA | Site | Quantile on Estimated Virgin Biomass(kg) | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | 0.010 | 0.050 | 0.100 | 0.250 | 0.500 | 0.750 | 0.900 | 0.950 | 0.990 |
| Jervis Inlet | 0 | 9768 | 10688 | 11798 | 14906 | 20005 | 25177 | 28309 | 29465 | 30977 |
| | 2 | 5764 | 6006 | 6154 | 6417 | 6820 | 7499 | 8641 | 9812 | 12696 |
| | 4 | 17251 | 19490 | 20747 | 22900 | 25045 | 26822 | 28217 | 28964 | 30305 |
| | 8 | 17502 | 19082 | 19876 | 21183 | 22514 | 23766 | 24807 | 25425 | 26465 |
| | 16 | 11025 | 11759 | 12232 | 13125 | 14380 | 15868 | 17329 | 18253 | 19860 |
| Laredo Inlet | 0 | 4090 | 4511 | 4811 | 5493 | 6561 | 7653 | 8466 | 8927 | 9705 |
| | 2 | 833 | 923 | 976 | 1085 | 1259 | 1692 | 2670 | 3147 | 3806 |
| | 4 | 7163 | 8530 | 9502 | 11320 | 13257 | 14803 | 15967 | 16565 | 17732 |
| | 8 | 2572 | 2764 | 2879 | 3089 | 3382 | 3698 | 3993 | 4196 | 4646 |
| | 16 | 8066 | 8624 | 8923 | 9469 | 10101 | 10758 | 11334 | 11697 | 12354 |
| Tolmie Channel | 0 | 22726 | 23604 | 24242 | 25845 | 28433 | 30982 | 32611 | 33374 | 34496 |
| | 2 | 33014 | 34448 | 35359 | 37283 | 39722 | 41816 | 43424 | 44269 | 45717 |
| | 4 | 23850 | 24584 | 24989 | 25701 | 26627 | 27809 | 29156 | 30112 | 32363 |
| | 8 | 33167 | 33923 | 34315 | 34965 | 35701 | 36413 | 37065 | 37463 | 38221 |
| | 16 | 24066 | 24617 | 24912 | 25396 | 25923 | 26452 | 26914 | 27202 | 27733 |
| Zeballos | 0 | 17365 | 18455 | 19174 | 20700 | 22816 | 25047 | 26690 | 27615 | 29200 |
| | 2 | 14195 | 15182 | 15709 | 16657 | 17853 | 19240 | 20907 | 22250 | 25793 |
| | 4 | 10449 | 11032 | 11343 | 11876 | 12515 | 13241 | 14006 | 14546 | 15698 |
| | 8 | 16830 | 17831 | 18389 | 19283 | 20315 | 21413 | 22469 | 23129 | 24586 |
| | 16 | 18007 | 19990 | 20959 | 22454 | 24301 | 26098 | 27606 | 28519 | 30161 |

*Table 3. Maximum sustainable harvest as a fraction of virgin biomass. Note that the equilibrium post-harvest stock level for a given harvest amount is greater than or equal to the truncation point applied to the productivity function.*

| EFA | Dataset | Harvest Interval (years) | Quantile on Maximum Sustainable Harvest (fraction of virgin biomass) | | | | |
|---|---|---|---|---|---|---|---|
| | | | 0.010 | 0.050 | 0.100 | 0.250 | 0.500 |
| Jervis Inlet | full | 1 | 0.088 | 0.107 | 0.118 | 0.138 | 0.162 |
| Jervis Inlet | to 2007 | 1 | 0.083 | 0.104 | 0.115 | 0.135 | 0.156 |
| Laredo Inlet | full | 1 | 0.037 | 0.046 | 0.050 | 0.059 | 0.072 |
| Laredo Inlet | to 2007 | 1 | 0.051 | 0.063 | 0.069 | 0.080 | 0.093 |
| Tolmie Channel | full | 1 | 0.054 | 0.057 | 0.059 | 0.062 | 0.065 |
| Tolmie Channel | to 2007 | 1 | 0.046 | 0.051 | 0.054 | 0.059 | 0.064 |
| Zeballos | full | 1 | 0.020 | 0.029 | 0.035 | 0.045 | 0.057 |
| Zeballos | to 2007 | 1 | 0.135 | 0.149 | 0.158 | 0.173 | 0.189 |
| Jervis Inlet | full | 2 | 0.171 | 0.206 | 0.225 | 0.261 | 0.302 |
| Jervis Inlet | to 2007 | 2 | 0.161 | 0.200 | 0.221 | 0.256 | 0.293 |
| Laredo Inlet | full | 2 | 0.075 | 0.091 | 0.100 | 0.117 | 0.141 |
| Laredo Inlet | to 2007 | 2 | 0.103 | 0.125 | 0.136 | 0.158 | 0.184 |
| Tolmie Channel | full | 2 | 0.107 | 0.113 | 0.116 | 0.121 | 0.127 |
| Tolmie Channel | to 2007 | 2 | 0.090 | 0.100 | 0.106 | 0.114 | 0.124 |
| Zeballos | full | 2 | 0.041 | 0.058 | 0.069 | 0.088 | 0.111 |
| Zeballos | to 2007 | 2 | 0.257 | 0.281 | 0.294 | 0.320 | 0.351 |
| Jervis Inlet | full | 3 | 0.249 | 0.294 | 0.321 | 0.367 | 0.419 |
| Jervis Inlet | to 2007 | 3 | 0.234 | 0.287 | 0.316 | 0.360 | 0.409 |
| Laredo Inlet | full | 3 | 0.112 | 0.135 | 0.149 | 0.173 | 0.208 |
| Laredo Inlet | to 2007 | 3 | 0.154 | 0.186 | 0.203 | 0.235 | 0.272 |
| Tolmie Channel | full | 3 | 0.159 | 0.166 | 0.170 | 0.177 | 0.186 |
| Tolmie Channel | to 2007 | 3 | 0.133 | 0.147 | 0.155 | 0.167 | 0.180 |
| Zeballos | full | 3 | 0.060 | 0.086 | 0.102 | 0.129 | 0.162 |
| Zeballos | to 2007 | 3 | 0.355 | 0.385 | 0.403 | 0.436 | 0.478 |
| Jervis Inlet | full | 4 | 0.321 | 0.373 | 0.404 | 0.457 | 0.515 |
| Jervis Inlet | to 2007 | 4 | 0.302 | 0.365 | 0.399 | 0.450 | 0.505 |
| Laredo Inlet | full | 4 | 0.148 | 0.179 | 0.197 | 0.228 | 0.271 |
| Laredo Inlet | to 2007 | 4 | 0.204 | 0.245 | 0.268 | 0.309 | 0.354 |
| Tolmie Channel | full | 4 | 0.207 | 0.217 | 0.222 | 0.231 | 0.241 |
| Tolmie Channel | to 2007 | 4 | 0.175 | 0.192 | 0.201 | 0.216 | 0.232 |
| Zeballos | full | 4 | 0.080 | 0.114 | 0.134 | 0.169 | 0.209 |
| Zeballos | to 2007 | 4 | 0.432 | 0.464 | 0.483 | 0.520 | 0.561 |
| Jervis Inlet | full | 5 | 0.384 | 0.442 | 0.476 | 0.532 | 0.594 |
| Jervis Inlet | to 2007 | 5 | 0.363 | 0.433 | 0.471 | 0.525 | 0.583 |
| Laredo Inlet | full | 5 | 0.185 | 0.222 | 0.243 | 0.280 | 0.331 |
| Laredo Inlet | to 2007 | 5 | 0.254 | 0.303 | 0.331 | 0.379 | 0.431 |
| Tolmie Channel | full | 5 | 0.253 | 0.265 | 0.271 | 0.281 | 0.292 |
| Tolmie Channel | to 2007 | 5 | 0.215 | 0.235 | 0.245 | 0.262 | 0.280 |

| EFA | Dataset | Harvest Interval (years) | Quantile on Maximum Sustainable Harvest (fraction of virgin biomass) | | | | |
|---|---|---|---|---|---|---|---|
| | | | 0.010 | 0.050 | 0.100 | 0.250 | 0.500 |
| Zeballos | full | 5 | 0.100 | 0.141 | 0.166 | 0.207 | 0.254 |
| Zeballos | to 2007 | 5 | 0.486 | 0.517 | 0.535 | 0.568 | 0.603 |

*Table 4. Minimum relative biomass during the EFAs.*

| EFA | Quantile of Minimum Relative Biomass During EFA (fraction of Virgin Biomass) | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Full Dataset | | | | | | | | | Data to 2007 | | | | | | | | |
| | 0.010 | 0.050 | 0.100 | 0.250 | 0.500 | 0.750 | 0.900 | 0.950 | 0.990 | 0.010 | 0.050 | 0.100 | 0.250 | 0.500 | 0.750 | 0.900 | 0.950 | 0.990 |
| Jervis Inlet | 0.057 | 0.077 | 0.089 | 0.109 | 0.133 | 0.158 | 0.181 | 0.196 | 0.224 | 0.056 | 0.079 | 0.091 | 0.111 | 0.135 | 0.160 | 0.184 | 0.198 | 0.223 |
| Laredo Inlet | 0.228 | 0.262 | 0.279 | 0.308 | 0.341 | 0.372 | 0.401 | 0.419 | 0.452 | 0.144 | 0.175 | 0.193 | 0.222 | 0.258 | 0.297 | 0.335 | 0.360 | 0.407 |
| Tolmie Channel | 0.085 | 0.093 | 0.098 | 0.105 | 0.114 | 0.122 | 0.130 | 0.135 | 0.144 | 0.214 | 0.226 | 0.233 | 0.244 | 0.257 | 0.270 | 0.282 | 0.289 | 0.303 |
| Zeballos | 0.126 | 0.141 | 0.151 | 0.169 | 0.193 | 0.220 | 0.242 | 0.254 | 0.274 | 0.247 | 0.273 | 0.288 | 0.316 | 0.348 | 0.382 | 0.413 | 0.432 | 0.468 |

*Table 5. Maximum sustainable harvest as a fraction of pre-harvest biomass. Note that the equilibrium post-harvest stock level for a given harvest amount is greater than or equal to the truncation point applied to the productivity function.*

| EFA | Dataset | Harvest Interval (years) | Quantile on Maximum Sustainable Harvest (fraction of pre-harvest biomass) | | | | |
|---|---|---|---|---|---|---|---|
| | | | 0.010 | 0.050 | 0.100 | 0.250 | 0.500 |
| Jervis Inlet | full | 1 | 0.295 | 0.363 | 0.402 | 0.468 | 0.544 |
| Jervis Inlet | to 2007 | 1 | 0.281 | 0.351 | 0.394 | 0.460 | 0.534 |
| Laredo Inlet | full | 1 | 0.051 | 0.071 | 0.086 | 0.114 | 0.150 |
| Laredo Inlet | to 2007 | 1 | 0.076 | 0.099 | 0.117 | 0.153 | 0.209 |
| Tolmie Channel | full | 1 | 0.226 | 0.298 | 0.320 | 0.341 | 0.362 |
| Tolmie Channel | to 2007 | 1 | 0.131 | 0.166 | 0.175 | 0.187 | 0.200 |
| Zeballos | full | 1 | 0.096 | 0.151 | 0.173 | 0.202 | 0.227 |
| Zeballos | to 2007 | 1 | 0.195 | 0.257 | 0.281 | 0.314 | 0.348 |
| Jervis Inlet | full | 2 | 0.461 | 0.530 | 0.567 | 0.627 | 0.692 |
| Jervis Inlet | to 2007 | 2 | 0.443 | 0.518 | 0.558 | 0.620 | 0.684 |
| Laredo Inlet | full | 2 | 0.100 | 0.137 | 0.164 | 0.211 | 0.263 |
| Laredo Inlet | to 2007 | 2 | 0.146 | 0.190 | 0.221 | 0.282 | 0.360 |
| Tolmie Channel | full | 2 | 0.402 | 0.471 | 0.485 | 0.506 | 0.527 |
| Tolmie Channel | to 2007 | 2 | 0.243 | 0.284 | 0.294 | 0.310 | 0.325 |
| Zeballos | full | 2 | 0.182 | 0.264 | 0.294 | 0.331 | 0.363 |
| Zeballos | to 2007 | 2 | 0.364 | 0.415 | 0.433 | 0.466 | 0.500 |
| Jervis Inlet | full | 3 | 0.558 | 0.617 | 0.651 | 0.703 | 0.758 |
| Jervis Inlet | to 2007 | 3 | 0.540 | 0.609 | 0.643 | 0.698 | 0.752 |
| Laredo Inlet | full | 3 | 0.147 | 0.199 | 0.238 | 0.294 | 0.350 |
| Laredo Inlet | to 2007 | 3 | 0.213 | 0.272 | 0.315 | 0.389 | 0.468 |
| Tolmie Channel | full | 3 | 0.535 | 0.571 | 0.582 | 0.600 | 0.620 |
| Tolmie Channel | to 2007 | 3 | 0.337 | 0.369 | 0.380 | 0.395 | 0.412 |
| Zeballos | full | 3 | 0.259 | 0.351 | 0.382 | 0.421 | 0.453 |
| Zeballos | to 2007 | 3 | 0.473 | 0.501 | 0.517 | 0.546 | 0.579 |
| Jervis Inlet | full | 4 | 0.621 | 0.671 | 0.701 | 0.747 | 0.794 |
| Jervis Inlet | to 2007 | 4 | 0.604 | 0.663 | 0.694 | 0.742 | 0.788 |
| Laredo Inlet | full | 4 | 0.192 | 0.257 | 0.304 | 0.364 | 0.419 |
| Laredo Inlet | to 2007 | 4 | 0.276 | 0.348 | 0.399 | 0.474 | 0.546 |
| Tolmie Channel | full | 4 | 0.615 | 0.636 | 0.646 | 0.661 | 0.679 |
| Tolmie Channel | to 2007 | 4 | 0.406 | 0.434 | 0.444 | 0.458 | 0.474 |
| Zeballos | full | 4 | 0.323 | 0.418 | 0.448 | 0.486 | 0.517 |
| Zeballos | to 2007 | 4 | 0.516 | 0.543 | 0.559 | 0.587 | 0.617 |
| Jervis Inlet | full | 5 | 0.662 | 0.707 | 0.733 | 0.774 | 0.816 |
| Jervis Inlet | to 2007 | 5 | 0.648 | 0.700 | 0.727 | 0.770 | 0.811 |
| Laredo Inlet | full | 5 | 0.237 | 0.312 | 0.363 | 0.422 | 0.474 |
| Laredo Inlet | to 2007 | 5 | 0.336 | 0.418 | 0.471 | 0.541 | 0.603 |
| Tolmie Channel | full | 5 | 0.665 | 0.681 | 0.690 | 0.703 | 0.720 |

| EFA | Dataset | Harvest Interval (years) | Quantile on Maximum Sustainable Harvest (fraction of pre-harvest biomass) | | | | |
|---|---|---|---|---|---|---|---|
| | | | 0.010 | 0.050 | 0.100 | 0.250 | 0.500 |
| Tolmie Channel | to 2007 | 5 | 0.461 | 0.483 | 0.492 | 0.506 | 0.521 |
| Zeballos | full | 5 | 0.377 | 0.471 | 0.500 | 0.536 | 0.564 |
| Zeballos | to 2007 | 5 | 0.528 | 0.559 | 0.576 | 0.603 | 0.633 |

*Table 6. Maximum sustainable harvest as a fraction of virgin biomass to maintain different biomass thresholds.*

| EFA | Post-Harvest Target Stock Level (Fraction of Virgin Biomass) | Harvest Interval (years) | Quantile of Sustaining Harvest Amount (fraction of **virgin** biomass) | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Full Dataset | | | | | Data to 2007 | | | | |
| | | | 0.010 | 0.050 | 0.100 | 0.250 | 0.500 | 0.010 | 0.050 | 0.100 | 0.250 | 0.500 |
| Jervis Inlet | 0.5 | 1 | 0.062 | 0.074 | 0.081 | 0.092 | 0.106 | 0.060 | 0.072 | 0.079 | 0.090 | 0.103 |
| Laredo Inlet | 0.5 | 1 | 0.035 | 0.042 | 0.047 | 0.054 | 0.065 | 0.048 | 0.057 | 0.063 | 0.074 | 0.085 |
| Tolmie Channel | 0.5 | 1 | 0.034 | 0.036 | 0.038 | 0.039 | 0.042 | 0.035 | 0.038 | 0.040 | 0.043 | 0.047 |
| Zeballos | 0.5 | 1 | 0.015 | 0.021 | 0.024 | 0.030 | 0.038 | 0.112 | 0.125 | 0.134 | 0.149 | 0.167 |
| Jervis Inlet | 0.5 | 2 | 0.118 | 0.139 | 0.150 | 0.170 | 0.192 | 0.113 | 0.136 | 0.148 | 0.167 | 0.188 |
| Laredo Inlet | 0.5 | 2 | 0.070 | 0.084 | 0.092 | 0.107 | 0.128 | 0.094 | 0.114 | 0.124 | 0.144 | 0.165 |
| Tolmie Channel | 0.5 | 2 | 0.066 | 0.070 | 0.073 | 0.076 | 0.080 | 0.067 | 0.074 | 0.078 | 0.084 | 0.091 |
| Zeballos | 0.5 | 2 | 0.029 | 0.040 | 0.047 | 0.059 | 0.074 | 0.202 | 0.225 | 0.239 | 0.267 | 0.302 |
| Jervis Inlet | 0.5 | 3 | 0.168 | 0.195 | 0.209 | 0.234 | 0.262 | 0.163 | 0.191 | 0.207 | 0.231 | 0.258 |
| Laredo Inlet | 0.5 | 3 | 0.104 | 0.124 | 0.136 | 0.157 | 0.186 | 0.140 | 0.166 | 0.182 | 0.209 | 0.240 |
| Tolmie Channel | 0.5 | 3 | 0.097 | 0.102 | 0.105 | 0.110 | 0.116 | 0.098 | 0.107 | 0.112 | 0.121 | 0.131 |
| Zeballos | 0.5 | 3 | 0.043 | 0.060 | 0.069 | 0.086 | 0.107 | 0.274 | 0.302 | 0.319 | 0.352 | 0.399 |
| Jervis Inlet | 0.5 | 4 | 0.213 | 0.243 | 0.260 | 0.287 | 0.317 | 0.207 | 0.240 | 0.257 | 0.284 | 0.313 |
| Laredo Inlet | 0.5 | 4 | 0.136 | 0.162 | 0.178 | 0.205 | 0.241 | 0.182 | 0.215 | 0.235 | 0.268 | 0.308 |
| Tolmie Channel | 0.5 | 4 | 0.125 | 0.131 | 0.135 | 0.142 | 0.149 | 0.127 | 0.139 | 0.145 | 0.155 | 0.168 |
| Zeballos | 0.5 | 4 | 0.057 | 0.078 | 0.090 | 0.111 | 0.139 | 0.329 | 0.358 | 0.377 | 0.411 | 0.459 |
| Jervis Inlet | 0.5 | 5 | 0.252 | 0.284 | 0.302 | 0.331 | 0.361 | 0.244 | 0.281 | 0.299 | 0.327 | 0.357 |
| Laredo Inlet | 0.5 | 5 | 0.168 | 0.199 | 0.218 | 0.250 | 0.292 | 0.222 | 0.261 | 0.284 | 0.321 | 0.366 |
| Tolmie Channel | 0.5 | 5 | 0.151 | 0.159 | 0.163 | 0.171 | 0.180 | 0.154 | 0.167 | 0.175 | 0.187 | 0.201 |
| Zeballos | 0.5 | 5 | 0.070 | 0.096 | 0.110 | 0.136 | 0.167 | 0.372 | 0.400 | 0.418 | 0.449 | 0.489 |
| Jervis Inlet | 0.6 | 1 | 0.052 | 0.061 | 0.067 | 0.076 | 0.087 | 0.050 | 0.060 | 0.066 | 0.075 | 0.086 |
| Laredo Inlet | 0.6 | 1 | 0.032 | 0.039 | 0.043 | 0.051 | 0.061 | 0.044 | 0.053 | 0.059 | 0.068 | 0.080 |

| EFA | Post-Harvest Target Stock Level (Fraction of Virgin Biomass) | Harvest Interval (years) | Quantile of Sustaining Harvest Amount (fraction of **virgin** biomass) | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Full Dataset | | | | | Data to 2007 | | | | |
| | | | 0.010 | 0.050 | 0.100 | 0.250 | 0.500 | 0.010 | 0.050 | 0.100 | 0.250 | 0.500 |
| Tolmie Channel | 0.6 | 1 | 0.028 | 0.030 | 0.031 | 0.032 | 0.034 | 0.029 | 0.032 | 0.033 | 0.036 | 0.039 |
| Zeballos | 0.6 | 1 | 0.012 | 0.017 | 0.020 | 0.025 | 0.032 | 0.093 | 0.105 | 0.113 | 0.129 | 0.149 |
| Jervis Inlet | 0.6 | 2 | 0.098 | 0.114 | 0.123 | 0.139 | 0.158 | 0.094 | 0.112 | 0.122 | 0.137 | 0.155 |
| Laredo Inlet | 0.6 | 2 | 0.064 | 0.077 | 0.085 | 0.099 | 0.117 | 0.086 | 0.103 | 0.114 | 0.131 | 0.153 |
| Tolmie Channel | 0.6 | 2 | 0.054 | 0.057 | 0.059 | 0.062 | 0.066 | 0.055 | 0.061 | 0.064 | 0.069 | 0.075 |
| Zeballos | 0.6 | 2 | 0.025 | 0.033 | 0.039 | 0.048 | 0.061 | 0.166 | 0.186 | 0.199 | 0.225 | 0.263 |
| Jervis Inlet | 0.6 | 3 | 0.139 | 0.160 | 0.171 | 0.191 | 0.214 | 0.133 | 0.157 | 0.170 | 0.189 | 0.211 |
| Laredo Inlet | 0.6 | 3 | 0.093 | 0.113 | 0.124 | 0.144 | 0.171 | 0.125 | 0.149 | 0.164 | 0.188 | 0.219 |
| Tolmie Channel | 0.6 | 3 | 0.078 | 0.083 | 0.085 | 0.090 | 0.095 | 0.081 | 0.088 | 0.092 | 0.100 | 0.108 |
| Zeballos | 0.6 | 3 | 0.036 | 0.049 | 0.057 | 0.071 | 0.088 | 0.223 | 0.247 | 0.262 | 0.292 | 0.338 |
| Jervis Inlet | 0.6 | 4 | 0.175 | 0.199 | 0.212 | 0.234 | 0.259 | 0.169 | 0.196 | 0.210 | 0.232 | 0.255 |
| Laredo Inlet | 0.6 | 4 | 0.121 | 0.146 | 0.160 | 0.186 | 0.219 | 0.161 | 0.191 | 0.208 | 0.238 | 0.276 |
| Tolmie Channel | 0.6 | 4 | 0.101 | 0.106 | 0.110 | 0.115 | 0.122 | 0.104 | 0.113 | 0.119 | 0.128 | 0.138 |
| Zeballos | 0.6 | 4 | 0.048 | 0.064 | 0.074 | 0.091 | 0.113 | 0.268 | 0.292 | 0.308 | 0.337 | 0.379 |
| Jervis Inlet | 0.6 | 5 | 0.206 | 0.232 | 0.246 | 0.269 | 0.294 | 0.199 | 0.229 | 0.243 | 0.267 | 0.290 |
| Laredo Inlet | 0.6 | 5 | 0.147 | 0.177 | 0.193 | 0.224 | 0.264 | 0.193 | 0.227 | 0.246 | 0.280 | 0.323 |
| Tolmie Channel | 0.6 | 5 | 0.122 | 0.129 | 0.132 | 0.139 | 0.147 | 0.126 | 0.137 | 0.143 | 0.153 | 0.165 |
| Zeballos | 0.6 | 5 | 0.059 | 0.079 | 0.090 | 0.111 | 0.137 | 0.302 | 0.324 | 0.339 | 0.365 | 0.397 |
| Jervis Inlet | 0.8 | 1 | 0.028 | 0.033 | 0.036 | 0.041 | 0.048 | 0.027 | 0.032 | 0.035 | 0.041 | 0.047 |
| Laredo Inlet | 0.8 | 1 | 0.020 | 0.025 | 0.029 | 0.036 | 0.047 | 0.028 | 0.035 | 0.039 | 0.048 | 0.060 |
| Tolmie Channel | 0.8 | 1 | 0.014 | 0.015 | 0.016 | 0.017 | 0.018 | 0.015 | 0.017 | 0.018 | 0.019 | 0.021 |
| Zeballos | 0.8 | 1 | 0.007 | 0.009 | 0.011 | 0.013 | 0.017 | 0.050 | 0.057 | 0.063 | 0.075 | 0.097 |
| Jervis Inlet | 0.8 | 2 | 0.052 | 0.061 | 0.066 | 0.074 | 0.085 | 0.051 | 0.060 | 0.065 | 0.074 | 0.083 |
| Laredo Inlet | 0.8 | 2 | 0.038 | 0.048 | 0.054 | 0.069 | 0.089 | 0.052 | 0.064 | 0.072 | 0.088 | 0.111 |

| EFA | Post-Harvest Target Stock Level (Fraction of Virgin Biomass) | Harvest Interval (years) | Quantile of Sustaining Harvest Amount (fraction of **virgin** biomass) | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Full Dataset | | | | | Data to 2007 | | | | |
| | | | 0.010 | 0.050 | 0.100 | 0.250 | 0.500 | 0.010 | 0.050 | 0.100 | 0.250 | 0.500 |
| Tolmie Channel | 0.8 | 2 | 0.028 | 0.029 | 0.031 | 0.033 | 0.035 | 0.029 | 0.032 | 0.034 | 0.037 | 0.041 |
| Zeballos | 0.8 | 2 | 0.013 | 0.018 | 0.021 | 0.026 | 0.032 | 0.087 | 0.099 | 0.108 | 0.126 | 0.157 |
| Jervis Inlet | 0.8 | 3 | 0.074 | 0.084 | 0.090 | 0.101 | 0.114 | 0.071 | 0.083 | 0.090 | 0.100 | 0.112 |
| Laredo Inlet | 0.8 | 3 | 0.055 | 0.068 | 0.077 | 0.097 | 0.127 | 0.074 | 0.090 | 0.100 | 0.121 | 0.150 |
| Tolmie Channel | 0.8 | 3 | 0.040 | 0.043 | 0.044 | 0.047 | 0.051 | 0.042 | 0.046 | 0.049 | 0.053 | 0.058 |
| Zeballos | 0.8 | 3 | 0.020 | 0.027 | 0.030 | 0.038 | 0.047 | 0.116 | 0.129 | 0.139 | 0.158 | 0.188 |
| Jervis Inlet | 0.8 | 4 | 0.092 | 0.104 | 0.111 | 0.123 | 0.136 | 0.089 | 0.103 | 0.110 | 0.122 | 0.135 |
| Laredo Inlet | 0.8 | 4 | 0.070 | 0.086 | 0.097 | 0.120 | 0.158 | 0.093 | 0.111 | 0.123 | 0.147 | 0.178 |
| Tolmie Channel | 0.8 | 4 | 0.052 | 0.055 | 0.057 | 0.060 | 0.065 | 0.054 | 0.059 | 0.062 | 0.067 | 0.074 |
| Zeballos | 0.8 | 4 | 0.026 | 0.035 | 0.040 | 0.049 | 0.060 | 0.138 | 0.151 | 0.160 | 0.178 | 0.199 |
| Jervis Inlet | 0.8 | 5 | 0.108 | 0.121 | 0.128 | 0.140 | 0.153 | 0.104 | 0.120 | 0.127 | 0.139 | 0.152 |
| Laredo Inlet | 0.8 | 5 | 0.084 | 0.102 | 0.115 | 0.140 | 0.182 | 0.110 | 0.129 | 0.142 | 0.166 | 0.195 |
| Tolmie Channel | 0.8 | 5 | 0.062 | 0.066 | 0.068 | 0.072 | 0.078 | 0.065 | 0.071 | 0.074 | 0.080 | 0.088 |
| Zeballos | 0.8 | 5 | 0.032 | 0.042 | 0.048 | 0.059 | 0.072 | 0.154 | 0.167 | 0.175 | 0.189 | 0.200 |

*Table 7. Harvest amounts (fraction of pre-harvest biomass) for combinations of harvest intervals and equilibrium post-harvest stock levels (reference points from Hand et al. 2009), using both the full and early data.*

| EFA | Post-Harvest Target Stock Level (Fraction of Virgin Biomass) | Harvest Interval (years) | Quantile of Sustaining Harvest Amount (fraction of **pre-harvest** biomass) | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Full Dataset | | | | | Data to 2007 | | | | |
| | | | 0.010 | 0.050 | 0.100 | 0.250 | 0.500 | 0.010 | 0.050 | 0.100 | 0.250 | 0.500 |
| Jervis Inlet | 0.5 | 1 | 0.111 | 0.129 | 0.139 | 0.156 | 0.175 | 0.107 | 0.127 | 0.137 | 0.153 | 0.171 |
| Laredo Inlet | 0.5 | 1 | 0.066 | 0.078 | 0.085 | 0.098 | 0.116 | 0.087 | 0.103 | 0.112 | 0.128 | 0.145 |
| Tolmie Channel | 0.5 | 1 | 0.064 | 0.068 | 0.070 | 0.073 | 0.077 | 0.065 | 0.071 | 0.074 | 0.080 | 0.086 |
| Zeballos | 0.5 | 1 | 0.029 | 0.039 | 0.045 | 0.057 | 0.071 | 0.183 | 0.201 | 0.211 | 0.229 | 0.251 |
| Jervis Inlet | 0.5 | 2 | 0.191 | 0.217 | 0.231 | 0.253 | 0.278 | 0.185 | 0.214 | 0.228 | 0.250 | 0.274 |
| Laredo Inlet | 0.5 | 2 | 0.123 | 0.143 | 0.156 | 0.176 | 0.203 | 0.159 | 0.185 | 0.199 | 0.223 | 0.249 |
| Tolmie Channel | 0.5 | 2 | 0.117 | 0.123 | 0.127 | 0.132 | 0.139 | 0.119 | 0.129 | 0.134 | 0.144 | 0.154 |
| Zeballos | 0.5 | 2 | 0.055 | 0.075 | 0.085 | 0.105 | 0.129 | 0.288 | 0.310 | 0.323 | 0.348 | 0.376 |
| Jervis Inlet | 0.5 | 3 | 0.251 | 0.280 | 0.295 | 0.319 | 0.344 | 0.246 | 0.277 | 0.293 | 0.316 | 0.340 |
| Laredo Inlet | 0.5 | 3 | 0.172 | 0.198 | 0.214 | 0.239 | 0.271 | 0.218 | 0.249 | 0.267 | 0.295 | 0.324 |
| Tolmie Channel | 0.5 | 3 | 0.162 | 0.169 | 0.174 | 0.180 | 0.189 | 0.164 | 0.177 | 0.184 | 0.195 | 0.207 |
| Zeballos | 0.5 | 3 | 0.079 | 0.106 | 0.121 | 0.146 | 0.177 | 0.354 | 0.376 | 0.389 | 0.413 | 0.444 |
| Jervis Inlet | 0.5 | 4 | 0.298 | 0.327 | 0.342 | 0.365 | 0.388 | 0.292 | 0.324 | 0.339 | 0.362 | 0.385 |
| Laredo Inlet | 0.5 | 4 | 0.214 | 0.245 | 0.263 | 0.291 | 0.325 | 0.267 | 0.301 | 0.320 | 0.349 | 0.381 |
| Tolmie Channel | 0.5 | 4 | 0.200 | 0.208 | 0.213 | 0.221 | 0.230 | 0.203 | 0.217 | 0.225 | 0.237 | 0.251 |
| Zeballos | 0.5 | 4 | 0.102 | 0.135 | 0.152 | 0.182 | 0.217 | 0.397 | 0.417 | 0.430 | 0.451 | 0.479 |
| Jervis Inlet | 0.5 | 5 | 0.335 | 0.363 | 0.377 | 0.398 | 0.419 | 0.328 | 0.359 | 0.374 | 0.396 | 0.416 |
| Laredo Inlet | 0.5 | 5 | 0.251 | 0.285 | 0.303 | 0.334 | 0.369 | 0.308 | 0.343 | 0.362 | 0.391 | 0.422 |
| Tolmie Channel | 0.5 | 5 | 0.232 | 0.241 | 0.246 | 0.255 | 0.265 | 0.235 | 0.251 | 0.259 | 0.272 | 0.287 |
| Zeballos | 0.5 | 5 | 0.123 | 0.161 | 0.180 | 0.213 | 0.251 | 0.427 | 0.445 | 0.455 | 0.473 | 0.494 |
| Jervis Inlet | 0.6 | 1 | 0.080 | 0.093 | 0.100 | 0.113 | 0.127 | 0.077 | 0.091 | 0.099 | 0.111 | 0.125 |
| Laredo Inlet | 0.6 | 1 | 0.051 | 0.062 | 0.067 | 0.078 | 0.092 | 0.069 | 0.082 | 0.089 | 0.102 | 0.117 |
| Tolmie Channel | 0.6 | 1 | 0.044 | 0.047 | 0.048 | 0.051 | 0.054 | 0.046 | 0.050 | 0.052 | 0.057 | 0.061 |
| Zeballos | 0.6 | 1 | 0.020 | 0.028 | 0.032 | 0.040 | 0.050 | 0.134 | 0.149 | 0.158 | 0.176 | 0.199 |

| EFA | Post-Harvest Target Stock Level (Fraction of Virgin Biomass) | Harvest Interval (years) | Quantile of Sustaining Harvest Amount (fraction of **pre-harvest** biomass) | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Full Dataset | | | | | Data to 2007 | | | | |
| | | | 0.010 | 0.050 | 0.100 | 0.250 | 0.500 | 0.010 | 0.050 | 0.100 | 0.250 | 0.500 |
| Jervis Inlet | 0.6 | 2 | 0.140 | 0.160 | 0.171 | 0.189 | 0.208 | 0.136 | 0.158 | 0.169 | 0.186 | 0.205 |
| Laredo Inlet | 0.6 | 2 | 0.096 | 0.114 | 0.124 | 0.142 | 0.164 | 0.126 | 0.147 | 0.160 | 0.180 | 0.204 |
| Tolmie Channel | 0.6 | 2 | 0.083 | 0.087 | 0.089 | 0.094 | 0.099 | 0.085 | 0.092 | 0.096 | 0.103 | 0.111 |
| Zeballos | 0.6 | 2 | 0.039 | 0.053 | 0.060 | 0.075 | 0.092 | 0.217 | 0.236 | 0.249 | 0.273 | 0.305 |
| Jervis Inlet | 0.6 | 3 | 0.188 | 0.210 | 0.222 | 0.242 | 0.263 | 0.182 | 0.208 | 0.220 | 0.240 | 0.260 |
| Laredo Inlet | 0.6 | 3 | 0.135 | 0.158 | 0.171 | 0.194 | 0.221 | 0.173 | 0.199 | 0.214 | 0.239 | 0.268 |
| Tolmie Channel | 0.6 | 3 | 0.115 | 0.121 | 0.124 | 0.130 | 0.137 | 0.118 | 0.128 | 0.134 | 0.142 | 0.152 |
| Zeballos | 0.6 | 3 | 0.057 | 0.076 | 0.086 | 0.105 | 0.128 | 0.271 | 0.291 | 0.304 | 0.328 | 0.360 |
| Jervis Inlet | 0.6 | 4 | 0.226 | 0.249 | 0.261 | 0.281 | 0.301 | 0.219 | 0.246 | 0.259 | 0.279 | 0.299 |
| Laredo Inlet | 0.6 | 4 | 0.168 | 0.196 | 0.211 | 0.236 | 0.267 | 0.211 | 0.241 | 0.257 | 0.284 | 0.315 |
| Tolmie Channel | 0.6 | 4 | 0.144 | 0.151 | 0.155 | 0.161 | 0.169 | 0.148 | 0.159 | 0.165 | 0.175 | 0.187 |
| Zeballos | 0.6 | 4 | 0.074 | 0.097 | 0.110 | 0.132 | 0.159 | 0.309 | 0.327 | 0.339 | 0.359 | 0.387 |
| Jervis Inlet | 0.6 | 5 | 0.256 | 0.278 | 0.291 | 0.309 | 0.329 | 0.249 | 0.277 | 0.289 | 0.308 | 0.326 |
| Laredo Inlet | 0.6 | 5 | 0.197 | 0.227 | 0.244 | 0.272 | 0.306 | 0.244 | 0.275 | 0.291 | 0.318 | 0.350 |
| Tolmie Channel | 0.6 | 5 | 0.169 | 0.176 | 0.181 | 0.188 | 0.197 | 0.173 | 0.186 | 0.193 | 0.203 | 0.216 |
| Zeballos | 0.6 | 5 | 0.090 | 0.116 | 0.131 | 0.156 | 0.185 | 0.335 | 0.351 | 0.361 | 0.378 | 0.398 |
| Jervis Inlet | 0.8 | 1 | 0.034 | 0.039 | 0.043 | 0.049 | 0.056 | 0.033 | 0.039 | 0.042 | 0.048 | 0.055 |
| Laredo Inlet | 0.8 | 1 | 0.024 | 0.031 | 0.035 | 0.044 | 0.056 | 0.033 | 0.041 | 0.047 | 0.056 | 0.070 |
| Tolmie Channel | 0.8 | 1 | 0.018 | 0.019 | 0.019 | 0.021 | 0.022 | 0.019 | 0.020 | 0.022 | 0.024 | 0.026 |
| Zeballos | 0.8 | 1 | 0.008 | 0.011 | 0.013 | 0.016 | 0.021 | 0.058 | 0.067 | 0.073 | 0.086 | 0.108 |
| Jervis Inlet | 0.8 | 2 | 0.062 | 0.070 | 0.076 | 0.085 | 0.096 | 0.059 | 0.070 | 0.075 | 0.084 | 0.094 |
| Laredo Inlet | 0.8 | 2 | 0.046 | 0.056 | 0.064 | 0.079 | 0.101 | 0.061 | 0.075 | 0.083 | 0.099 | 0.122 |
| Tolmie Channel | 0.8 | 2 | 0.033 | 0.036 | 0.037 | 0.039 | 0.042 | 0.035 | 0.039 | 0.041 | 0.044 | 0.048 |
| Zeballos | 0.8 | 2 | 0.016 | 0.022 | 0.025 | 0.031 | 0.039 | 0.098 | 0.110 | 0.119 | 0.136 | 0.164 |
| Jervis Inlet | 0.8 | 3 | 0.084 | 0.095 | 0.102 | 0.112 | 0.124 | 0.082 | 0.094 | 0.101 | 0.111 | 0.123 |
| Laredo Inlet | 0.8 | 3 | 0.064 | 0.078 | 0.088 | 0.108 | 0.137 | 0.085 | 0.101 | 0.111 | 0.131 | 0.158 |

| EFA | Post-Harvest Target Stock Level (Fraction of Virgin Biomass) | Harvest Interval (years) | Quantile of Sustaining Harvest Amount (fraction of **pre-harvest** biomass) | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Full Dataset | | | | | Data to 2007 | | | | |
| | | | 0.010 | 0.050 | 0.100 | 0.250 | 0.500 | 0.010 | 0.050 | 0.100 | 0.250 | 0.500 |
| Tolmie Channel | 0.8 | 3 | 0.048 | 0.051 | 0.052 | 0.055 | 0.060 | 0.050 | 0.055 | 0.057 | 0.062 | 0.068 |
| Zeballos | 0.8 | 3 | 0.024 | 0.032 | 0.037 | 0.045 | 0.055 | 0.127 | 0.139 | 0.148 | 0.165 | 0.191 |
| Jervis Inlet | 0.8 | 4 | 0.103 | 0.115 | 0.122 | 0.133 | 0.145 | 0.100 | 0.114 | 0.121 | 0.132 | 0.144 |
| Laredo Inlet | 0.8 | 4 | 0.081 | 0.097 | 0.108 | 0.131 | 0.165 | 0.104 | 0.122 | 0.134 | 0.155 | 0.182 |
| Tolmie Channel | 0.8 | 4 | 0.061 | 0.064 | 0.066 | 0.070 | 0.075 | 0.063 | 0.069 | 0.072 | 0.078 | 0.084 |
| Zeballos | 0.8 | 4 | 0.031 | 0.042 | 0.047 | 0.058 | 0.070 | 0.147 | 0.159 | 0.167 | 0.182 | 0.199 |
| Jervis Inlet | 0.8 | 5 | 0.119 | 0.131 | 0.138 | 0.149 | 0.161 | 0.115 | 0.130 | 0.137 | 0.148 | 0.159 |
| Laredo Inlet | 0.8 | 5 | 0.095 | 0.113 | 0.125 | 0.149 | 0.186 | 0.121 | 0.139 | 0.151 | 0.172 | 0.196 |
| Tolmie Channel | 0.8 | 5 | 0.072 | 0.076 | 0.078 | 0.083 | 0.088 | 0.076 | 0.082 | 0.085 | 0.091 | 0.099 |
| Zeballos | 0.8 | 5 | 0.038 | 0.050 | 0.057 | 0.069 | 0.083 | 0.162 | 0.172 | 0.179 | 0.191 | 0.200 |

# 12. FIGURES

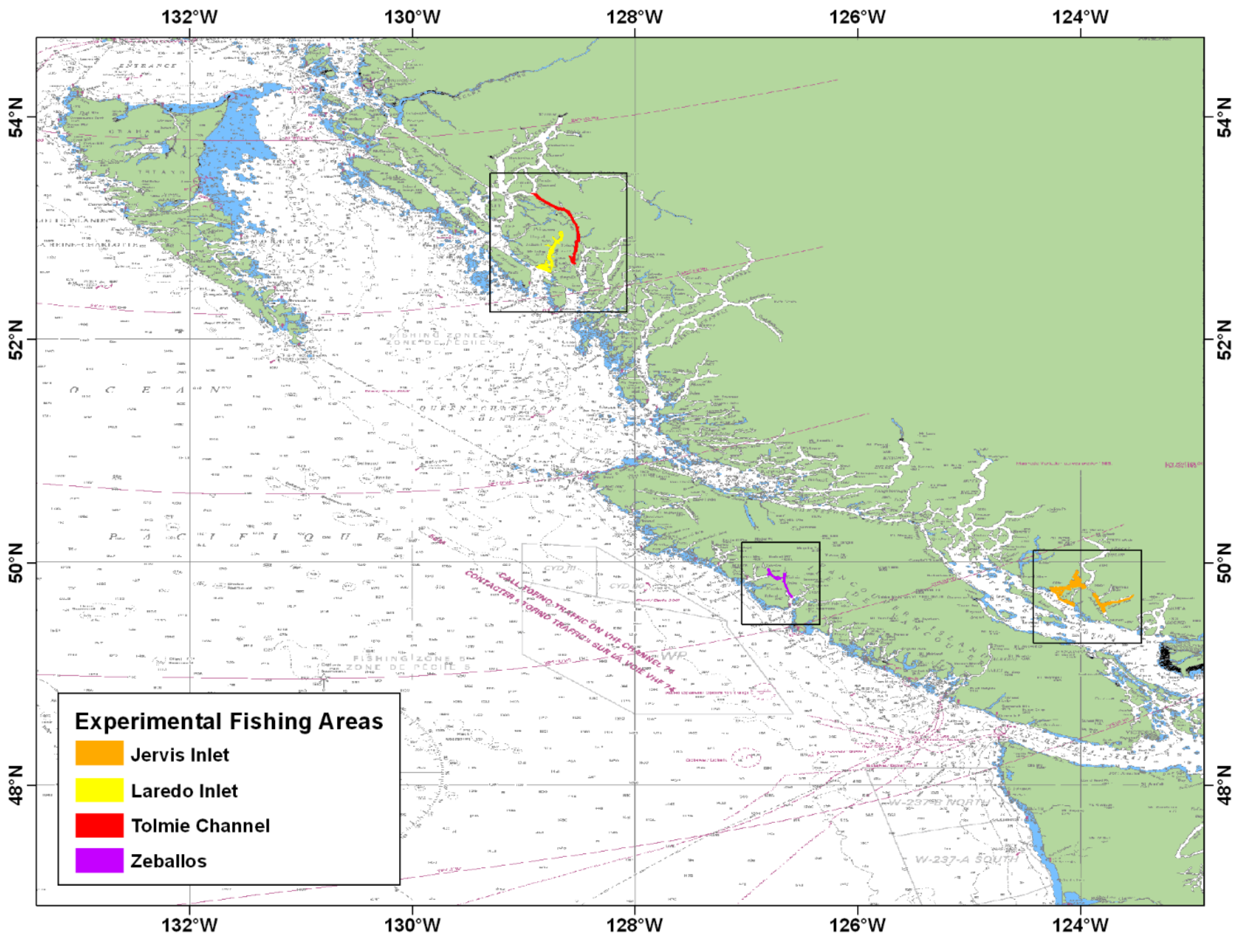



*Figure 1. Location of Experimental Fishing Areas on the coast of British Columbia.*

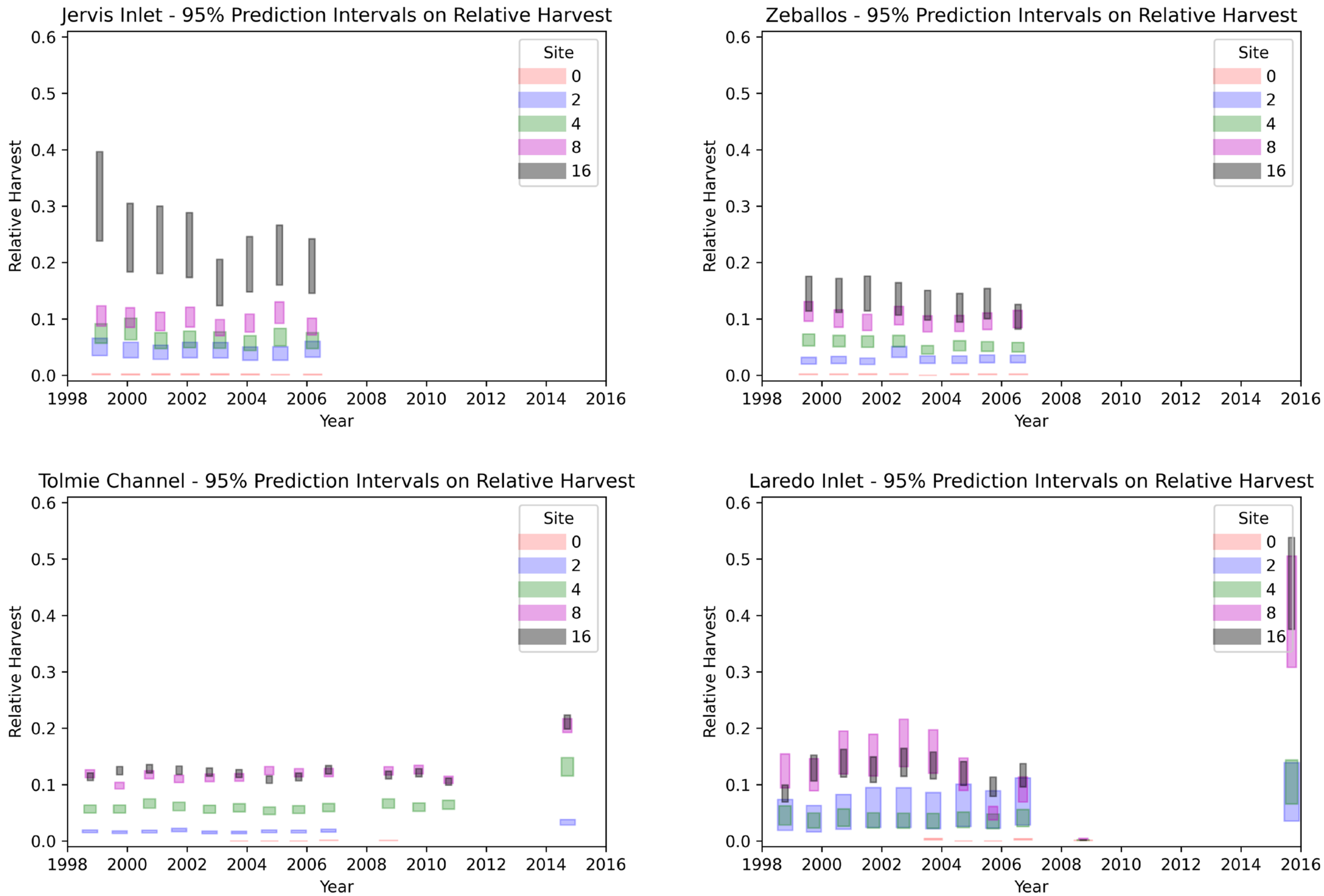



*Figure 2. 95% Credible intervals on harvest amounts for the EFAs. Harvest amounts are expressed as a fraction of the virgin biomass affected by harvest.*

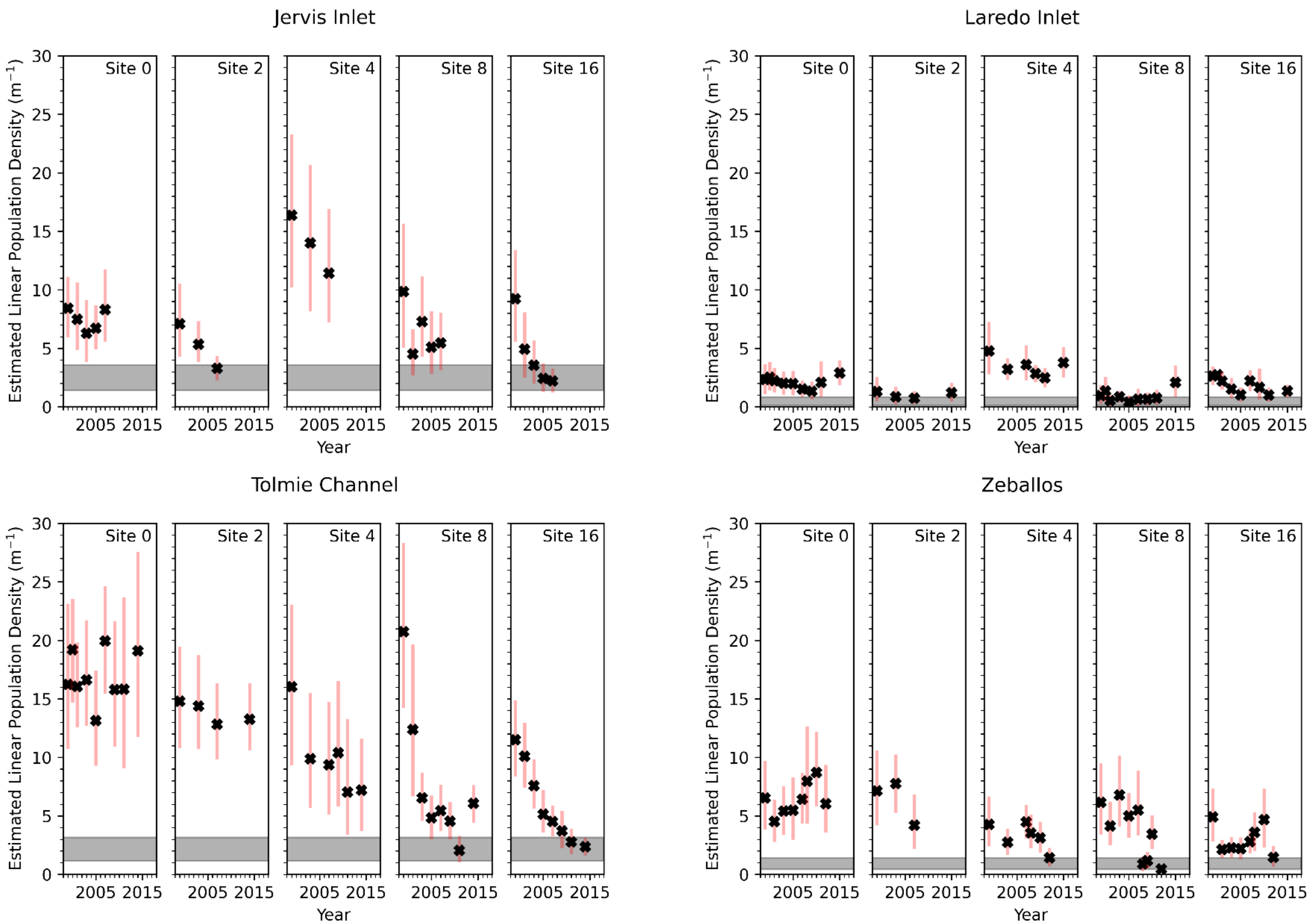



*Figure 3. Estimated linear population densities by EFA, site and year. Pink lines show the 95% confidence bounds on estimated mean linear population density (m$^{-1}$), x's show medians, and grey bars show estimated 95% confidence intervals for the minimum density from each EFA (excluding final density estimates).*

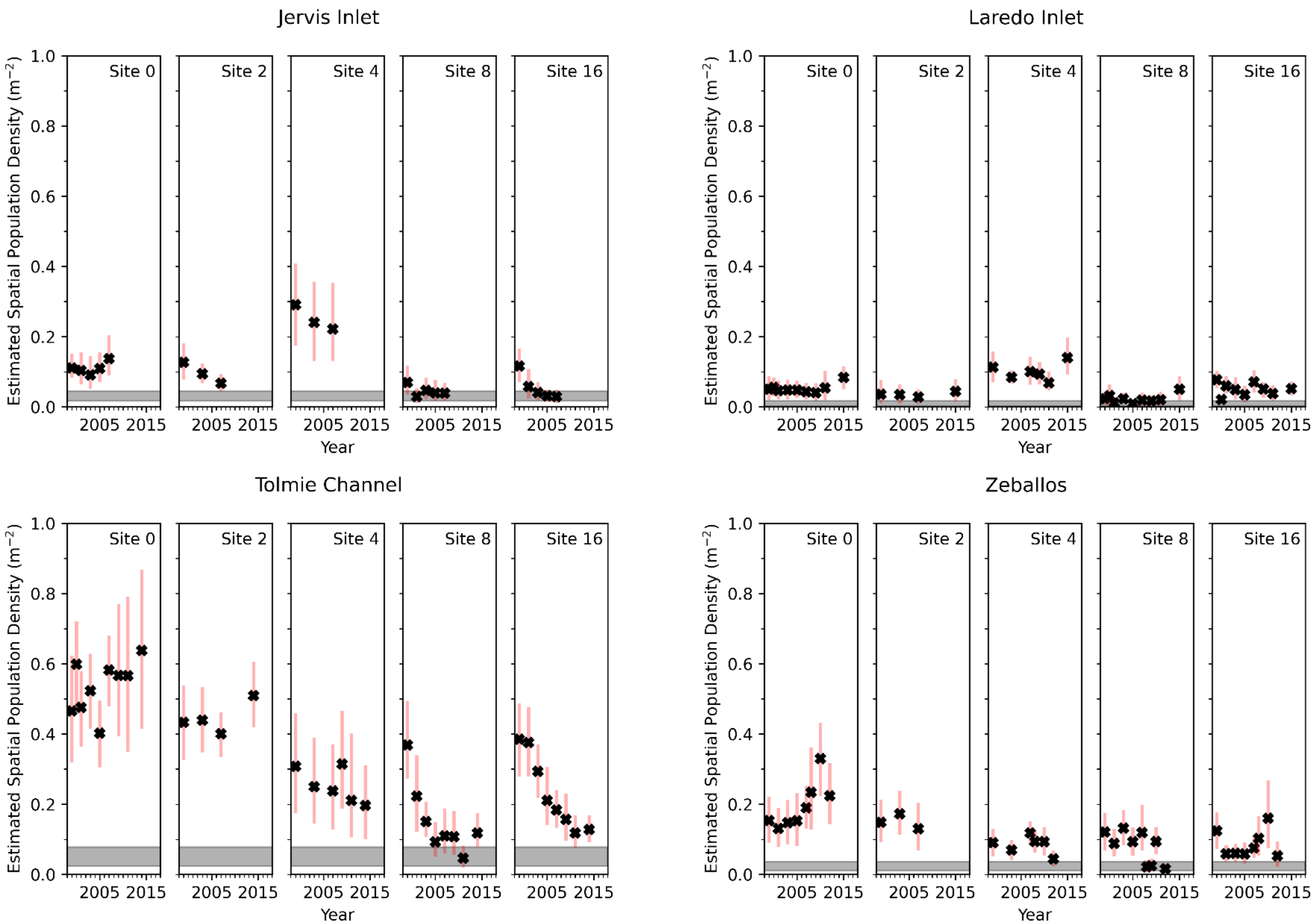



*Figure 4. Estimated spatial population densities by EFA, site and year. Pink lines show the 95% confidence bounds on estimated mean spatial population density (m$^{-2}$), x's show medians, and grey bars show estimated 95% confidence intervals for the minimum density from each EFA (excluding final density estimates).*

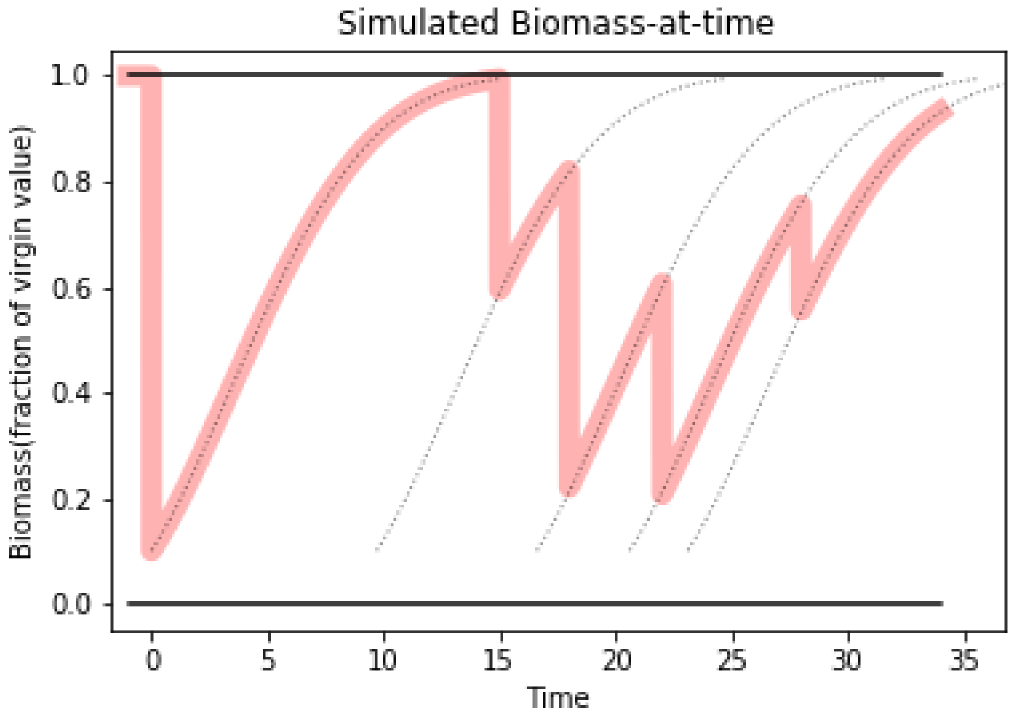



*Figure 5. A deterministic demonstration of the effects of harvest and productivity on a stock, where harvest is instantaneous. The pink line represents stock-level as a function of time and the dotted parallel curves represent the productivity curve. Note that stock levels may not reach zero in this demonstration.*

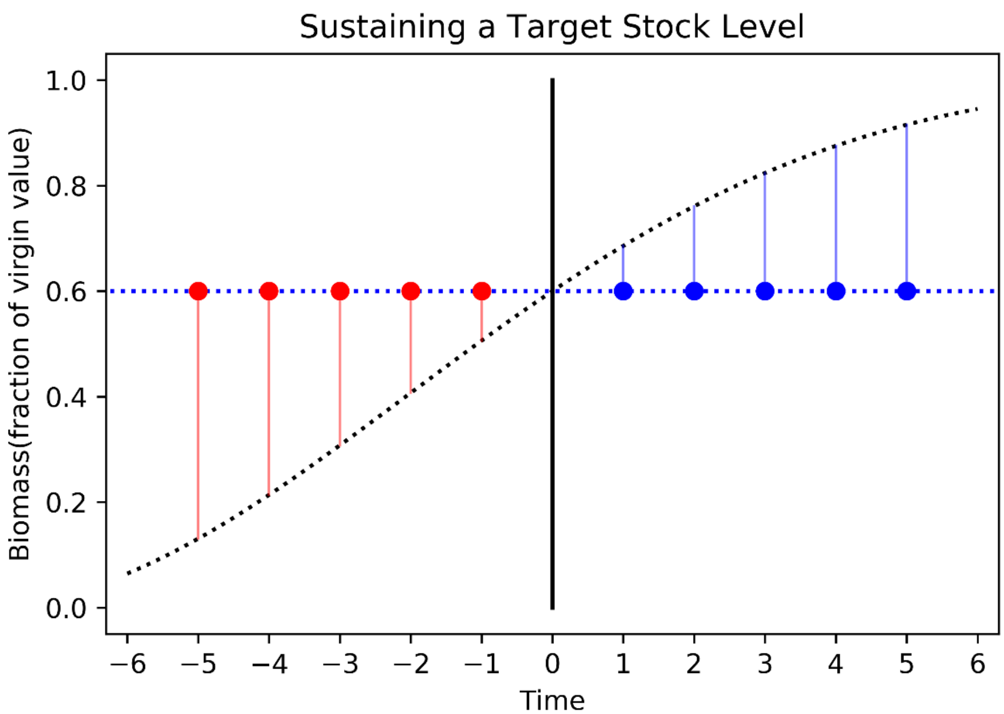
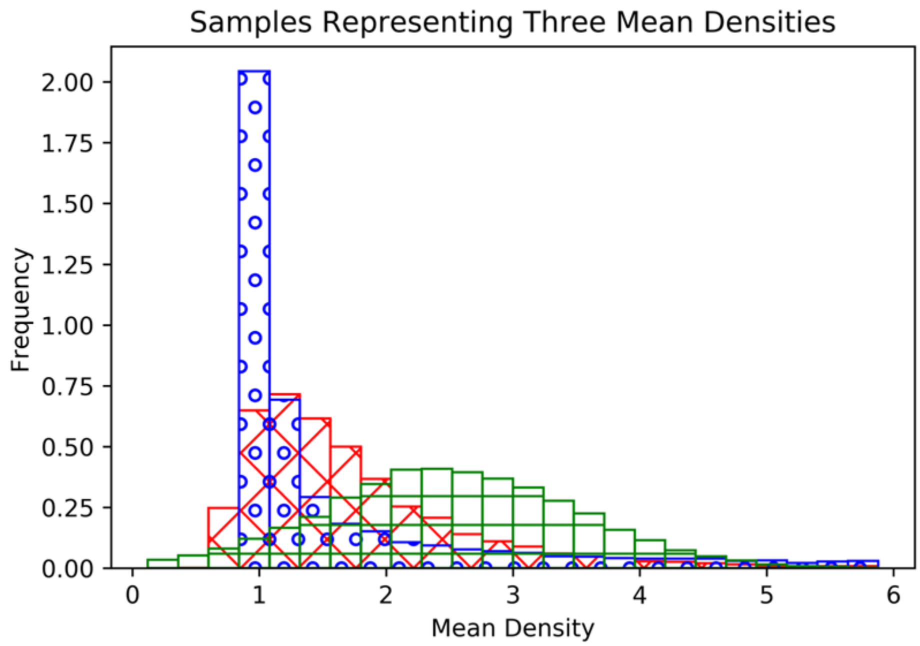



*Figure 6. A graphical representation of harvesting to maintain an equilibrium stock level. The horizontal line is the equilibrium stock level, the grey curve is one of the hypothetical parallel tracks that stock-levels follow when there is no harvest. The distance from the vertical centre line is length of the harvest cycle. The lengths of the blue vertical lines represent the harvests that will sustain the equilibrium stock-level as a post-harvest value. The lengths of the red vertical lines represent the harvests that will sustain the equilibrium stock-level as a pre-harvest value.*

A.




B.

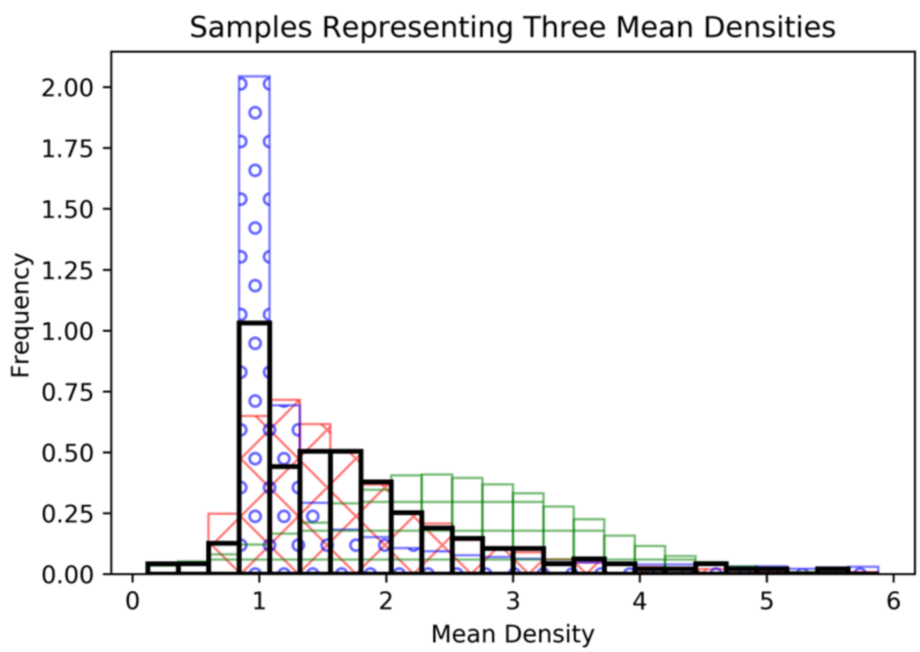



*Figure 7. Mean Density of Three Minima. Panel A (top) shows hypothetical distributions of three samples of values: green striped bars, red hatched bars and blue dotted bars. Panel B (bottom) shows the sample of 100 values generated to represent the smallest of the three original samples with black bars.*

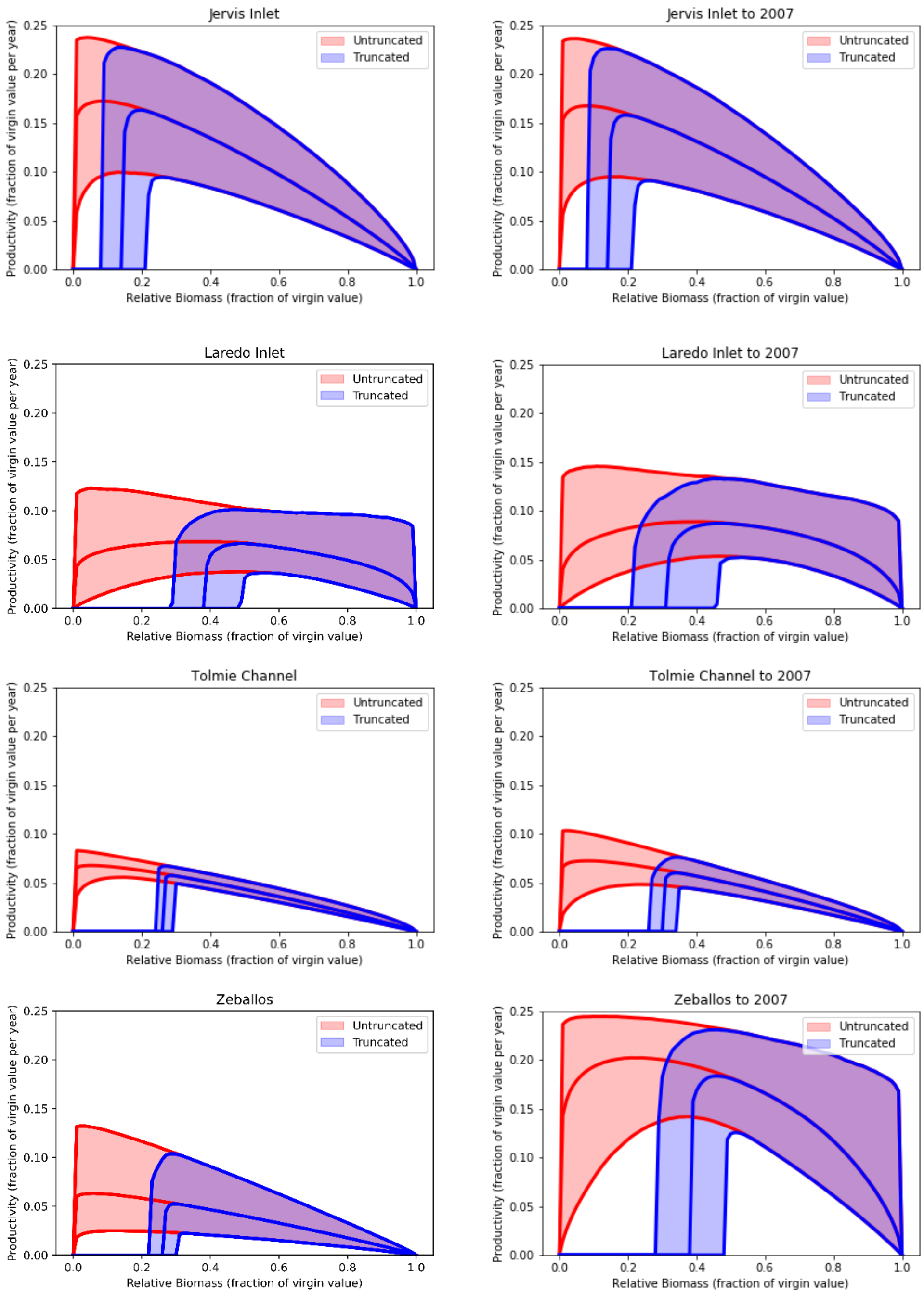



*Figure 8. Probabilistic productivity curves from a Bayesian analysis. 95% credible intervals and the medians of the posterior distribution are shown. For the truncated (blue) curves, productivity is conservatively assumed to be zero outside the range of stock-levels that occurred in the EFA. For untruncated (red) curves, extrapolation is used to estimate productivity beyond the range of stock-levels that occurred in the EFAs.*

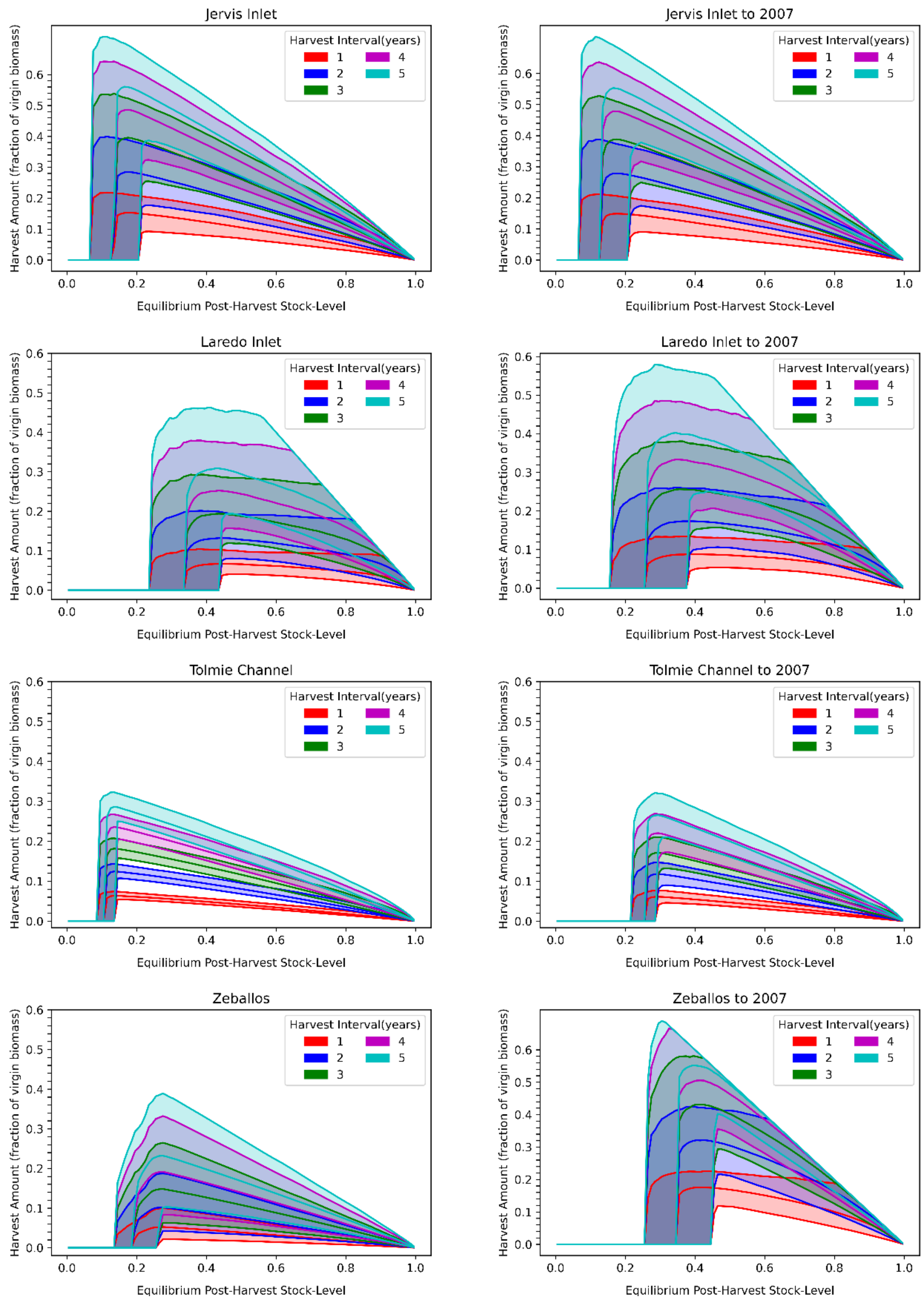



*Figure 9. Harvest Amount to Maintain Post-Harvest Stock-Levels. Harvest amounts and stock-levels are shown as a fraction of virgin stock-level. Results are shown for harvest intervals of 1,2,3,4 and 5 years. Solid lines the 0.025, 0.50 and 0.975 quantiles of the estimated posterior distribution. The shaded areas show the 95% credible intervals. Plots on the left use all the available data. Plots on the right use data that was available before 2008. For Jervis Inlet, the last surveys occurred in 2007 and therefore the same data was used for both plots but small differences will occur due to the random seeds used in the calculations.*

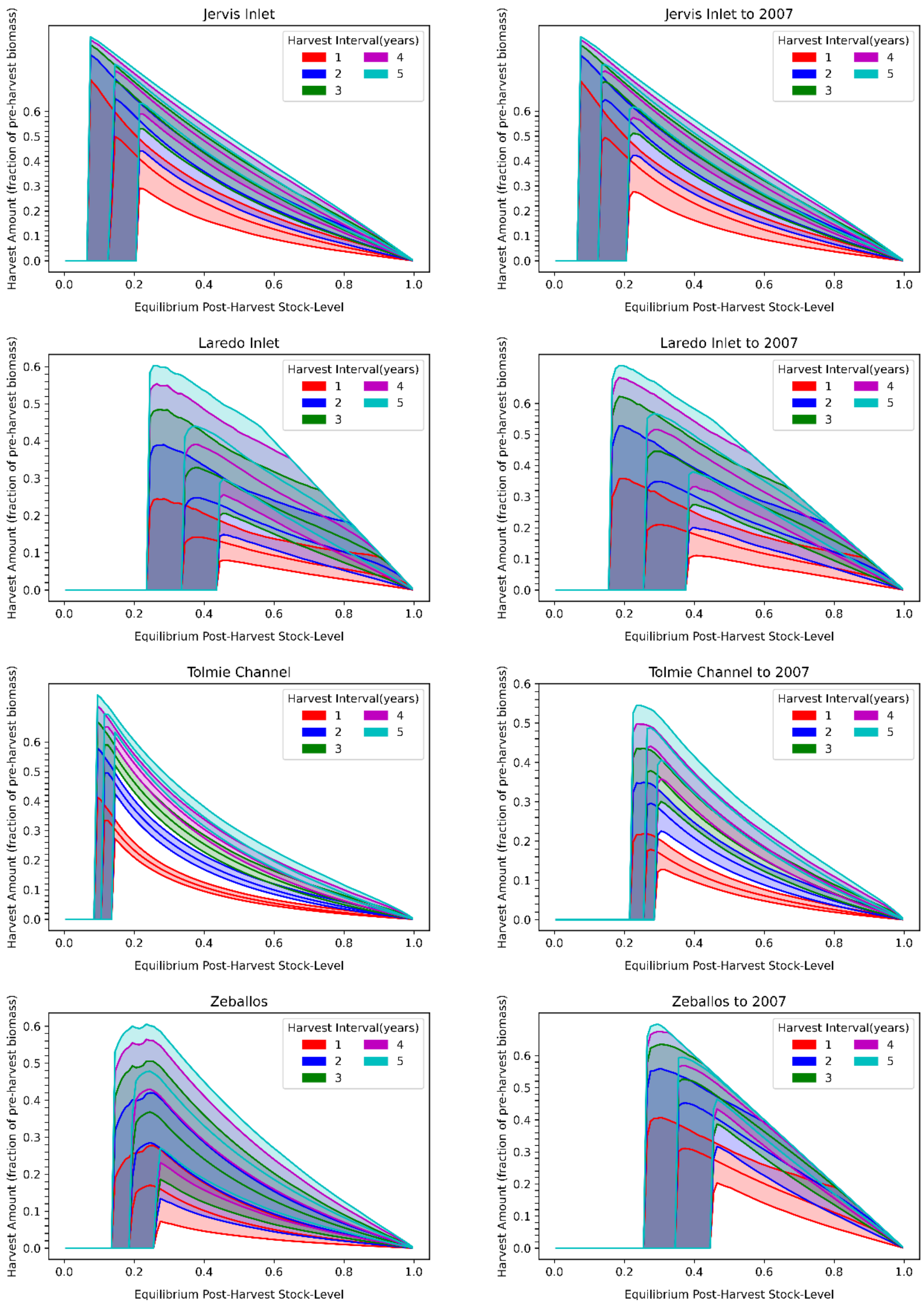



*Figure 10. Harvest Amount to Maintain Post-Harvest Stock-Levels. Harvest amounts are shown as a fraction of the pre-harvest stock-level and post-harvest stock-levels are shown as a fraction of the virgin value. Results are shown for harvest intervals of 1,2,3,4 and 5 years. Solid lines the 0.025, 0.50 and 0.975 quantiles of the estimated posterior distribution. The shaded areas show the 95% credible intervals. Plots on the left use all the available data. Plots on the right use data that was available before 2008. For Jervis Inlet, the last surveys occurred in 2007 and therefore the left and right plots are the same.*

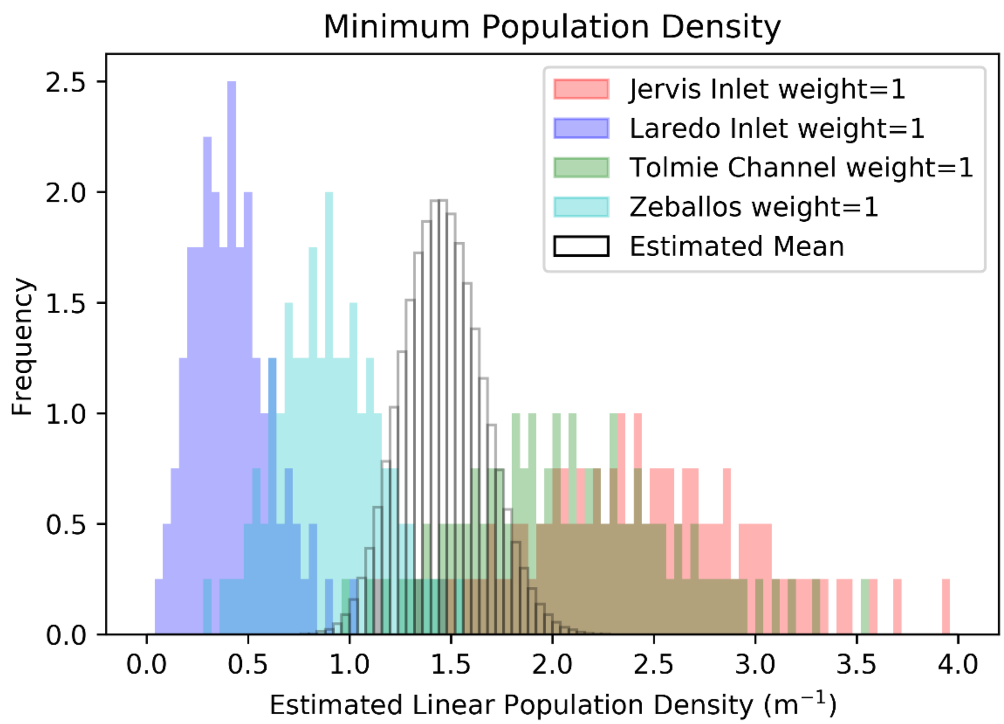



*Figure 11. Average of the estimated minimum linear population densities for the EFAs.*

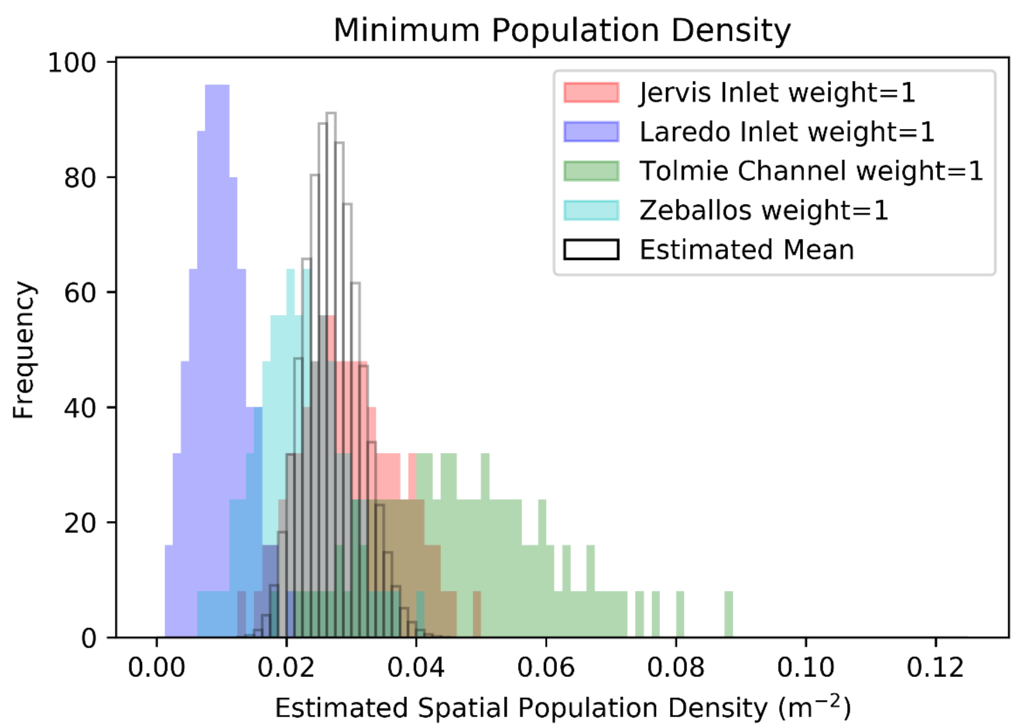



*Figure 12. Average of the estimated minimum spatial population densities for the EFAs.*

# APPENDIX A. TRIMMING TRANSECTS

Transects were surveyed quadrat-by-quadrat from deep to shallow, and results were recorded for each quadrat along the way. Gauge depth was recorded for each quadrat and tide height was used to convert gauge depth to chart depth.

As much as possible, divers reused transect locations from year to year. With this strategy, year-to-year differences in stock level are less affected by the random effects of the transect locations. The year-to-year changes in the survey results will be better representations of year effects, harvest and productivity.

Despite best efforts, the location of a transect will change every time it is surveyed. Some of the changes will be directly related to navigational issues. Global Positioning System (GPS) is less than perfect, especially when the EFAs just began. Currents were at least slightly different every time a transect was surveyed and that all contributed to changes in the transect location.

Other changes will be environmental. Since divers can only work efficiently over a limited range of gauge depths (0 to 18 m), they will work further out to sea or closer to shore depending on the tide height at the time. Even with perfect navigation, a transect will be different every time it is surveyed (Figure A-1).

In order to make a transect location as consistent as possible from year to year, data was trimmed from the tips. A different amount was trimmed for each time the transect was surveyed. As a result of the trimming process:

- the transect length is the same every time the location is surveyed, and
- the depth profile is as similar as possible from survey to survey.

The first step was to find the common depth range that occurred every time the transect surveyed.

The second step was to determine the minimum transect length associated with this depth range. For every instance the transect location was surveyed, the first and last quadrats in the common depth range were identified and used to define a transect segment. The length of the shortest of these segments became the reference length for the transect location.

Both the old (Hand et al. 2009) and the current versions of the transect-trimming process use the same method to generate the transect length. For the old version, the shortest transect segment that matched the depth range became the reference depth profile. If the shortest transect segment occurred multiple times, it was arbitrary which of the corresponding transect segments contributed the reference depth profile.

For the current version of the process, the reference depth profile was chosen according to a best-fit criterion. The ‘best’ part of the criterion means there was only one reference depth profile and therefore a unique set of transect segments that represent the transect.

Given the reference length, a brute force approach was used to determine the best reference depth profile. Every possible transect segment of the required length, from any year, regardless of the depth range, was evaluated for how well its depth profile matched depth profiles that occurred the other times the transect was surveyed.

Two depth-profiles can be compared on the basis of a sum-of-squares of the differences in depth, $\sum_{i=1}^{m}(q_i - r_i)^2$, where $q_i$ and $r_i$ are the depths from the two transect segments at the $i^{th}$ quadrat. A smaller sum of squares indicates a better fit.

To evaluate a candidate transect segment against the depth values from another year, the sum-of-squares calculation was applied to all transect segments of the same length from the other year. The smallest of these sums of squares represents how well the candidate segment matches the depth profile of the other year.

To evaluate a candidate transect segment against the multiple times the transect was surveyed, the minimum sum of squares was applied to each of the other years. The sum of these minima indicates how well the depth profile of the candidate segment matches depth profiles from the other years.

The sum of minima (of sum of squares) was calculated for each possible transect segment. The depth profile with the smallest value was used as a reference. For each year's data, the ends of the transect were trimmed so that what remained had the reference length and matched the reference depth profile as closely as possible.

Laredo Channel, transect #5, is provided here as an example to illustrate the trimming method (Figure A-1). The location was surveyed 10 times from 1998 to 2015. The lines show the depth profiles as they were before the transects were trimmed, and the symbols represent the end depth of the 5 m long transects. The common depth range was 0 to 10 metres. There were two surveys, 2001 and 2003, where only three quadrats were within that depth range and therefore three quadrats was chosen as the reference length. For 2003, quadrats 3, 4 and 5 (quadrat 5 not shown in Figure A-1) have depths within 0 to 10 m. When fitting to the reference depth profile, quadrats 2, 3, and 4 (shown in Figure A-1) best fit the reference depth profile, see below.

The three quadrat segment that best represents the transect location occurred in 2009. The consecutive chart depths were 10, 8 and 5 metres (quadrats 1, 2 and 3). The symbols in the figure show the three quadrat segment from each survey that best fits the reference depth profile. These are the trimmed transects that were used in the analyses.

Hajas et al. (2011) and Hand et al. (2009) used a different criteria for selecting a reference transect segment. The reference transect segment was simply chosen as the shortest to fall within the reference depth range. When this shortest length occurred more than once, it was arbitrary which transect segment was chosen as the reference. This new method that choses the reference depth profile according to a best fit criterion is an improvement because it is more repeatable.

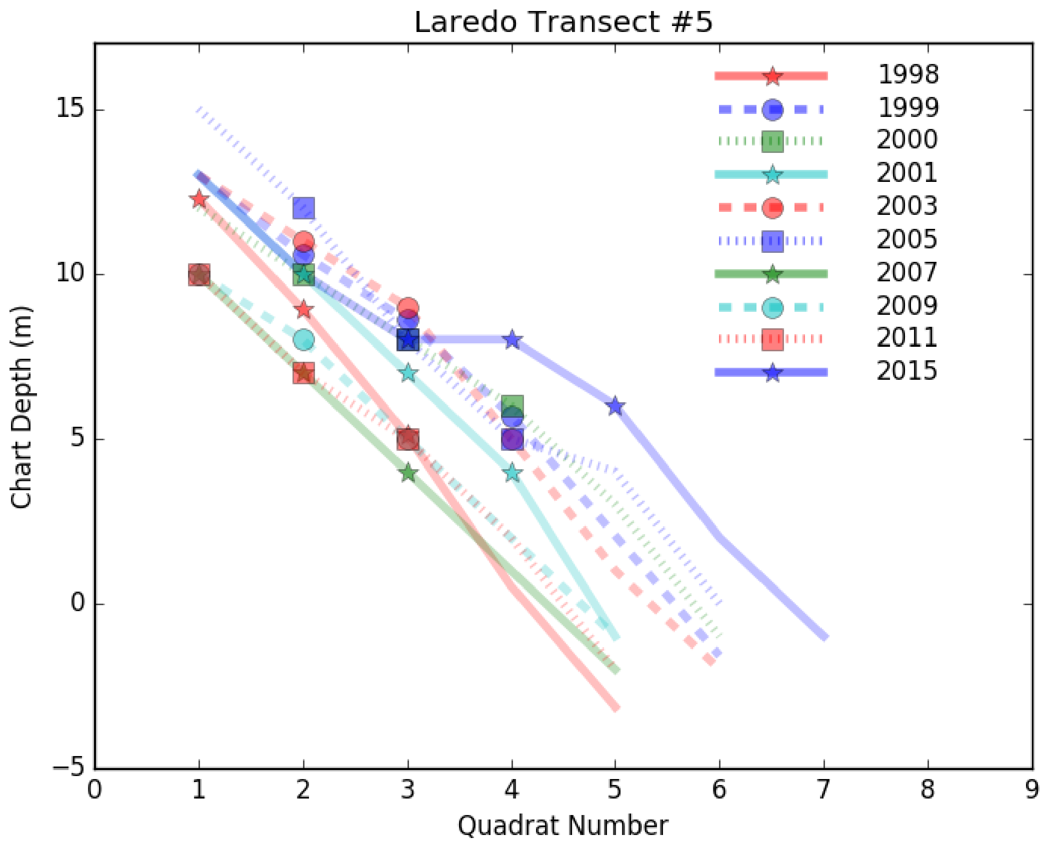



*Figure A-1. Reference depth profile for transect #5 in Laredo Channel. The lines represent all the quadrats where data was collected (untrimmed transects). Markers represent the quadrats included in the trimmed transects. The trimmed transects all have the same length (three quadrats) and the depth profiles agree as much as possible.*

# APPENDIX B. MATHEMATICAL MODELS USED IN THE BAYESIAN ANALYSES

## B.1. HARVEST

Harvest is modelled as an instantaneous drop in relative biomass. Relative harvest is the harvest amount divided by the estimated virgin biomass. If the relative harvest is greater than the pre-harvest relative biomass, the post-harvest relative biomass is set to zero. Otherwise, the post-harvest relative-biomass is just the pre-harvest stock-level less the relative harvest.

## B.2. PRODUCTIVITY

For these analyses, the productivity function is taken from (Hajas et al. 2011);

$P(B|a, b, B_{max}, f_{max}) = f_{max} * \frac{B}{B_{max}}^{a} * \frac{1-B}{1-B_{max}}^{b}$ where:

- $f_{max}$ is the maximum possible value of productivity with units of year$^{-1}$,
- $0 < B_{max} < 1$ is the value of relative-biomass where maximum productivity occurs, $P(B = B_{max}|a, b, B_{max}, f_{max}) = f_{max}$
- $0 < a < 1$ and $0 < b = a * \frac{1-B_{max}}{B_{max}} \leq 1$ control the width of the productivity curve, and
- $\theta = (a, b, B_{max}, f_{max})$ is the vector of productivity parameters.

The important characteristics of this productivity function are:

- Productivity is greater than or equal to zero. Stock levels never decrease except when there is harvest.
- Productivity is zero when biomass is zero; i.e. the stock will never recover after it has been completely depleted.
- Productivity is zero when biomass is at its virgin value; i.e. the virgin state represents the largest possible amount of biomass.
- There is a single maximum in the productivity curve.
- Relative biomass can be reduced to any non-zero value and it will return to its virgin state in a finite amount of time.
- Biomass is either increasing, holding steady at zero, or holding steady at the virgin state.

The values of $a$ and $b$ are constrained to be less than one in order to manage a mathematical artefact of the productivity function. With this constraint, relative biomass can start out at any non-zero value and return to the virgin state ($B = 1$) in a finite amount of time. If $a$ and $b$ are greater than or equal to one, there are situations where the virgin state is not achievable and the model becomes conceptually inconsistent.

The familiar Scheafer model (Schaefer 1954) is a special case of the current model where; $a = 1$, $b = 1$ and $B_{max} = {}^{1}/_{2}$.

As a further cautious and simple assumption, productivity is assumed to be zero when relative-biomass is less than the minimum that occurred during the EFA. There is no data to suggest productivity low stock-levels. If the model is used as an extrapolation-tool, there are very optimistic estimates of productivity at low stock-levels (Figure 8).

Between harvests, biomass increases at the rate of $\frac{dB}{d\tau} = P(B|a, b, B_{max}, f_{max})$ where $\tau$ is time. Numerical methods were implemented to solve the equation.

## B.3. SAMPLING MODEL

The sampling model represents random variability in the survey results. Random effects associated with the year of survey, site-locations and transect-locations are considered.

Even for sites with no significant harvest, survey results vary from year-to-year. Some of the variability may be due to year-to-year changes in abundance or migration in and out of sites and diveable depths. To account for this variability, the year-effects are given by $Y_y \sim norm(0, \sigma_y^2)$ and $\sum_y Y_y = 0$ where:

- $y = y(\tau)$ is an index corresponding to the calendar year as determined from the time of survey, $\tau$,
- $Y_y$ is the year effect and
- $\sigma_y^2$ is the variance of the year effects and is also used as a proxy for natural year-to-year variability in abundance.

Similarly, within the same EFA, there will be effects associated with different sites that are not associated with the harvest treatment. Site effects are treated the same as year-effects; $S_s \sim norm(0, \sigma_s^2)$ and $\sum_s S_s = 0$ where:

- s is an index for sites,
- $S_s$ is the site effect and
- $\sigma_s^2$is the variance of the site effects.

The above-noted requirements for the values of year-effects and site-effects are less restrictive than those of Hajas et al. (2011). Appendix C provides more details on how the current restrictions on the values of $Y_y$ and of $S_s$ were applied.

Transect-location effects are different because the sum-to-zero requirement is applied on a site-by-site basis. For the t[th] transect location in the s[th] site, the transect effect is $T_{s,t} \sim norm(0, \sigma_t^2)$ and $\sum_t T_{s,t} = 0$.

Hajas et al. (2011) applied more restrictive requirements to the values of the effects. Appendix C gives more details on how the sum-to-zero restrictions on the effects were applied.

Given these effects, for a virgin-state, the biomass density at a specific transect-location and particular year is $U_{s,y,t} = G * \exp\left(S_s + Y_y + T_{s,t}\right)$ where:

- $G$ is a grand geometric mean of spatial biomass density for the EFA.

For a transect in one of the EFAs, the expected spatial biomass density is $H_{s,t}(\tau) = U_{s,y(\tau),t} * B_s(\tau)$ where:

- $B_s(\tau)$ is the relative biomass, as calculated from the productivity model, for the s[th] site at time equals $\tau$.

The expected biomass on the t[th] transect of the s[th] site is $M_{s,t}(\tau) = A_{s,t} * B_s(\tau)$ where:

- $A_{s,t}$ is the area of the trimmed transect. The trimming process for transects is described in Appendix A.

Finally, the expected number of sea cucumbers on the transect is $P_{s,t}(\tau) = M_{s,t}(\tau)/W_s(\tau)$ where:

- $W_s(\tau)$ is the estimated mean weight at the $s^{th}$ site at time equals $\tau$.

The relationship between the expected and observed number of sea cucumbers is $O_{s,t}(\tau) \sim poisson(P_{s,t}(\tau))$. Under the poisson distribution, the possible number of sea cucumbers on a transect must be a non-negative integer.

## B.4. CHANGES SINCE HAND ET AL. (2009)

The current version of the model is implemented in pymc2 (Patil et al. 2010). Previously the model ran on WinBUGS (Lunn et al. 2009) with an extension to solve the differential equation for the productivity model. The code for the extension was lost and re-writing that extension would have been cumbersome. Implementing new functions or statistical distributions is much easier with pymc2 as the new platform.

1. pymc2 is tightly integrated with the PYTHON (van Rossum & Drake 2011) and inherits many program constructs (e.g. object orientation) from the language.
2. WinBUGS uses Gibbs sampling while pymc2 uses one-at-a-time Metropolis-Hastings sampling (Gelman et al. 2013).
3. With pymc2, it is much easier to generate meaningful node-names because they are completely specified by the user.
4. In the previous version of the model, the estimated effect of the first year was incorrectly included in the estimate of virgin biomass. In the current model, virgin biomass is unaffected by year-effects.
5. For the transect-trimming process, the new version of the model is more repeatable (see Appendix A for details).
6. The previous version of the model implemented productivity as a second order numerical approximation with a fixed time interval of one month. The current version uses a fourth order approximation with an adaptive time interval, which is preferred because the current version is faster and more numerically accurate.
7. Random effects associated with the year of survey, site locations and transect locations are considered in the model. For an array of effects in the previous model, the mean had to equal zero and the estimated standard deviation was forced to equal a sampled value. In the current version, the members of the array sum to zero and there are prior distributions with a variability defined in terms of a sampled standard deviation. Appendix C gives more details on how the sum-to-zero restrictions on the effects were applied in the current version.
8. There was an error in the previous version. The prior distribution for the mean transect length used a standard error instead of tau-value. The error has been corrected in the current version.

# APPENDIX C. ARRAY OF EFFECTS

In the sampling model, there is an array of year effects, an array of site effects and for every site there is an array of transect effects.

In non-Bayesian statistics there is a common requirement that an array of effects sums to zero. This requirement is quite reasonable. Otherwise, all the effects in an array could be increased by one, the grand mean could be decreased by one and the fit to the data would be just the same. It would just appear that all the effects were more positive.

In Bayesian analyses there usually is not a sum-to-zero requirement. Instead some sort of zero-centered prior distribution is applied independently to each effect; e.g. $\partial_i \sim norm(0, {\theta_\partial}^2)$. These prior distributions are not as restrictive as the sum-to-zero requirement. The posterior distribution will include combinations of parameter values that are effectively redundant to each other. The Markov chain will converge more slowly because it has to explore a larger parameter space.

These analyses implemented a sum-to-zero requirement in a Bayesian analysis. There are $n$ effects in an array. The first $n-1$ members of an array are assigned prior distributions of $\partial_i \sim norm(0, {\theta_\partial}^2)$. The final member fulfills the sum-to-zero requirement; $\partial_{n-1} = -\sum_{i=0}^{n-2} \partial_i$.

Without any correction, the implicit prior distribution on the last effect in the array is wider than the prior distributions applied to the other members of the array; $\partial_{n-1} \sim norm(0, (n-1) * {\theta_\partial}^2)$. An extra prior distribution is applied to the last effect in the array so that cumulatively there is the same prior distribution as for the other members of the array.

We want the probability density function for the prior for last member to be $f(\partial_{n-1}; \mu = 0, \sigma) = \frac{1}{\sqrt{2*\pi}*\sigma} * \exp\left(\frac{-{\partial_{n-1}}^2}{2*\sigma^2}\right)$. The uncorrected probability density function is $f(\partial_{n-1}; \mu = 0, \sigma, n) = \frac{1}{\sqrt{2*\pi*(n-1)}*\sigma} * \exp\left(\frac{-{\partial_{n-1}}^2}{2*(n-1)*\sigma^2}\right)$. The correction is made by applying an extra prior distribution where the probability density function is the ratio of the required and uncorrected probability density function of $f(\partial_{n-1}; \mu = 0, \sigma, n) = \sqrt{n-1} * \exp\left(-\frac{-{\partial_{n-1}}^2}{2*\sigma^2}\frac{n-2}{n-1}\right)$.

pymc2 does not allow a node to be both deterministic and probabilistic. Fortunately the additional prior distribution is symmetric in $\partial_{n-1}$ and $\mu$. The additional prior distribution can be applied by assuming a dummy data value with a value of zero and a distribution of $f(0; \mu = \partial_{n-1}, \sigma, n)$.

The following figure (Figure C-1) demonstrates the manipulation of the prior distribution for the last member of an array of effects.

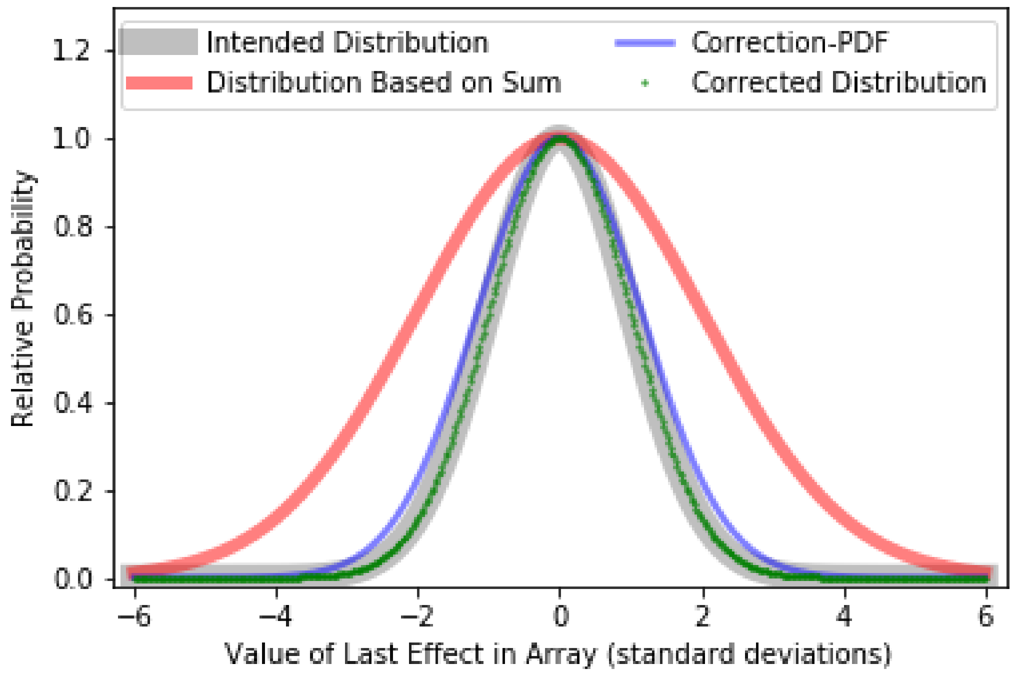



*Figure C-1.Probability density function for last of an array of effects.*

## APPENDIX D. THE MARKOV CHAIN

A precise mathematical definition of a Markov chain can be found in Gilks et al. (1995). For the purpose of post analysis, it is convenient to think of a Markov chain as a table of values.

Each column in the table represents a different parameter. For example, in the current analyses we decided to record a column of values for each parameter in the productivity function (Table D-1). When the model is implemented in pymc2, the analyst specifies parameter-values to save to the output and those values are written for each iteration of the Markov chain. In the current analyses, the number of model parameters depends on the number of times each site is surveyed and harvested. For example, 401 parameter-values are saved to file for each iteration of the Bayesian analysis of the Tolmie Channel EFA.

Each row in the table represents an iteration of the Markov chain. An iteration is a plausible explanation for the data. An iteration is also a single multi-dimensional parameter value drawn from the posterior distribution.

Some relationships between parameter values are explicitly specified in the model, i.e. $b = a * \frac{1-B_{max}}{B_{max}}$ (Appendix B). These relationships are maintained for every iteration in the Markov chain. Other relationships are not written into the model or prior distributions and only occur when data is considered. For example, there is a negative correlation between the estimated values $f_{max}$ and $B_{max}$ (Figure C-1). In the model and in the prior distributions, $f_{max}$ and $B_{max}$ are independent of each other. As a result of the full Bayesian analysis, which incorporates data, it becomes apparent that there is a relationship between the two estimated values. Large values of $f_{max}$ and large estimates of $B_{max}$ do not occur at the same time (Figure C-1). Any post-analysis results for Tolmie Channel are invalid if they simultaneously use high values of $f_{max}$ and $B_{max}$.

Often there is a need to perform post analyses where results of the Bayesian analysis are used to calculate other quantities. To be meaningful, any post analysis must incorporate these relationships between parameter values. The most accurate and convenient way to maintain these relationships is to perform the post analyses iteration by iteration.

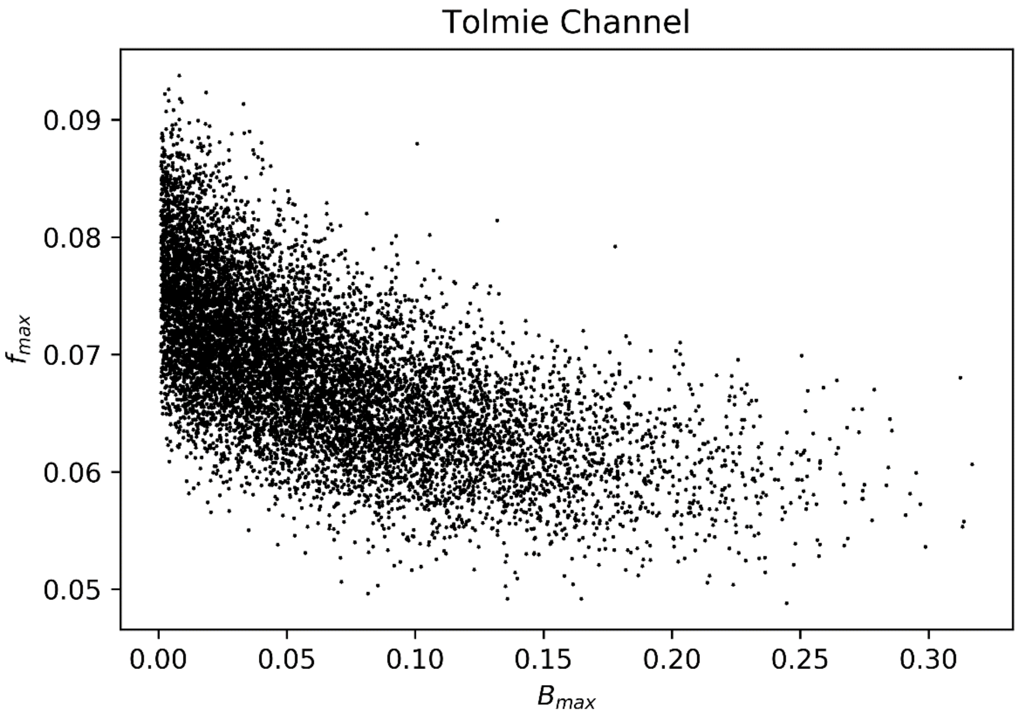



*Figure D-1. An example of an unanticipated negative correlation between the values of model parameters $f_{max}$ (maximum productivity) and $B_{max}$ (relative biomass where maximum productivity occurs) for Tolmie Channel.*