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Pre-COSEWIC review of DFO information on Northern Abalone (*Haliotis kamtschatkana*) along the Pacific Coast of Canada

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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

This review presents updated DFO data on Northern Abalone (*Haliotis kamtschatkana*) for use in a Committee on the Status of Endangered Wildlife in Canada (COSEWIC) status report. Northern Abalone were first designated as “Threatened” in 1999 by COSEWIC and re-designated as “Endangered” in 2009, and have been legally listed as “Endangered” under the Species At Risk Act since 2009. Northern Abalone occur from Salisbury Sound, Alaska to Bahía Tortugas, Baja California. Genetic studies show no evidence for more than one population of Northern Abalone in BC. Adults generally occupy exposed and semi-exposed coastal waters of less than 10 m depth, but have been observed from the low intertidal zone to 40 m depth. The extent of occurrence in BC waters was estimated at 6,985 km² based on a recently developed habitat suitability index model. The largest recorded shell length for a Northern Abalone in BC is 165 mm. Northern Abalone reach 50 mm in 2-5 years and 100 mm in 6-9 years. Fifty percent of individuals are sexually mature around 50 mm and 100% are mature at 70 mm. Estimated total mortality (0.20 – 0.50 y⁻¹), varied by region and with the presence/absence of Sea Otters (*Enhydra lutris*). All fisheries for Northern Abalone have been closed since 1990, including commercial, recreational, and First Nations’, but illegal harvest continues to be a major concern for this species. Density time series based on the DFO Northern Abalone Index Site Surveys show that estimated Northern Abalone densities have declined since the start of the time series (1978 in Northern BC), but have shown recent large increases in juvenile (shell length ≥ 20 mm to < 70 mm) densities and small increases in adult (≥ 70 mm) densities in Northern BC. However, the survey is marked by high variability in observed and estimated densities. Densities from a repeated transect survey near Kitkatla, BC, in 2000 and 2016, show similar trends to the densities estimated from the DFO Northern Abalone Index Site Surveys in Northern BC. Patterns are less clear in Southern BC where densities are much lower and have not shown large increases in any size category.

1 INTRODUCTION

1.1 PURPOSE

The Northern or Pinto Abalone (*Haliotis kamtschatkana*) is a marine snail, patchily distributed along the coast of British Columbia (BC), Canada and is the only species of abalone found in Canada (McLean 1966; Campbell 2000; Geiger 2000). Historically, this species supported First Nations', recreational and commercial fisheries (Sloan and Breen 1988; Farlinger 1990) until the closure of all fisheries in 1990, following large declines in the surveyed densities of Northern Abalone. Despite the closure of the fisheries, surveyed densities of Northern Abalone did not increase (Harbo 1997) and Northern Abalone were first designated as "Threatened" in 1999 by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) (Jamieson 2001), and re-designated as "Endangered" in 2009 (COSEWIC 2009). Following the COSEWIC status assessment, Northern Abalone were first legally listed as "Threatened" in 2003, and then re-listed as "Endangered" in 2009 under the Species at Risk Act (DFO 2012). The purpose of this paper is to provide an updated summary of DFO information relevant to the upcoming COSEWIC status re-assessment for Northern Abalone in Canadian waters. The results of this report will be made available to COSEWIC, the authors of the species status report, and the co-chairs of the applicable COSEWIC Species Specialist Subcommittee. Northern Abalone will henceforth be referred to simply as abalone, except when other species of abalone are also being discussed, then abalone species will be clearly identified.

1.2 AVAILABLE DATA AND LOCATIONS

The data used for the majority of the analyses herein were collected during Fisheries and Oceans Canada (DFO) Northern Abalone Index Site Surveys, hereafter referred to as index site surveys. These surveys are currently conducted in six survey regions in BC: Central Coast (CC); East Coast Haida Gwaii (ECHG); West Coast Haida Gwaii (WCHG); Queen Charlotte Strait (QCS); Georgia Basin (GB); and West Coast Vancouver Island (WCVI) (Figure 1) on an approximately five year rotation (see Table 1, Section 5.1 and Hansen et al. 2020 for more details). The index site surveys have been ongoing in some regions since 1978, thereby creating a time series on which most DFO science advice has been based, including closure of the fishery in 1990 and previous advice and analyses provided to COSEWIC. While the analyses herein rely heavily on the index sites surveys, a significant portion of our knowledge of the ecology and biology of abalone comes from other studies led by DFO (Table 2) and other groups. Most of these studies are conducted over small areas and usually for a limited period of time. For example, programs like the Aboriginal Fund for Species at Risk (AFSAR) and the Habitat Stewardship Program for Species at Risk (HSP) have enabled many First Nations to develop their own monitoring surveys or rebuilding projects. Notably, Gitxaala Nation, Haida Nation, Huu-ay-aht First Nations, Kitasoo/Xai'xais Nation, and Heiltsuk Nation collected data over many years. Others - Gitga'at First Nation, Metlakatla First Nation, Musgamagw Territorial Marine Management Society, Nisga'a Nation, Nuu-chah-nulth First Nations - were involved in smaller projects to collect abalone data and/or enhance stewardship. In addition, several university researchers have been conducting abalone research (Watson 2000; Griffiths and Gosselin 2008; Crim et al. 2011; Read et al. 2012, 2013; Hansen and Gosselin 2013, 2016; Lee et al. 2016). While abalone aquaculture is now defunct in BC, important knowledge gaps were filled in by the development of aquaculture projects (see Lessard et al. 2002; DFO 2015a). While these programs, surveys and research are valuable sources of information for evaluating the biology and status of abalone in BC, this pre-COSEWIC report focuses solely upon data collected by DFO.

Table 1. Northern Abalone Index Site Survey regions, years each region was sampled and corresponding Species at Risk Act Recovery Strategy (DFO 2007) biogeographic zones. Data from 2017-2019 are previously unpublished (2019 data were not available in time for this report).

Survey region	Years	Biogeographic zone
East Coast Haida Gwaii (ECHG)	1978, 1979, 1984, 1987, 1990, 1994, 1998, 2002, 2007, 2012, 2017	Haida Gwaii
Central Coast (CC)	1978, 1979, 1980, 1983, 1985, 1989, 1993, 1997, 2001, 2006, 2011, 2016	North and Central Coast
Queen Charlotte Strait (QCS)	2004, 2009, 2014, 2019	Queen Charlotte and Johnstone Straits
Georgia Basin (GB)	1982, 1985, 2005, 2009, 2019	Georgia Basin
West Coast Vancouver Island (WCVI)	2003, 2008, 2013, 2018	West Coast Vancouver Island
West Coast Haida Gwaii (WCHG)	2008, 2013, 2018	Haida Gwaii

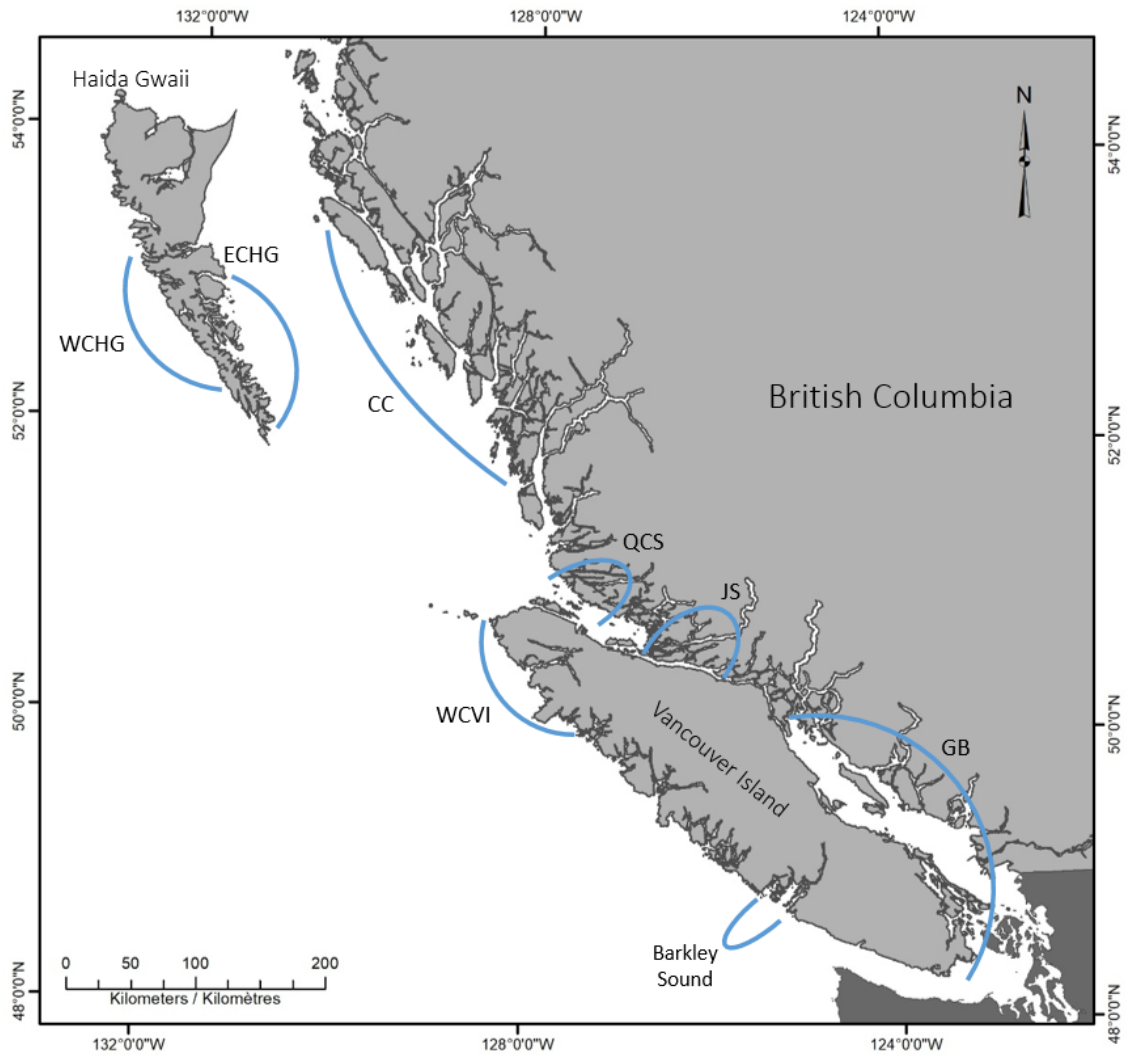


Figure 1. Map of regions surveyed in the DFO Northern Abalone Index Site Surveys in British Columbia. Index site data are available from six regions: East Coast Haida Gwaii (ECHG), West Coast Haida Gwaii (WCHG), Central Coast (CC), Queen Charlotte Strait (QCS), Georgia Basin (GB), and West Coast Vancouver Island (WCVI). Johnstone Strait (JS) was surveyed in 1982 and 2004, but is no longer surveyed. Although not an index site survey region, many DFO research studies have been conducted in Barkley Sound.

Table 2. DFO Northern Abalone data collected outside the scope of the Northern Abalone Index Site Surveys. Asterisks denote that Northern Abalone were seized by DFO; the location of seizure may not reflect the location of harvest.

Study location	Years	Northern Abalone Index Site Survey Region	Focus of study	Publication
McIntosh Island	1963	-	Growth, morphometry and breeding	Quayle (1971)
Hand Island	1963	-	Growth, morphometry and breeding	Quayle (1971)
Gilbert Island	1964, 1965	-	Growth, morphometry and breeding	Quayle (1971)
Bauke Island	1964, 1965	-	Growth, morphometry and breeding	Quayle (1971)
Sivart Island	1965, 1966	ECHG	Growth, morphometry and breeding	Quayle (1971)
Ramsbotham Reef	1966	GB	Growth, morphometry and breeding	Quayle (1971)
Hornby Island	1968	CC	Growth, morphometry and breeding	Quayle (1971)
Barkley Sound	1977, 1978	-	Growth rate	Breen (1986)
Haida Gwaii	1980, 1981, 1982	ECHG	Growth rate	Breen (1986)
Barkley Sound	1991, 1992, 1993	-	Growth and ageing - mark recapture	this report
Dallain Point	1995	CC	Density, population size and weight structure	Cripps and Campbell (1998)
Port Hardy*	1995	QCS	Length - weight relationship	this report
Higgins Pass	1996	CC	Density, population size and weight structure	Cripps and Campbell (1998)
Port McNeill*	1996	QCS	Length - weight relationship	this report
Goschen Island	2000; 2016	CC	Density estimate using transect survey method	Lucas et al. (2002); this report
Prager Islands	2000; 2016	CC	Density estimate using transect survey method	Lucas et al. (2002); this report
Dolphin Island	2000; 2016	CC	Density estimate using transect survey method	Lucas et al. (2002); this report
Barkley Sound	2002, 2003, 2004, 2005, 2006	-	Growth rate	Zhang et al. (2009)
Selwyn Inlet	2018	ECHG	Genetic distribution - population structure	unpublished
Tanu Island	2018	ECHG	Genetic distribution - population structure	unpublished
Upper Juan Perez Sound	2018	ECHG	Genetic distribution - population structure	unpublished
Lower Juan Perez Sound	2018	ECHG	Genetic distribution - population structure	unpublished

2 BIOLOGY

Abalone are dioecious, synchronous broadcast spawners with a life history that consists of a pelagic lecithotrophic larval phase (7-14 days) and a much longer benthic stage (Strathmann 1987; Sloan and Breen 1988; Pearce et al. 2003). During the benthic stage, recently settled abalone veligers metamorphose into juveniles and eventually mature into sexually reproductive adults (Strathmann 1987; Sloan and Breen 1988; Pearce et al. 2003). The earliest phases of this life history are generally associated with considerable mortality, as is typical of marine invertebrates (Thorson 1950, 1966; Moss and Tong 1992; Gosselin and Qian 1997), and settlement failure is not uncommon, particularly at low spawner densities (Breen 1986; Rothaus et al. 2008; Neuman et al. 2018; Carson et al. 2019, note that settlement failure is referred to as recruitment failure elsewhere). Causes for settlement failure may include unfavourable environmental conditions, a recruitment Allee effect, asynchronous spawning and high predation rates (e.g., failure of predator dilution at low densities, Shepherd 1990; Farlinger and Campbell 1992; McShane 1995; Rothaus et al. 2008). Predation can also be limiting at the juvenile and adult stages. Predators of the abalone include sea stars (e.g., *Pycnopodia helianthoides*), octopus (e.g., *Enteroctopus dofleini*), crabs (e.g., *Cancer productus*), fish (e.g., *Scorpaenichthys marmoratus*), and mammals (e.g., *Enhydra lutris*) (Sloan and Breen 1988). The vulnerability of abalone to certain predators decreases as they grow (Sloan and Breen 1988; Griffiths and Gosselin 2008), and they may exhibit behaviours such as crypsis to reduce their vulnerability to predation (Hansen and Gosselin 2016; Lee et al. 2016). The biology of abalone will be described in greater detail in the following sections, particularly as it pertains to the cryptic, mortality and Bayesian hurdle models used herein for population trend analysis. Moreover, Sloan and Breen (1988) provide a synopsis of abalone life history for BC, which remains one of the most comprehensive sources of information on abalone in BC. Some other helpful synopses include Lessard et al. (2007b) and COSEWIC (2009). Additionally, Neuman et al. (2018) recently reviewed the status of abalone for the west coast of North America, including a review of abalone biology.

2.1 GROWTH AND AGE

Growth and age information are used for mortality rate estimation. Growth is reasonably well described for Northern Abalone and other Haliotids (Sloan and Breen 1988). Most DFO growth information comes from tagging mark-recapture studies (e.g., Quayle 1971; Breen 1986; Zhang et al. 2009). Abalone growth varies with habitat and environmental conditions, with faster growth in locations with high-quality food sources, such as giant kelp (*Macrocystis pyrifera*) or bull kelp (*Nereocystis luetkeana*) (Breen 1986; Sloan and Breen 1988) and slower growth in high wave energy environments (Breen 1986; Lessard and Campbell 2007). Temperature also affects abalone growth (Sloan and Breen 1988). Given the influence of environmental conditions on abalone growth, growth might be expected to change over time as environmental conditions change.

Abalone growth is assumed to follow the von Bertalanffy model (Zhang et al. 2009):

$$\hat{L}_t = L_\infty(1 - e^{-K(t-t_0)}) \quad (1)$$

where \hat{L}_t is the expected shell length at age t , L_∞ is the asymptotic shell length, K is a growth rate coefficient that determines how quickly the maximum shell length is reached, t is age in years, and t_0 is the theoretical age at which the shell length is zero. Estimates of the von Bertalanffy growth parameters, L_∞ and K , are available from DFO mark-recapture studies in the 1960s-1980s (Breen 1986) and 2000s (Zhang et al. 2009). Breen (1986) estimated the growth

parameters using Ford-Walford plots of length at release and recovery for several tagging experiments coast-wide (1964-1982). Zhang et al. (2009) used Bayesian hierarchical models to estimate the growth parameters from a DFO translocation experiment in Barkley Sound (2002-2006) and incorporated individual variability in expected sizes into the parameter estimates. Data from another DFO mark-recapture experiment conducted from 1991 to 1993 in Barkley Sound (Hankin Island, Dempster Island, and Turret Island) are currently unpublished, and provide an opportunity to re-assess abalone growth parameters in BC using additional data.

In the absence of age data, the von Bertalanffy growth parameters (L_∞ and K) were estimated from the 1991-1993 mark-recapture data using Gulland and Holt plots (Gulland and Holt 1959; Murray and Neilson 2002) based on the change in shell length (mm) between tagging (t_1) and recapture (t_2) of each individual abalone (j):

$$\frac{L_{2,j} - L_{1,j}}{t_2 - t_1} = K \cdot L_\infty - K \cdot \frac{L_{1,j} + L_{2,j}}{2} \quad (2)$$

where $L_{1,j}$ and $L_{2,j}$ are the shell lengths measured at the time of tagging (t_1) and the time of recapture (t_2), respectively. The t_0 parameter in the von Bertalanffy growth equation (Equation 1) is assumed to be zero, as it cannot be estimated from mark-recapture data alone (Zhang et al. 2009). L_∞ is derived from the Gulland and Holt plot as the intercept (a) divided by K , and K is equal to the negative value of the slope (b):

$$K = -b \quad (3)$$

$$L_\infty = \frac{a}{K} \quad (4)$$

The boot package (Davison and Hinkley 1997; Canty and Ripley 2020) in R version 4.0.2 (R Core Team 2020) was used to estimate 95% confidence intervals (CIs) around the von Bertalanffy growth parameters estimated for Hankin Island, Dempster Island and Turret Island (5000 replicates with replacement). Diagnostic plots (histograms and quantile plots) of the bootstrap estimates revealed a normal distribution with only slight deviations at the tails. Bootstrap CIs were accordingly calculated using the basic (empirical) CI method built into the boot.ci function in the boot package, which is robust to deviations at the tails of the distribution (Canty and Ripley 2020).

The von Bertalanffy parameters, L_∞ and K , estimated from the 1991-1993 mark-recapture data are similar to the those estimated by Breen (1986) and Zhang et al. (2009) (Table 3, Figure 2). A null hypothesis of no difference between the parameters estimated from the 1991-1993 mark-recapture study and those in Breen (1986) cannot be rejected based on evidence from ANOVAs (ANOVA for K : $F_{1,10} = 0.001$, $p = 0.97$; ANOVA for L_∞ : $F_{1,10} = 0.65$, $p = 0.439$). Similarly, a cursory assessment of growth curves generated from the von Bertalanffy parameter estimates and their 95% confidence intervals does not suggest that a null hypothesis of no difference between sources (Breen 1986; Zhang et al. 2009, and the 1991-1993 mark-recapture study) could be rejected, and we have therefore not pursued additional analyses (Figure 2). The growth parameter values also appear consistent with those derived by Schnute and Fournier (1980) from length-frequency data in Breen and Adkins (1979), where L_∞ was 132.8 and K was 0.216. These comparisons are intended solely to demonstrate that additional data are not outliers. Greater variability between the estimated growth curves exists between locations within one study (Breen 1986) than between the three sources (Figure 2). Note that Ellis Islet, west coast of Vancouver Island, was removed from the figures as its K parameter range encompassed

zero. The observation that abalone growth in BC is highly site dependent is consistent with other studies, for example declining growth and shell length occur with increasing exposure (Breen 1986; Lessard and Campbell 2007).

Table 3. Northern Abalone von Bertalanffy growth parameters, L_{∞} (asymptotic shell length) and K (growth rate coefficient that determines how quickly the maximum shell length is reached) and their 95% confidence intervals (CIs) in British Columbia. Regions are HG (Haida Gwaii), CC (Central Coast), and BS (Barkley Sound), which do not correspond to the Northern Abalone Index Site Surveys. Derived from Breen (1986), Zhang et al. (2009), and a 1991-1993 tagging study (these additional data are identified by asterisks). Note that Zhang et al. (2009) involved transplantations among four sites in Barkley Sound.

Location	Year	K			L_{∞}		
		Mean	Lower 95% CI	Upper 95% CI	Mean	Lower 95% CI	Upper 95% CI
Sivart Is., HG	1966	0.230	0.128	0.346	129.8	126.8	132.9
Lyll Is., HG	1980	0.505	0.366	0.668	100.6	98.2	103.0
Newberry Cove, HG	1980	0.195	0.144	0.249	95.2	94.6	95.9
Murchison Is., HG	1982	0.267	0.070	0.510	124.2	116.3	132.2
Hickey Is., CC	1981	0.241	0.129	0.365	113.8	112.0	115.6
Bauke Is. (a), BS	1965	0.317	0.103	0.580	123.7	118.8	128.5
Gilbert Is., BS	1965	0.204	0.074	0.353	137.3	133.5	141.1
Ellis It., BS	1977	0.158	0.000	0.434	122.6	116.1	129.1
Bauke Is. (b), BS	1978	0.351	0.234	0.483	114.2	111.0	117.4
Hankin Is., BS *	1993	0.232	0.185	0.279	110.8	100.7	117.2
Turret Is., BS *	1993	0.306	0.214	0.394	111.8	102.6	117.3
Dempster Is., BS *	1993	0.292	0.245	0.338	111.8	107.6	114.9
Four locations, BS	2006	0.590	0.510	0.690	98.9	95.8	102.5

Limited information on ageing currently exists for abalone. Growth curves based on data in Breen (1980a) show that abalone reach 50 mm shell length around 2-5 years and 100 mm around 6-9 years with the purported age based on shell characteristics (Sloan and Breen 1988). Breen (1986) suggested it took 6 years to reach 100 mm. Quayle (1971) estimated that an abalone reaches approximately 20 mm shell length in 1 year, 35 mm length in 2 years, 50-60 mm in 3 years, and 90 mm in 6 years, and that an abalone of 140 mm might be about 15 years old (Quayle 1971). The maximum recorded shell length for an abalone in BC is 165 mm (Breen 1980b). The maximum recorded shell length in the DFO Northern Abalone Database is 158 mm. Growth curves project an estimated maximum age of about 15-20 years based on maximum size (Quayle 1971; Sloan and Breen 1988), which appears reasonable based on age determined using spire growth rings (Shepherd et al. 2000; Lessard et al. 2007b). Such ageing methods are currently being verified using shell microchemistry. The longevity estimates of 15-20 years have been previously used to estimate a natural generation time of approximately 10 years (COSEWIC 2009), with the caveat that the recent rarity of large individuals is suggestive of a decline in generation time. COSEWIC (2009) states that generation time may be only 2-5 years in areas with Sea Otters (*Enhydra lutris*). No new information is available to update these estimates.

2.2 LENGTH-WEIGHT RELATIONSHIP

The length-weight relationship is used to estimate spawning biomass in the mortality rate estimation process. Limited recent data exist on abalone length-weight relationships in BC, with Sloan

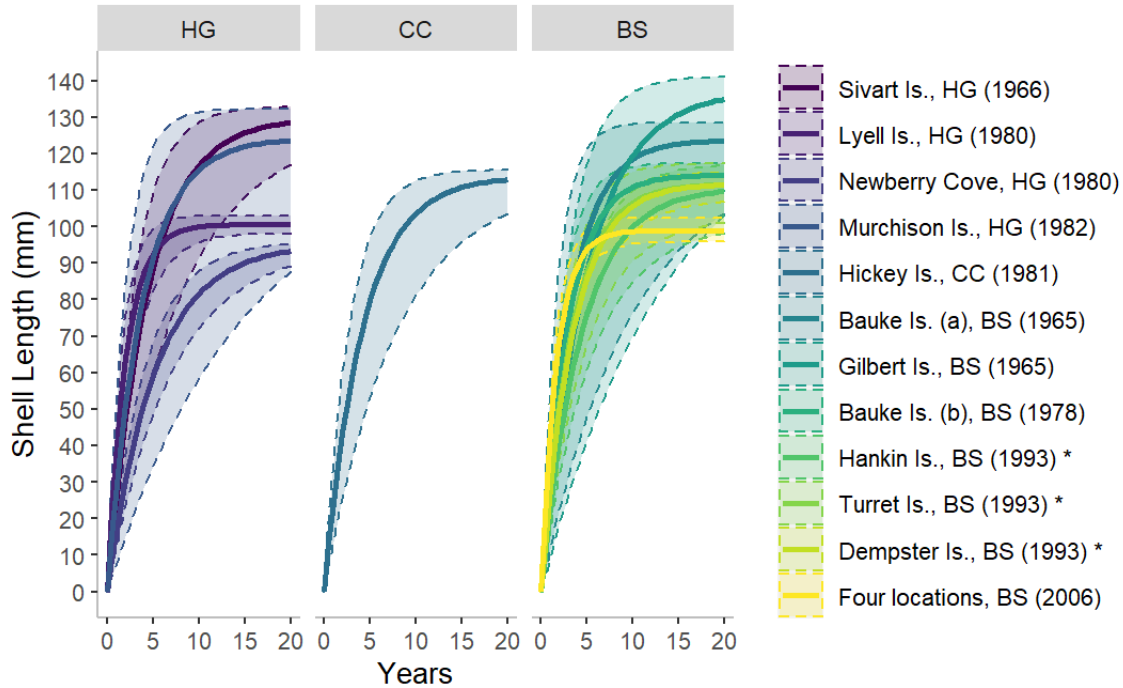


Figure 2. Northern Abalone von Bertalanffy growth curves derived from 95% confidence intervals of L_{∞} (asymptotic shell length) and K (growth rate coefficient that determines how quickly the maximum shell length is reached) parameters from studies in British Columbia. Additional data from the 1991-1993 tagging study are denoted by asterisks. Regions are Haida Gwaii (HG), the Central Coast (CC), and Barkley Sound (BS), and do not correspond with the Northern Abalone Index Site Surveys. Note that t_0 was not required for von Bertalanffy parameter estimation, however it has been set to 0 for the purpose of visualizing the growth curves.

and Breen (1988), citing data from Quayle (1971), still representing one of the leading references on this subject. Weight data were also collected by Breen and Adkins (1982) and Cripps and Campbell (1998). Breen and Adkins (1982) data have not yet been digitized and are not currently available in the DFO Northern Abalone database.

However, length-weight data collected from seized abalone in 1995 and 1996 were available and were analyzed as an update to the Quayle (1971) and Cripps and Campbell (1998) length-weight relationships. These seizures occurred at Beaver Cove, near Port Hardy, on April 5, 1995 and in the Port McNeill area on April 12, 1996, and included 860 (846 intact) and approximately 200 abalone, respectively. Given the source of these abalone collections, they consist primarily of large abalone, whereas size-frequency distributions from Quayle (1971) and Cripps and Campbell (1998) encompass a broader range of sizes. A non-linear least-squares approach was used to estimate the parameters of the length-weight relationship:

$$W = a \cdot L^z \quad (5)$$

where W is wet weight (g), L is the shell length (mm), and a and z are constants. The estimated length-weight relationships were compared by location, as well as by data source (Quayle 1971; Cripps and Campbell 1998, versus seized abalone). Although abalone are dioecious (separate sexes), and sexes can be distinguished based on gonad colouration (dark green in females and pink to beige in males), the literature provides no evidence of sexual dimorphism in shell

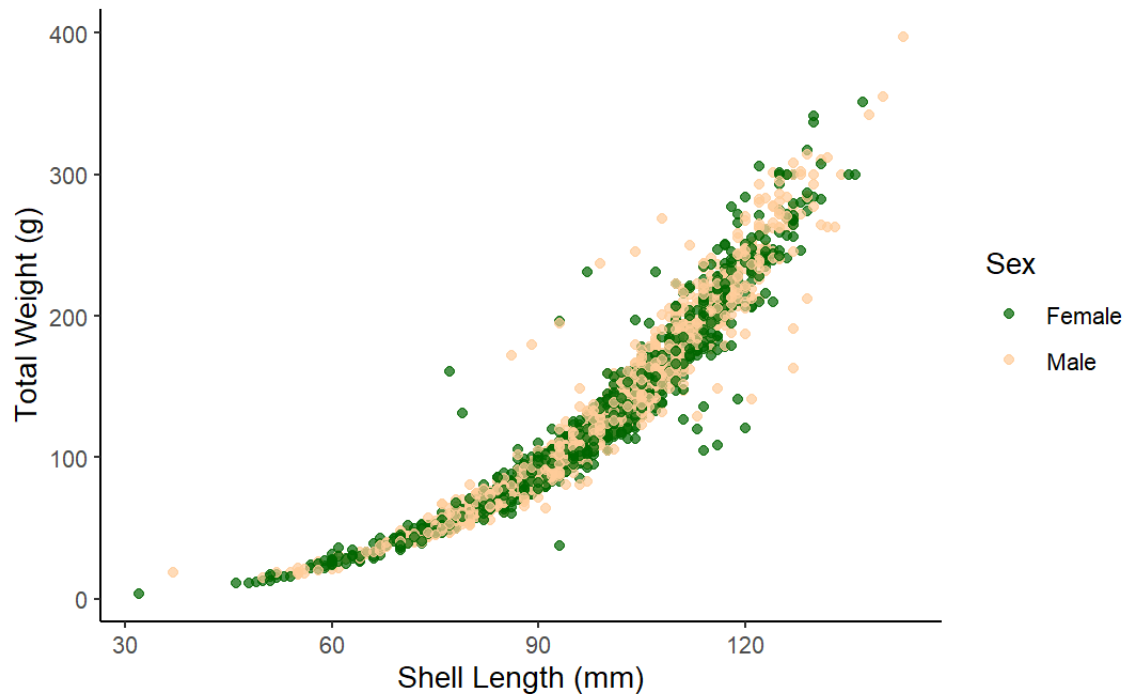


Figure 3. Length-weight relationship of dioecious Northern Abalone in British Columbia, based on data from Quayle (1971).

structure or morphometrics (McLean 1966; Breen and Adkins 1982). Re-analysis of the data collected by Quayle (1971) (Figure 3) using an ANCOVA with site and sex effects ($\log(W) = \alpha + \beta_{\log(L)} \cdot \log(L) + \beta_{Site} \cdot Site + \beta_{Sex} \cdot Sex + \epsilon$) showed that while site has a significant effect on the length-weight relationship ($F_{2,2021} = 10.7$, $p < 0.001$), sex does not have a significant effect, visually or statistically at $\alpha = 0.05$ ($F_{1,2021} = 3.451$, $p = 0.063$). Given the lack of influence of sex on morphometrics, sex was excluded from further analyses.

Although it appears that the abalone seized in Port Hardy and Port McNeill generally had a lower condition (z) than those measured by Quayle (1971) or Cripps and Campbell (1998) (Figure 4, Table 4), this was largely a site effect (Figures 4 and 5), driven by abalone seized in Port Hardy having a lower estimated weight-at-length at large sizes than abalone in Port McNeill (also seized) or any sites in Quayle (1971) or Cripps and Campbell (1998). However, it is important to note that the location of seizure may not reflect the location from which abalone were poached. Parameter estimates are presented in Table 4. These comparisons are intended to demonstrate that the additional (seizure) data do not represent outliers relative to previously analysed data.

2.3 MATURITY

Information on maturity is used to determine the length of mature abalone in the mortality rate estimation process. Abalone become sexually mature around 50 mm, with 50% observed to reach sexual maturity around 50 mm (44-55 mm depending on location) and 100% at 70 mm (Quayle 1971; Campbell et al. 1992, 2003). It is important to note that these lengths at maturity were estimated in the absence of Sea Otters and there is currently no data available for lengths at maturity in otter occupied areas. Abalone in Sea Otter occupied areas may have slower

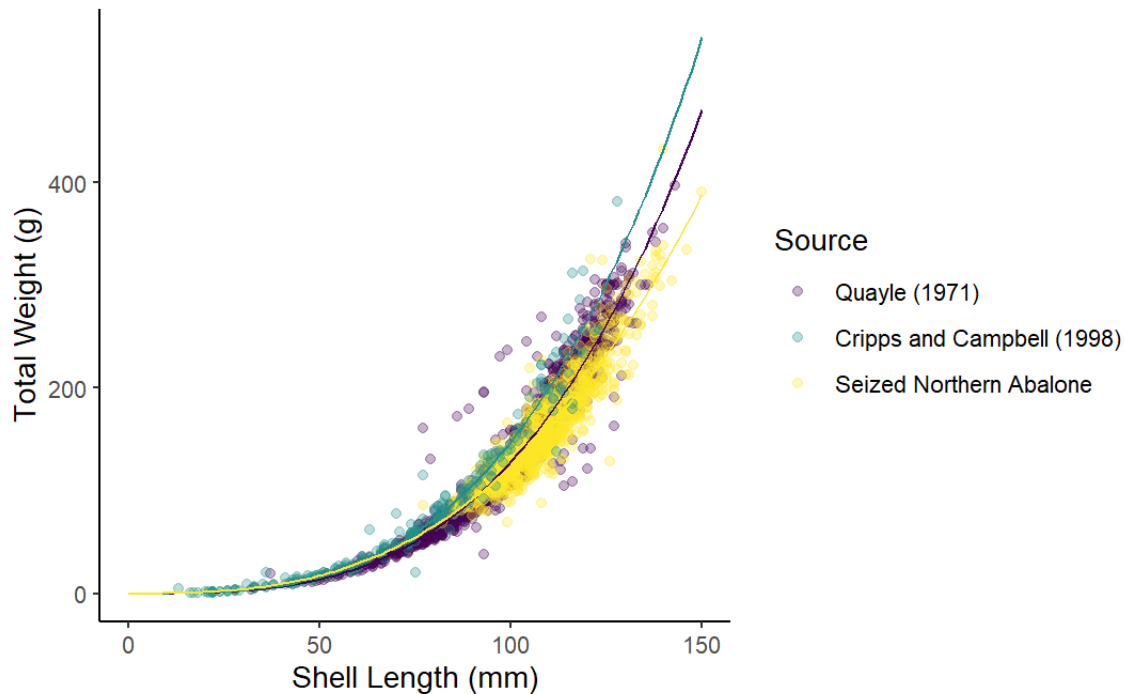


Figure 4. Northern Abalone length-weight relationships derived from different sources of data: Quayle (1971), Cripps and Campbell (1998), and seizures of Northern Abalone.

growth, reach maturity at smaller sizes and might accordingly have higher fecundity at smaller sizes, however these relationships need to be examined.

Table 4. Northern Abalone length-weight relationship parameters at several sites in British Columbia, estimated using three data sources: Quayle (1971); Cripps and Campbell (1998), and seized Northern Abalone. Averages are the mean \pm standard error across sites for each data source. Regions are Barkley Sound (BS), Haida Gwaii (HG), Georgia Basin (GB), Central Coast (CC), and Queen Charlotte Strait (QCS), and do not correspond with the Northern Abalone Index Site Surveys.

Source	Location	a	z
Quayle (1971)	Bauke Island, BS (1964)	3.87e-05	3.258
Quayle (1971)	Sivart Island, HG (1966)	6.63e-05	3.146
Quayle (1971)	Hornby Island, GB (1968)	7.94e-05	3.119
Quayle (1971)	Ramsbotham Reef, CC (1966)	5.49e-05	3.178
	Average	5.98e-05\pm8.65e-06	3.175\pm0.030
Cripps and Campbell (1998)	Dallain Point, CC (1995)	3.53e-05	3.316
Cripps and Campbell (1998)	Higgins Pass, CC (1996)	2.14e-04	2.910
	Average	1.25e-04\pm8.92e-05	3.113\pm0.203
Seized Northern Abalone	Port Hardy, QCS (1995)	2.05e-04	2.885
Seized Northern Abalone	Port McNeill, QCS (1996)	2.21e-04	2.895
	Average	2.13e-04\pm8.24e-06	2.890\pm0.005
	Overall Average	1.14e-04\pm2.94e-05	3.088\pm0.060

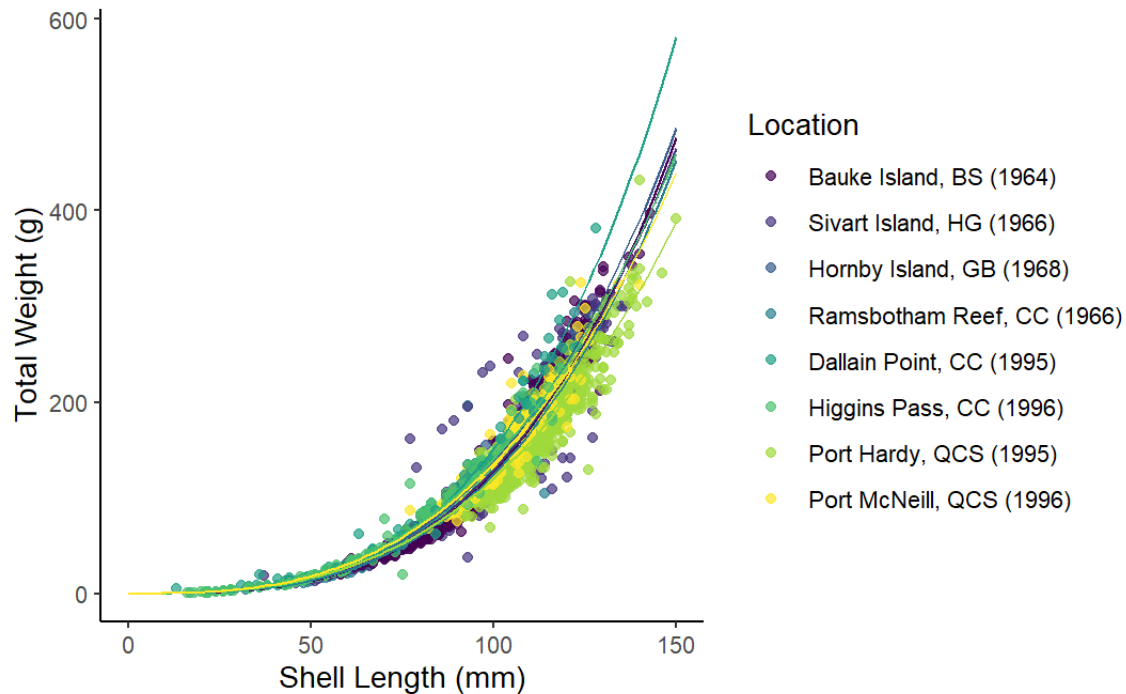


Figure 5. Northern Abalone length-weight relationships at different locations in British Columbia. Port Hardy and Port McNeill relationships are derived from data based on seized Northern Abalone. Dallain Point and Higgins Pass are from Cripps and Campbell (1998) data. All others (Bauke Island, Sivart Island, Hornby Island and Ramsbotham Reef) are from Quayle (1971) data. Regions are Barkley Sound (BS), Haida Gwaii (HG), Georgia Basin (GB), Central Coast (CC), and Queen Charlotte Strait (QCS), and do not correspond with the Northern Abalone Index Site Surveys.

2.4 FECUNDITY

Fecundity is not applied to the models herein, however it is important to contextualize the implications of shifting population structure. Abalone are dioecious broadcast spawners whose fecundity increases with size and age (Sloan and Breen 1988; Campbell et al. 2003). Factors that may affect both size-at-maturity and fecundity are food availability, water temperature and other environmental conditions (Neuman et al. 2018). Studies involving histologic sections of abalone gonads reveal that abalone fecundity ranges from 156,985 (57 mm shell length female) to 11.56 million eggs (139 mm shell length female) (Campbell et al. 1992, 2003; COSEWIC 2009). Abalone may participate in multiple spawning events in a given year, releasing only a portion of their gametes (30,000 to 2.3 million eggs) per event (Neuman et al. 2018; Carson and Ulrich 2019). See Breen and Adkins (1980a) for descriptions of abalone spawning aggregations and behaviour. Given the relationship between fecundity and size or age, loss of large mature individuals from the population may have disproportionate impacts on population-level fecundity (Curtis and Zhang 2018). Curtis and Zhang (2018) estimated that despite recent increases in abalone population size in some parts of BC, overall egg production had declined approximately 28% between 1990 and 2012 (ECHG survey region) due to a smaller proportion of large individuals.

2.5 MORTALITY RATE AND SIZE-SPECIFIC CRYPTIC PROBABILITIES

Size-specific cryptic probabilities are used to estimate the total number of abalone based on the observed number of emergent abalone, as part of the mortality rate estimation process. Total instantaneous annual mortality rates are only estimated for abalone in the CC and ECHG survey regions (Figure 1), as stock-recruitment relationships are only available for these two regions (Zhang et al. 2007). Total instantaneous annual mortality rates are estimated using shell lengths collected during index site surveys that occurred after the closure of the fishery in 1990. However, these surveys focus on emergent abalone, so an estimate of the cryptic portion of the population in the surveyed transects is necessary, particularly as juvenile (≥ 20 mm to < 70 mm) and adult (≥ 70 mm) abalone exhibit different cryptic behaviours (Sloan and Breen 1988; Cripps and Campbell 1998). Indeed, abalone generally undergo an ontogenetic shift in habitat use and cryptic behavior that is likely associated with their declining vulnerability to predation with increasing size (Sloan and Breen 1988; Lessard et al. 2007b; Zhang et al. 2007; Griffiths and Gosselin 2008). Mature abalone (≥ 70 mm) tend to occupy exposed rock surfaces, whereas juveniles (≥ 20 mm to < 70 mm) are more commonly found in cryptic habitats such as crevices or the undersides of rocks (Sloan and Breen 1988; Cripps and Campbell 1998). Methods for estimating size-specific cryptic probabilities are in Appendix A.

For the ECHG survey region, the probability of being cryptic declined with shell length, with smaller abalone being more cryptic than larger abalone (Figure 6). This finding is consistent with previous models (Lessard et al. 2007b; Zhang et al. 2007) and observations of abalone behaviour (Sloan and Breen 1988; Cripps and Campbell 1998). The posterior means for the α and β model parameters (see Equation A.2, Appendix A) were estimated as 1.973 (95% credible interval 1.244 to 2.726) and -0.070 mm⁻¹ (95% credible interval -0.089 to -0.052 mm⁻¹), respectively.

For the CC survey region, the probability of being cryptic also declined with shell length, but the model did not fit the data well, likely because the observations came from index sites both with and without Sea Otters present (Figure 6). The posterior mean α and β parameters were estimated as 0.790 (95% credible interval 0.380 to 1.210) and -0.026 mm⁻¹ (95% credible interval -0.035 to -0.018 mm⁻¹).

The cryptic behaviour of abalone appears to be affected by Sea Otters (Campbell 1996; Watson 2000; Lee et al. 2016). Therefore, Sea Otter occupancy (presence/absence over time) was estimated for every index site in the index site surveys (see Appendix B for methods). Spring/summer Sea Otter rafts are present in portions of the CC survey region, but are absent from the ECHG survey region. The index sites with cryptic abalone observations in the CC survey region were divided based on the presence/absence of Sea Otters at each index site and reanalyzed for abalone shell lengths between 10 mm and 90 mm. For areas without Sea Otters in the CC survey region, the probability of being cryptic declined with increasing shell length (Figure 6), similar to the ECHG survey region (Figure 6). The posterior mean α and β model parameters for these Sea Otter-free areas were estimated as 1.570 (95% credible interval 0.881 to 2.288) and -0.042 mm⁻¹ (95% credible interval -0.057 to -0.028 mm⁻¹). For areas with Sea Otters present in the CC survey region, the probability of being cryptic did not decline with increasing shell length, meaning larger abalone were more likely to be cryptic in the presence of Sea Otters than in their absence (Figure 6). This result is consistent with other observations of abalone in areas where Sea Otters are present (Watson 1993, 2000; Lee et al. 2016). The posterior mean α and β parameters in Sea Otter occupied areas in CC were estimated as -0.351 (95% credible interval -0.974 to 0.252) and 0.004 mm⁻¹ (95% credible interval -0.011 to 0.018 mm⁻¹).

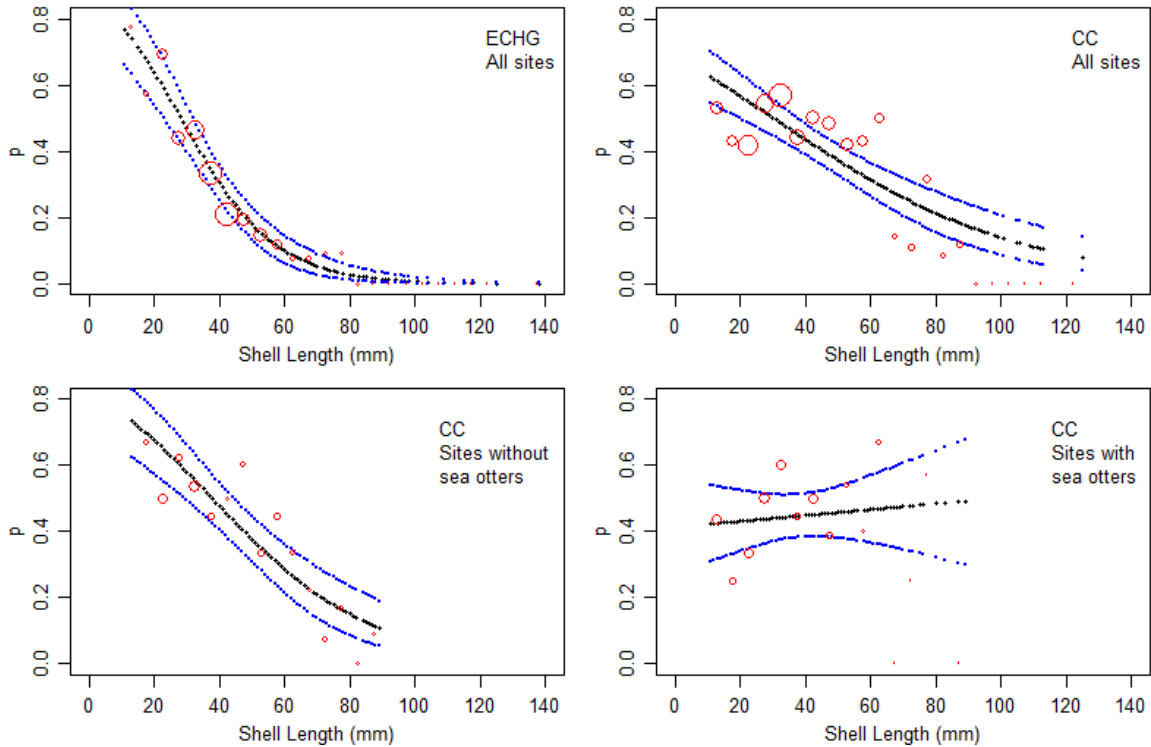


Figure 6. Size-specific probability of a Northern Abalone in the East Coast Haida Gwaii (ECHG) or Central Coast (CC) survey regions being cryptic, based on shell length (mm). Size-specific probabilities at CC index sites with and without Sea Otters present are based on a restricted data set (shell lengths 10-90 mm). Data are from the 2016 and 2017 Northern Abalone Index Site Surveys. Red circles are observed data and the size of the circle represents the sample size.

Based on the size-specific cryptic probabilities and the stock-recruitment models of Zhang et al. (2007), the total instantaneous annual mortality rate for the ECHG survey region (1990-2017) was estimated to be $0.50 \pm 0.04 \text{ y}^{-1}$ (\pm sd, Figure 7). The total instantaneous annual mortality rate for the period 1990 to 2012 was estimated at $0.28 \pm 0.02 \text{ y}^{-1}$ (\pm sd, Figure 7) and at $0.60 \pm 0.05 \text{ y}^{-1}$ for 2012 to 2017 (\pm sd, Figure 7). The particularly high total instantaneous annual mortality rate in recent years appears to be due to the lack of increase in adult abalone in the ECHG survey region, relative to the large increases in the density of juvenile abalone. The total instantaneous annual mortality rate for the CC survey region (1993-2016) was estimated at $0.20 \pm 0.02 \text{ y}^{-1}$ in areas where Sea Otters were absent (Figure 8) and at $0.42 \pm 0.07 \text{ y}^{-1}$ in areas where Sea Otters were present (Figure 8). However, it is difficult to separate the specific contributions of Sea Otter predation (see Section 8.4), illegal harvest (see Section 8.2) or other sources to total instantaneous annual mortality, and to understand precisely why the increased density of abalone juveniles in recent years is not translating into recruitment into the adult stage at the same proportion as in the past (see Sections 2.6 and 5.1).

Abalone densities vary substantially within the survey regions. Observed means are highly imprecise in each year (coefficient of variation ≥ 1.0 for 58% of the year-survey region combinations, Hansen et al. 2020). Additionally, the Sea Otter occupation time based on presence/absence of at least three Sea Otters during summer, may not be a good measure of Sea Otter predation effects on abalone. It cannot account for the difference between a large raft of Sea Otters foraging in an area versus a small raft, or for different amounts of time spent foraging at the index

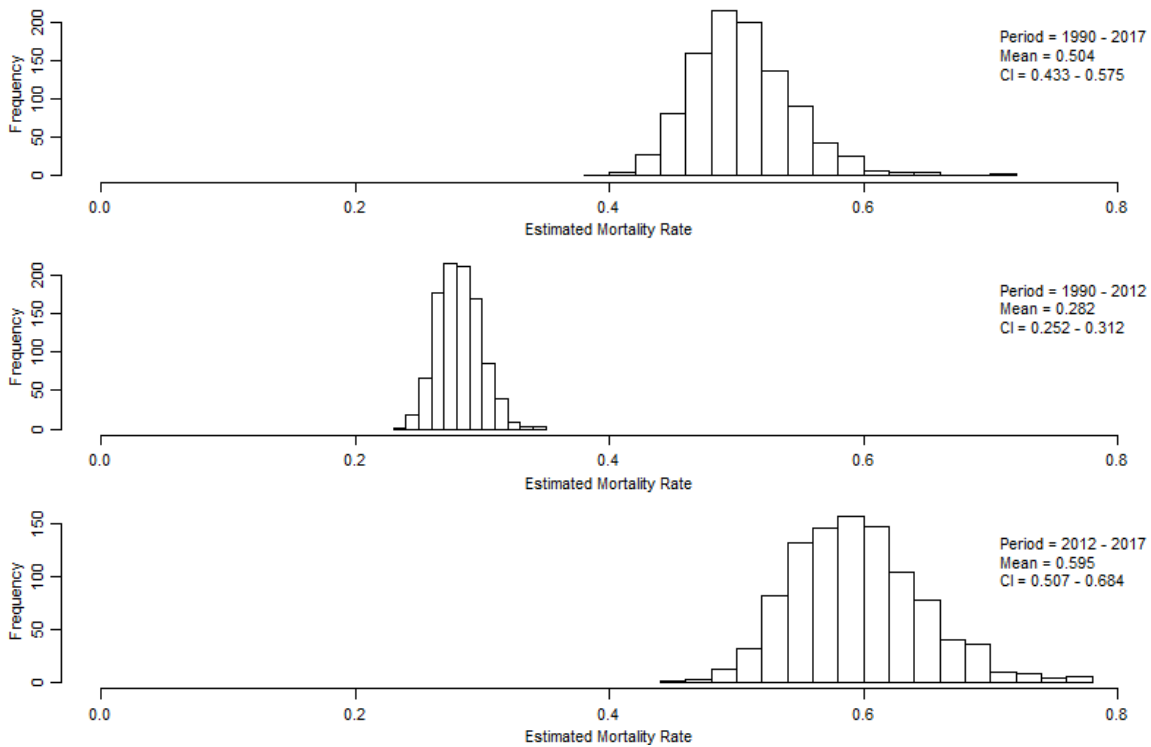


Figure 7. Bootstrapped estimated total instantaneous annual mortality rate (Z ; y^{-1}) for Northern Abalone in the East Coast Haida Gwaii (ECHG) survey region between 1990 and 2017, based on densities of individuals > 70 mm. The top panel includes data from 1990-2017, while the middle and bottom panels include only data from 1990-2012 and 2012-2017, respectively.

site, which may have different impacts on abalone density. The present analyses also do not include the abundance of other Sea Otter prey at the index sites, such as sea urchins, which may contribute to variation in predation pressure on abalone between the index sites.

Annual mortality rates estimated by Zhang et al. (2007) for abalone in the ECHG (1990-2002) and CC (1993-2001) survey regions were $0.29 \pm 0.05 y^{-1}$ ($\pm se$) and $0.36 \pm 0.07 y^{-1}$, respectively. Curtis and Zhang (2018) estimated the instantaneous annual mortality rates to be $0.25 \pm 0.02 y^{-1}$ for the ECHG (1990-2012) and $0.30 \pm 0.02 y^{-1}$ for the CC (1993-2016). These estimates are lower than the present estimates for the ECHG survey region and the CC survey region in areas with Sea Otters present, but higher than the estimate for the CC survey region in areas where Sea Otters are absent. Breen (1986) estimated instantaneous total mortality in areas where there was no commercial fishery at $0.15-0.20 y^{-1}$, but at $0.21-0.41 y^{-1}$ in areas where the commercial fishery was operating. All estimates here, except for the areas of the CC survey region where Sea Otters were absent, are within the range or higher than those estimated for areas where the commercial fishery was operating. The increases in total instantaneous annual mortality rates appear to result from the large increases in juvenile abalone densities in 2016/2017 that are not reflected in adult densities (Figures 11-12).

2.6 RECRUITMENT

Estimated recruitment models are used for mortality rate estimation. Recruitment is defined here as the rate at which abalone become part of the adult size category (≥ 70 mm). Zhang

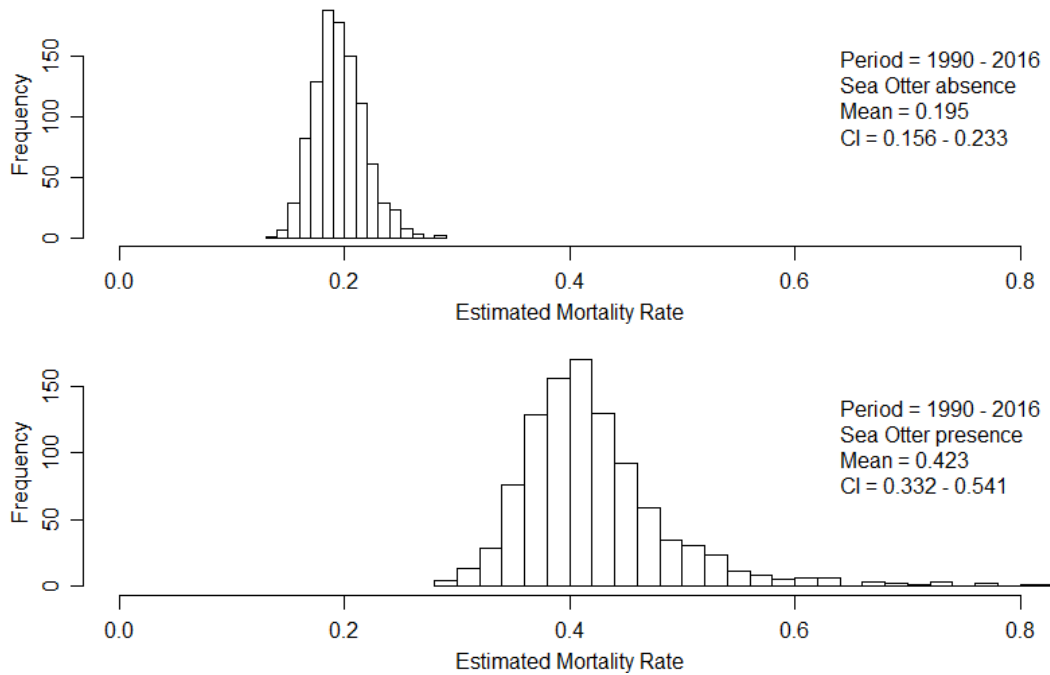


Figure 8. Bootstrapped estimated total instantaneous annual mortality rate ($Z; y^{-1}$) for Northern Abalone in the Central Coast (CC) survey region between 1993 and 2016, based on densities of individuals > 70 mm. The top panel only includes data from index sites where Sea Otters were absent in 2016, while the bottom panel only includes data from index sites where Sea Otters were present in 2016.

et al. (2007) fitted stock-recruitment curves for the ECHG and CC survey regions, using data from 1990 to 2002. These fitted stock-recruitment curves were relatively flat and linear, with recruitment decreasing or increasing almost proportionally with decreasing or increasing stock size, such that the ratio of recruitment to stock size did not change appreciably when stock size changes. This relatively fixed ratio is indicative of a lack of compensation or depensation at low spawning densities $< 0.05 \text{ kg/m}^2$ (i.e. a disproportionate increase or decrease in the number of recruits at low spawning biomass was not detected). Recruitment varied considerably with spawning stock biomass (Zhang et al. 2007). Recent recruitment rates for abalone are not available. However, large increases in the density of juvenile abalone (≥ 20 mm to < 70 mm) have been observed in all areas of Northern BC (CC, ECHG, WCHG survey regions) starting in the late 2000s (Curtis and Zhang 2018, Figures 10-13, Appendix E, Tables E.1-E.3). In contrast, large increases in juvenile density have not been observed in Southern BC (WCVI, QCS, GB survey regions, Curtis and Zhang 2018, Figures 14-15, Appendix E, Tables E.4-E.5). Curtis and Zhang (2018) suggested that the ECHG and CC survey regions may have been experiencing settlement failure (i.e. few larval abalone surviving to the post-settlement stage) prior to 2006/2007 due to the low numbers of small abalone (< 40 mm in shell length) observed in those years. Sloan and Breen (1988) suggested that abalone displayed recruitment failure (where recruitment was defined as individuals reaching the legal size for the fishery i.e. ≥ 100 mm shell length) prior to the intense harvesting in 1976 and that may have been due to poor settlement. Bouma et al. (2012) and Carson and Ulrich (2019) also found low densities of juvenile abalone in recent years in the San Juan Islands in Washington State.

It is difficult to compare these recent estimates to the early years of the index site surveys as the search effort for small abalone increased around 1994 (Curtis and Zhang 2018). Quayle (1971) noted that small abalone were difficult to find for tagging studies, few small abalone were seen in early years, and therefore searches for cryptic abalone were initiated in early years of the index site surveys (P. Breen, Breen Consulting, Wellington, New Zealand, pers. comm., 2018). Breen (1986) also noted the scarcity of juvenile abalone, but Sloan and Breen (1988) found that numbers of small abalone varied with habitat type and some locations had high numbers of small abalone. Since abalone are broadcast spawners (Breen and Adkins 1980b), recruitment at an index site may be influenced by connectivity to other abalone aggregations and broader oceanographic conditions in the region rather than local drivers. McShane (1995) reviewed the literature on stock-recruitment relationships for various abalone species and reported that spawner abundance contributed little to the variation in recruitment.

3 GENETIC DESCRIPTION

Few published studies on the genetic population structure of Northern Abalone exist. Withler et al. (2003) examined 8 polymorphic microsatellite loci for Northern Abalone from 31 sites in BC and one site in southeastern Alaska. Among these sites, 99.6% of the genetic variation existed within the sites and only 0.4% between sites, indicating little geographic structure and differentiation among the sites. The results suggest extensive gene flow among Northern Abalone spawning aggregations and support that historically these Northern Abalone sites were not isolated populations, and that the low abundance of mature Northern Abalone was not restricting gene flow at that time. Withler et al. (2003) estimated a mean effective population size of 370,000 Northern Abalone based on the high values of heterozygosity observed in the samples (mean H_e = 0.92, range of 0.88-0.97). Effective population size is defined as the number of individuals in a population who contribute offspring to the next generation.

Recently, comparison of Single Nucleotide Polymorphisms (SNPs) has been used to look at differentiation in two abalone species, *H. rufescens* and *H. fulgens* (De Wit and Palumbi 2013; Gruenthal et al. 2014). A similar approach was applied to Northern Abalone tissue samples collected in BC (J. Supernault and R. Withler, DFO Science, Nanaimo, British Columbia, pers. comm., 2019) as part of a collaborative study of Northern Abalone genetics involving several Abalone Recovery Implementation Group (AbRIG) member groups. A total of 119 species-specific SNPs in Northern Abalone were chosen for development and preliminary genotyping based on the work of Timmins-Schiffman et al. (2013). Of these 119 SNPs, only 77 met the criteria for further analysis, including SNPs of both mitochondrial and nuclear genes. Tissue samples collected from four areas in the ECHG survey region (specifically Selwyn Inlet, Tanu Island, Upper Juan Perez, and Lower Juan Perez, Figure 1) were compared with 95 historical DNA samples from Northern Abalone individuals in Barkley Sound (west coast Vancouver Island), previously analyzed in Withler et al. (2001) and Withler et al. (2003). These two regions were expected to show the greatest difference based on microsatellite analysis by Withler et al. (2003). Analysis of the 77 SNPs revealed no difference in allele frequencies between the two regions, nor among three smaller sampling areas (i.e. Selwyn Inlet, Tanu Island, Upper Juan Perez) within Haida Gwaii.

These results are consistent with earlier findings (Withler et al. 2003) for microsatellite data, and similar genetic analysis of some other abalone species (De Wit and Palumbi 2013; Gruenthal et al. 2014). Studies from southern Australia and California provide evidence for varied spatial scales of population structure among abalone species (e.g., Brown and Murray 1992; Burton

and Tegner 2000; Hamm and Burton 2000; Hancock 2000; Huang et al. 2000). Several species, including Northern Abalone, show genetic similarity over large areas (Brown and Murray 1992; Burton and Tegner 2000; Withler et al. 2003).

At present, the collaborative study of BC Northern Abalone genetics is proceeding by comparing the results from ECHG survey region and Barkley Sound to samples collected in the northern Strait of Georgia in 2019 (GB survey region, Figure 1).

Implementation of genomic techniques has enabled the identification of SNPs associated with adaptive differentiation in other abalone species (De Wit and Palumbi 2013; Sandoval-Castillo et al. 2018). Similarly, population structure based on local adaptation to environmental conditions may exist in Northern Abalone and, if so, may be detected by screening SNPs associated with the adaptive gene sequences. The genomic information presently available for Northern Abalone is insufficient for identification of adaptive SNPs, thus ongoing research being led by DFO is focused on sequencing the entire Northern Abalone genome and subsequently screening the sequence for SNPs associated with local adaptation (J. Supernault and R. Withler, DFO Science, Nanaimo, British Columbia, pers. comm., 2019). Application of a set of suitable SNPs to Northern Abalone samples collected throughout BC would be expected to reveal more fine-scale geographic variation within the species, if it exists.

Although the trends and magnitude of the estimated Northern Abalone densities differ between Northern and Southern BC (Curtis and Zhang 2018, Section 5.1), the present genetic studies show no evidence for more than one population of Northern Abalone in BC.

4 DISTRIBUTION

Northern Abalone exist exclusively on the west coast of North America; the current known range extends from Bahía Tortugas, Baja California, north to Salisbury Sound, Alaska (Neuman et al. 2018, Figure 9). Adults generally occupy exposed and semi-exposed coastal waters of less than 10 m depth, but have been observed from the low intertidal zone to 40 m depth (Sloan and Breen 1988; Neuman et al. 2018).

Historically, Northern Abalone have been categorized into two subspecies, but the existence of subspecies is currently debated due to considerable range overlap and a lack of genetic differentiation (see Neuman et al. 2018). The northern subspecies, *Haliotis kamtschatkana kamtschatkana*, occupies the majority of the species' total range, from Alaska to Point Conception in California. The less abundant southern subspecies, *Haliotis kamtschatkana assimilis*, or Threaded Abalone, is found only in central California and south to Bahía Tortugas (Geiger 2000). Northern Abalone in the southern portion of the range are often found in deeper subtidal habitat (12-40 m) than those in the north (Geiger and Owen 2012).

4.1 CANADIAN DISTRIBUTION

Northern Abalone in Canada are found solely in the waters of BC (Figure 9), and with the very rare exception of Red Abalone (*H. rufescens*) individuals and unverified reports of Flat Abalone (*H. walallensis*), they are generally considered to be the only species of abalone present in BC (Campbell et al. 2010). Overall spatial distribution of Northern Abalone in Canada has remained largely unchanged in recent decades. Northern Abalone can occur anywhere appropriate habitat is present, which is not considered to be a limiting factor to Canadian populations (Lessard and Campbell 2007). Certain areas of the coast, such as the Georgia Basin, support only sparse



Figure 9. Global distribution (orange line) of Northern Abalone.

populations of Northern Abalone, and remain relatively inhospitable to Northern Abalone due to low salinity (Thompson 1914).

The last estimate for extent of occurrence of Northern Abalone in Canada was 207,478 km², but this was based on a coarse scale polygon of the coast that included land and other areas known to be uninhabitable for Northern Abalone (COSEWIC 2009). A knowledge-based habitat suitability index (HSI) model was recently developed to predict the probability of occurrence for Northern Abalone in the North Central Coast area (Nephtin et al. 2020). This model was extrapolated to the rest of the BC coast generating a new estimate of 6,985 km² for the extent of occurrence of Northern Abalone in BC waters (see methods in Appendix C). The considerably lower estimate is due to the incorporation of higher quality bathymetric and environmental data. In other words, the decline in estimated extent of occurrence does not reflect a change in possible abalone habitat, but rather an improvement in the method of estimating that habitat. For example, land and deep waters are no longer included in the estimate of extent of occurrence, making the new estimate far more realistic. The projected area of occupancy is currently unknown. Density estimates obtained from the index site surveys cannot be extrapolated to the entire coast of BC, as these surveys are restricted to only medium and high quality Northern Abalone habitat and do not represent a random selection of all available habitat (DFO 2016).

5 POPULATION TRENDS

5.1 NORTHERN ABALONE INDEX SITE SURVEYS

The index site surveys are the longest DFO time series available to estimate trends in abalone densities in BC (1978-present, e.g., Lessard et al. 2007b; Curtis and Zhang 2018). Surveys began in the ECHG and CC survey regions in 1978 and in the 2000s in all other survey regions. Johnstone Strait was surveyed in 1986 (2 locations, Adkins 1996) and in 2004 (36 locations, Davies et al. 2006), but is not included here as these sites contained limited abalone habitat (Lessard and Egli 2011) and are no longer surveyed as part of the index site surveys. DFO (2016) details the Breen Survey Method used in the index site surveys, which samples 16 quadrats (1 m x 1 m) at each index site. Emergent abalone, those that can be seen without overturning rocks, are counted and measured (shell length in mm) in all quadrats. Emergent abalone are also referred to as exposed in other DFO publications (e.g., DFO 2016).

The count of emergent abalone at each index site was binned into four size categories based on shell length (mm): (1) total abalone (≥ 20 mm); (2) juvenile abalone (≥ 20 mm to < 70 mm); (3) adult abalone (≥ 70 mm); and (4) large adult abalone (≥ 100 mm). The large adult category is a subset of the adult category and is an artefact of earlier studies in which it represented those individuals that had recruited to the fishery (minimum legal size during the legal fishery was 100 mm shell length). One hundred percent of abalone are sexually mature at 70 mm (Quayle 1971; Campbell et al. 1992, 2003). Total abalone counts do not include individuals smaller than 20 mm due to changes in diver search behaviour over the time series and lower detectability of very small abalone (Campbell 2000; Curtis and Zhang 2018). Lessard et al. (2007b) and Zhang et al. (2007) found that abalone less than 20 mm had a high probability of being cryptic (close to 100%), whereas recent surveys in the CC (2016) and ECHG (2017) survey regions had slightly lower probabilities of cryptic (70-80%) for this size category (see Section 2.5). Campbell (2000) did not include juveniles in density estimates (other than a total of all sizes measured) due to the difficulty of finding small abalone and because early surveys are thought to have underestimated juvenile densities since they did not conduct searches for cryptic abalone (Sloan and Breen 1988). Thus, care must be taken when interpreting trends in juvenile abundance as methods

of searching for the smallest abalone were not consistent until about 2004 (Curtis and Zhang 2018).

Counts by size category were converted into densities (Abalone/m²) by dividing by the number of quadrats (1 m²) sampled at each index site. These densities were corrected for differences between the number of emergent abalone observed in the quadrats and the number of abalone measured, based on Lessard et al. (2007a). The count of emergent abalone included both those that were measured and those that were emergent, but unable to be measured. In recent years, an increased percentage of emergent abalone could not be measured (0.09% ± 0.23% (± sd) during 1978-2005 and 2.80% ± 3.37% during 2006-2018). Trends in densities are presented instead of total numbers as the area of occupancy for abalone in BC is unknown (Section 4.1) and densities cannot be extrapolated over the total habitat in BC, since only abalone habitat of medium to high quality is surveyed (DFO 2016). Corrections to the densities for changes in survey protocols over time, and the list of excluded index sites (missing data or part of one-off surveys) are detailed in Hansen et al. (2020). Further details on the survey design, methods and data collected can be found in DFO (2016), Curtis and Zhang (2018), and Hansen et al. (2020), with adjustments to the survey methods detailed in the survey reports (see Table 1 summary in Hansen et al. 2020).

An attempt was made to integrate the data from all the survey regions into one abundance index, as the current genetic analyses indicate only a single population of abalone in BC (Section 3). However, the data were subsequently grouped into a Northern BC dataset (CC, ECHG, WCHG) and a Southern BC dataset (WCVI, QCS, GB), since mean densities in these regions were similar over time and the means were highly imprecise in each year (coefficient of variation ≥ 1.0 for 58% of the year-survey region combinations, Hansen et al. 2020). Additionally, the number of index sites surveyed has changed over time. These changes were greatest in the CC and ECHG survey regions (see Appendix E and Table 1 in Hansen et al. 2020). For example, 76 sites were surveyed in the CC survey region in 2016, but only 12 index sites were surveyed at the start of the time series in 1978. However, the overall trend in total abalone densities (≥ 20 mm) across index sites from all survey regions was similar between the full set of index sites and a restricted set, where only those index sites that were surveyed in most years were included for each survey region (Hansen et al. 2020). The greatest difference in mean densities between the full and restricted set of index sites occurred in the early years of the Northern BC time series (1978-1980) (Hansen et al. 2020). The restricted set of index sites showed a decline in mean density that was delayed in the full set of index sites, indicating that the decline in total abalone density in the early years may have been masked by the changing number of index sites in the CC and ECHG survey regions during 1978-1980. Analyses in this report include the full set of index sites, as the restricted set had a smaller sample size, which further increased variability around the mean densities (Hansen et al. 2020).

The Northern BC dataset and Southern BC dataset were analyzed using generalized additive modelling (GAM) to identify environmental variables that could be used in standardizing the time series (Hansen et al. 2020). Standardization using covariates is applied to attempt to remove the impact of these sources of variability on the index of abundance (Maunder and Punt 2004). However, for the Northern BC and Southern BC datasets, the majority of the deviance explained in the GAM models was explained by the year term (76-92% for the Northern BC survey regions and 40-73% for the Southern BC survey regions). The year term in the GAMs was a combination of the effect of year and region due to the grouping of survey regions in Northern BC and Southern BC. For the grouped Southern BC survey regions, the standardized densities changed greatly year to year as the region surveyed changed. Although the standardized densities for

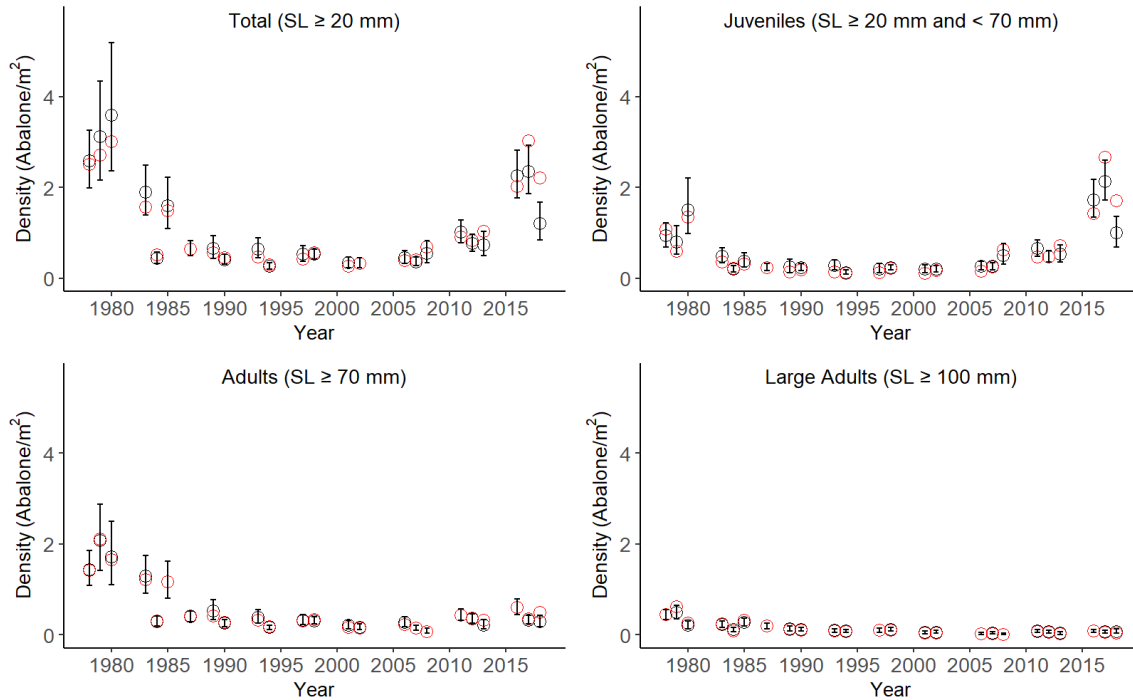


Figure 10. Posterior mean Northern Abalone densities and 95% credible intervals based on index site data from the pooled Northern BC survey regions: Central Coast (CC), East Coast Haida Gwaii (ECHG) and West Coast Haida Gwaii (WCHG) from 1978 to 2018. Northern Abalone observations were grouped into the four size categories based on shell length (SL). Black circles represent posterior means while red circles represent observed means. Note that here the differences in mean density between years are a combination of the effect of year and the effect of survey region, as index site data were only collected in one survey region per year, except in 1978 and 1979.

the grouped Northern BC survey regions also changed year to year as the region surveyed changed, the variation among the three Northern BC regions in recent years (i.e. 2016-2018) was generally less than the difference with the previous period the three regions were surveyed (i.e. 2011-2013).

A Bayesian hurdle model, including environmental covariates, was used to estimate the annual posterior mean abalone densities and 95% credible intervals. The significant environmental variables from the best-fitting GAM model for each size category from each of the Northern BC and Southern BC datasets were included in their respective Bayesian hurdle model (see Appendix D for methods). The estimated mean densities from this standardized hurdle model cannot be directly compared to the mean densities of the Population and Distribution Objectives in the DFO Northern Abalone Species at Risk Action Plan (DFO 2012). The time series for the grouped Northern BC survey regions is included here along with time series for each of the survey regions (i.e. CC, ECHG, WCHG, QCS, and WCVI). As no sites were repeated in any of the GB surveys that used the Breen Survey Method (1982, 1985, 2005, 2009), a time series is not produced for this survey region and observed densities are presented instead.

The trends in posterior mean abalone densities were similar across all the survey regions in Northern BC (CC, ECHG, WCHG), with a decline in estimated mean total densities (≥ 20 mm shell length) during the 1970s and 1980s, followed by a period of low estimated mean total densities until the late 2000s, when estimated mean total densities began to increase (Figures 10-13).

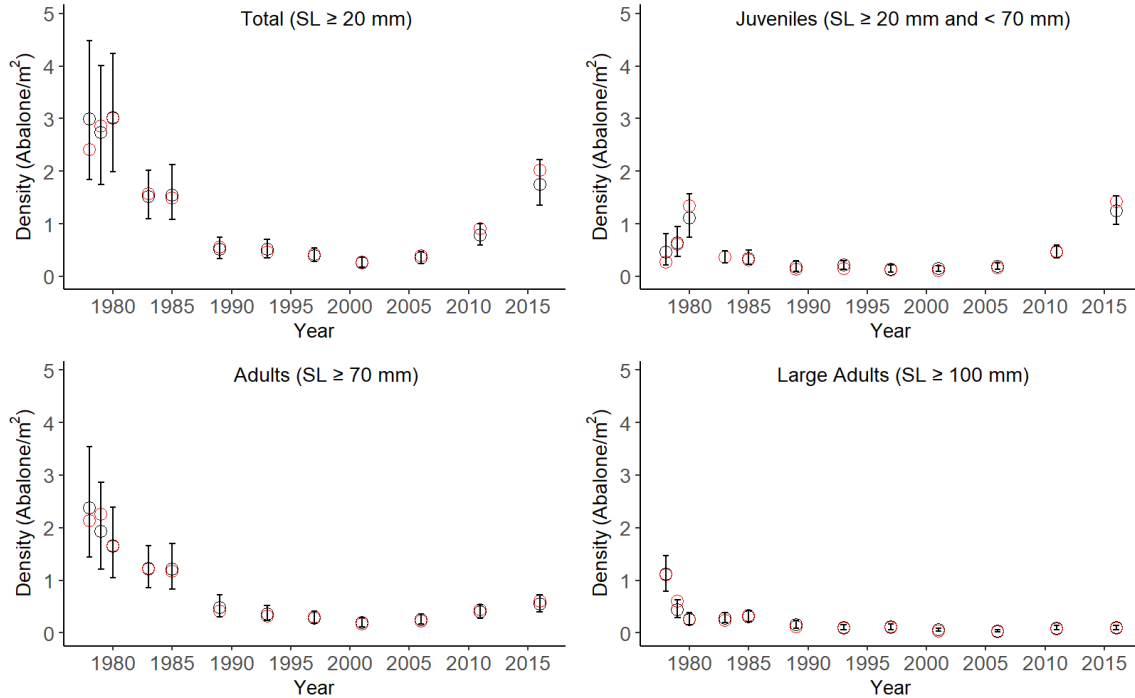


Figure 11. Posterior mean Northern Abalone densities and 95% credible intervals based on index site data from the Central Coast survey region (CC) for 1978 to 2016. Northern Abalone observations were grouped into the four size categories based on shell length (SL). Black circles represent posterior means while red circles represent observed means.

The commercial fishery for abalone operated in BC from the early 1900s and landings peaked in the 1970s (Breen 1986; Sloan and Breen 1988; Campbell 2000). Concern over large declines in the surveyed densities of abalone culminated in a total closure of all fisheries in 1990 (Farlinger 1990; Campbell 2000). The history of the abalone commercial fishery and management are described in Sloan and Breen (1988), Farlinger (1990), and Farlinger and Campbell (1992). The recent increase in estimated mean total abalone densities was driven primarily by an increase in the estimated mean densities of juvenile abalone (≥ 20 mm to < 70 mm shell length), with small increases in estimated mean adult densities, and little to no increase in estimated mean large adult densities in the survey regions (Figures 10-13).

There is a high level of variability in the estimated mean densities at the index sites within the survey regions. This is particularly apparent for the estimated mean densities early in the time series, where the number of index sites sampled was small (Figures 11-15, Appendix E, Tables E.1-E.5). Curtis and Zhang (2018) found that density trends vary across areas within the survey regions, with some areas showing larger or smaller increases in estimated mean adult densities than the average (e.g., Oswald Bay versus Stryker Island in the CC survey region). The overall trends are generally consistent at the level of the survey region and across all of Northern BC.

For the ECHG survey region, the 2017 estimated mean density for the total abalone size category (≥ 20 mm shell length) was slightly lower than the 1978 estimated mean total abalone density, but the credible intervals overlap. For the CC survey region, the 2016 estimated mean total abalone density was lower than the 1978 estimated mean total abalone density, but not

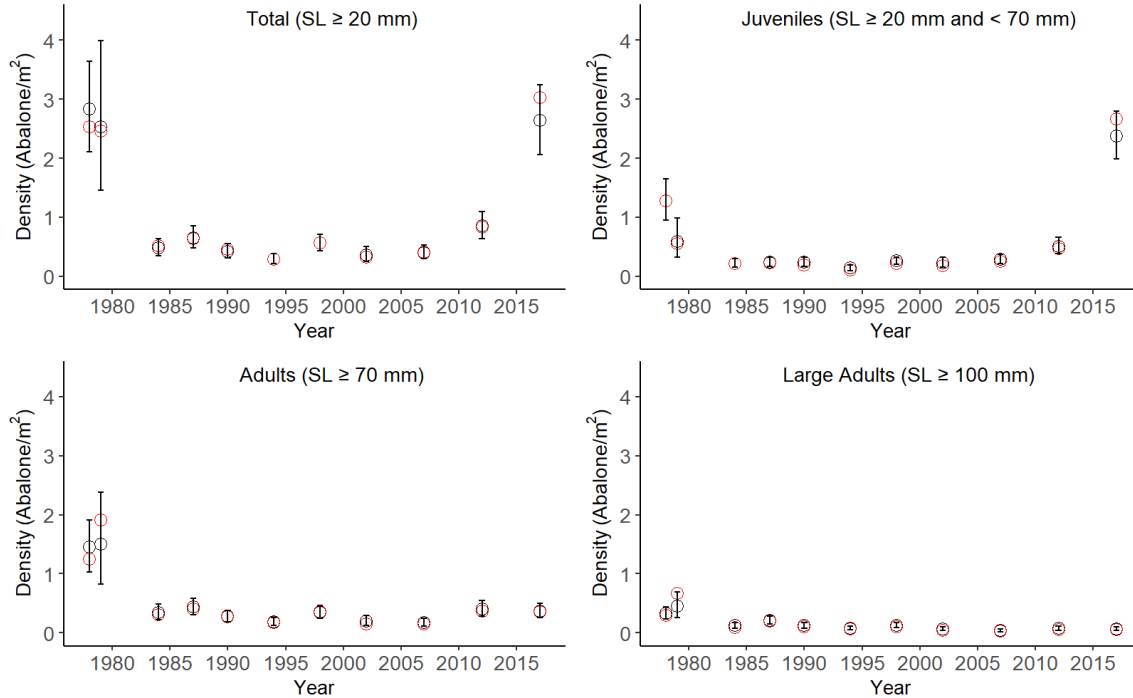


Figure 12. Posterior mean Northern Abalone densities and 95% credible intervals based on index site data from the East Coast Haida Gwaii survey region (ECHG) for 1978 to 2017. Northern Abalone observations were grouped into the four size categories based on shell length (SL). Black circles represent posterior means while red circles represent observed means.

significantly so since the credible intervals overlap. For adult abalone (≥ 70 mm), the 2016/2017 density estimates were significantly ($\alpha = 0.05$) lower than the early estimates for the ECHG and CC survey regions. Based on the 95% credible intervals, there is at least a 95% probability that the 2016 estimated mean adult density for CC is lower than the 1978 estimated mean adult density (the start of the time series). For the ECHG, there is also at least a 95% probability that the 2017 estimated mean adult density is lower than the 1978 estimated mean adult density. For the WCHG region, estimated mean densities for the total, juvenile, and adult size categories increased over the time series (2008-2018, $> 95\%$ probability).

Mean shell length (mm) for the total size category (≥ 20 mm shell length) decreased over the time series for the ECHG survey region, with a noticeable decrease in the proportion of the largest abalone and an increase in the juvenile size category in the 2000s, compared to earlier years (Hankewich et al. 2008; Curtis and Zhang 2018, Appendix F, Figure F.2). Mean shell length (\pm se) for the total size category for surveys in 1978-1987 was 74.9 ± 0.4 mm and 54.1 ± 0.3 mm for surveys in 2002-2017. The maximum shell length observed decreased from 146 mm to 138 mm between these two survey periods. The mean shell length of the adult size category also decreased from 93.0 ± 0.3 mm (\pm se) in 1978-1987 to 86.2 ± 0.4 mm in 2002-2017. A similar pattern exists for the CC survey region, with the distribution of adult sizes shifting to smaller sizes over time (Hankewich and Lessard 2008; Curtis and Zhang 2018, Appendix F, Figure F.1). Mean shell length (\pm se) for the total size category for surveys between 1978-1989 was 80.3 ± 0.3 mm and 61.9 ± 0.4 mm for surveys between 2001-2016. The maximum shell length observed decreased from 149 mm to 132 mm between these two survey periods, and it was also noted by Curtis and Zhang (2018), that max shell length has remained low since the

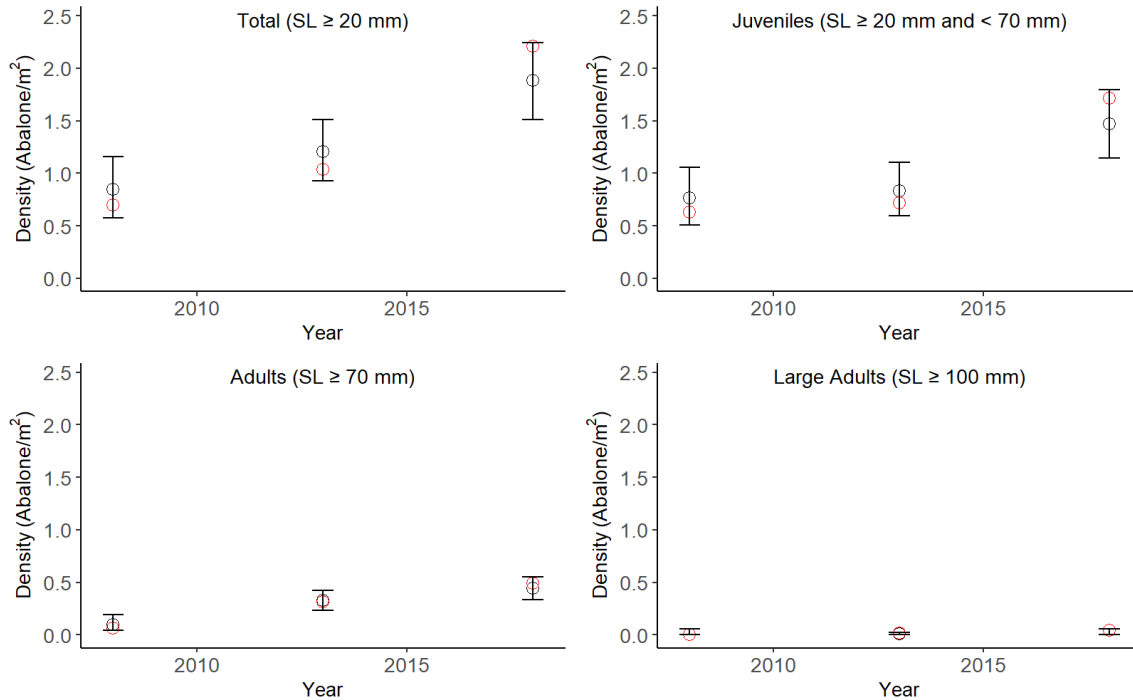


Figure 13. Posterior mean Northern Abalone densities and 95% credible intervals based on index site data from the West Coast Haida Gwaii survey region (WCHG) for 2008 to 2018. Northern Abalone observations were grouped into the four size categories based on shell length (SL). Black circles represent posterior means while red circles represent observed means.

large decline during the commercial fishery (Hankewich and Lessard 2008). The mean shell length of the adult size category also decreased from 91.0 ± 0.3 mm (\pm se) in 1978-1989 to 86.8 ± 0.3 mm in 2001-2016. For the WCHG survey region, the mean shell length is lower than the size at 100% maturity (70 mm), and as with other regions in Northern BC, there are relatively high proportions of juvenile abalone observed (Appendix F, Figure F.3). The WCHG survey region has few large abalone, likely due to the higher wave exposure in this region, which is negatively correlated with shell length in abalone (Lessard and Campbell 2007).

For the shorter time series in the Southern BC survey regions (QCS and WCVI), the trends were less clear due to much lower estimated mean abalone densities and high variability in the observed densities at the index sites (Figures 14-15). For both the QCS and WCVI survey regions, there was an increase in the estimated mean densities of the total, juvenile and adult size categories of abalone between the first year of the surveys and the last year in each region (2004 to 2014 for QCS and 2003 to 2018 for WCVI, Figures 14-15). However, the 95% credible intervals overlapped for all these estimates, meaning the probability that the true densities were different was less than 95%. Mean estimated densities of large adults in the QCS survey region did show an increase over the time series, but did not for the WCVI survey region, and again the 95% credible intervals overlapped for these years. Size-frequency data were sparse for these survey regions (Appendix F, Figures F.4-F.5). The proportion of large abalone (≥ 100 mm) was low in both regions, but larger abalone were noticeably absent from the WCVI survey region, where Sea Otters, an abalone predator (Watson 2000), have been present at the index sites for up to 42 years in some areas (Appendix B), as predicted by Hankewich and Lessard (2008).

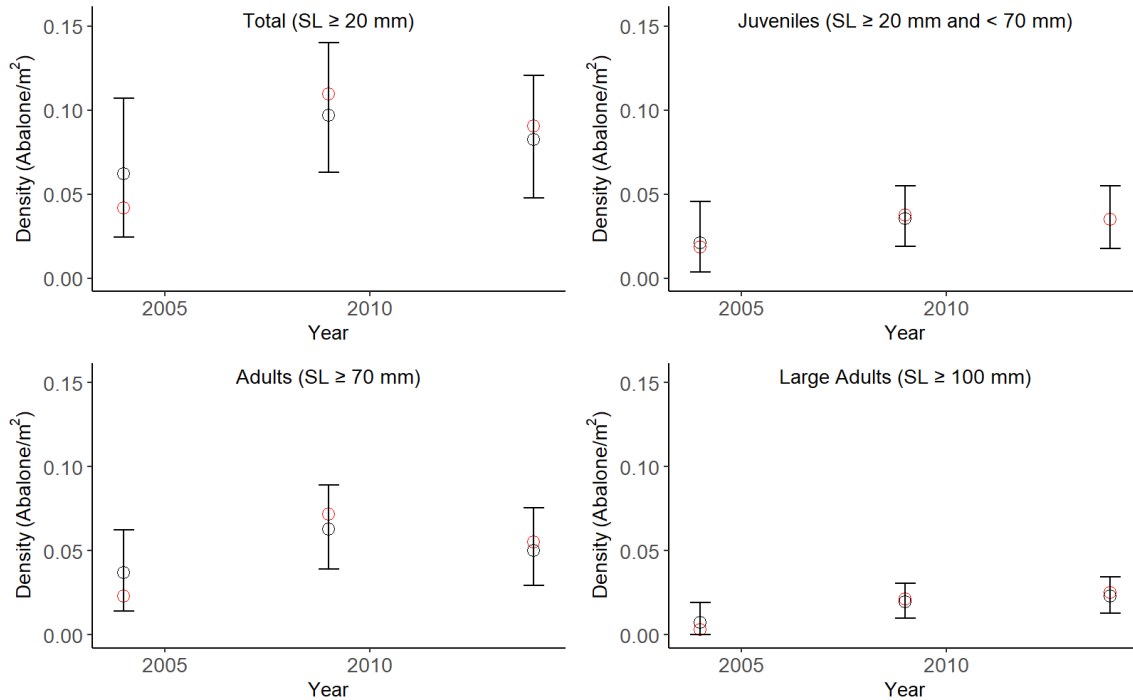


Figure 14. Posterior mean Northern Abalone densities and 95% credible intervals based on index site data from the Queen Charlotte Strait survey region (QCS) for 2004 to 2014. Northern Abalone observations were grouped into the four size categories based on shell length (SL). Black circles represent posterior means while red circles represent observed means.

Too few overlapping surveys using the Breen Survey Method were available for the GB survey region to estimate density trends using the Bayesian hurdle model. No sites were repeated in this region until 2019. In 1982, a mean density of 0.73 ± 0.91 Abalone/m² (\pm sd) was found at three sites in the southeast area of Vancouver Island (Adkins 1996). In 1985, 12 sites in the southeast area of Vancouver Island were surveyed and the mean (\pm se) total abalone (≥ 20 mm shell length) density was 1.165 ± 0.198 Abalone/m², while mean (\pm se) density for juveniles, adults, and large adults were 0.090 ± 0.034 Abalone/m², 1.075 ± 0.180 Abalone/m², and 0.655 ± 0.108 Abalone/m², respectively. In 2005, 19 sites in the Sooke area were surveyed. Only three abalones were observed on this survey, for a mean (\pm se) total abalone density of 0.010 ± 0.007 Abalone/m². Mean (\pm se) density of juveniles, adults, and large adults were 0.000 ± 0.000 Abalone/m², 0.010 ± 0.007 Abalone/m², and 0.010 ± 0.007 Abalone/m², respectively on this survey. A similar result was found in 2019, with only four abalones observed in the same 19 index sites in the Sooke area. All of these abalones were ≥ 99 mm in shell length (unpublished data). Lessard et al. (2007b) also noted that an aggregation of abalones found in the Sooke area near the William Head prison in 1996/1997 (Wallace 1999) had disappeared by the 2005 survey. Additionally, in 2009, 30 sites in the northern Strait of Georgia were surveyed, with only six abalones present. The total mean (\pm se) density of abalones (≥ 20 mm shell length) was 0.012 ± 0.007 Abalone/m². Mean (\pm se) density of juveniles, adults and large adults were 0.004 ± 0.003 Abalone/m², 0.008 ± 0.007 Abalone/m², and 0.004 ± 0.003 Abalone/m², respectively on this survey. In 2019, 12 abalones (≥ 20 mm shell length) were found in 28 sites in the northern Strait of Georgia, of which four were in the juvenile size category and eight were in the adult size category (size range of 54-112 mm, unpublished data). Similarly, Bouma et al. (2012) and

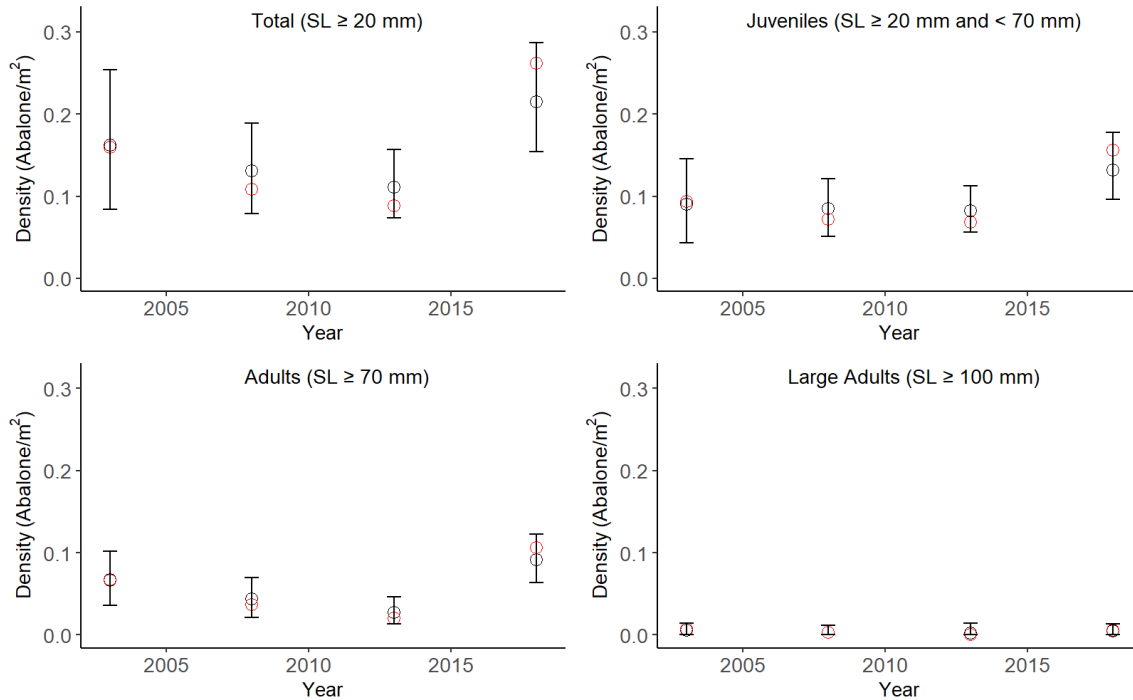


Figure 15. Posterior mean Northern Abalone densities and 95% credible intervals based on index site data from the West Coast Vancouver Island survey region (WCVI) for 2003 to 2018. Northern Abalone observations were grouped into the four size categories based on shell length (SL). Black circles represent posterior means while red circles represent observed means.

Carson and Ulrich (2019) also found low densities of abalone in recent years in the nearby San Juan Islands in Washington State.

There is limited information on abalone abundance in the Southern BC survey regions prior to the initiation of the new index site surveys during the 2000s and densities obtained by other survey methods are not directly comparable to those from the Breen Survey Method. Thompson (1914) is one of the earliest reports on abundance in Southern BC with observations made during a Province-wide intertidal clam survey. Thompson (1914) provided anecdotal evidence that abalone were absent in the Gulf of Georgia, but were dispersed throughout the whole outer coast of BC, including the west coast of Vancouver Island, and at Port Neville in the Johnstone Strait, but not in the inner end or among the passages of Queen Charlotte Sound. As this was an intertidal survey, a significant portion of abalone habitat would have been overlooked. However, trends in landings are also suggestive of fewer abalone in southern BC. While the commercial abalone fishery recorded landings in all of the coastal Pacific Fisheries Management Areas (PFMAs) except for many of the areas in the Strait of Georgia and Sooke area (Sloan and Breen 1988; Curtis and Zhang 2018), landings in Northern BC were generally much higher than those in Southern BC. Indeed, Northern BC was the focus of the intensive fishery in the 1970s (Sloan and Breen 1988). Furthermore, landings in the Georgia Basin made up only $4.32 \pm 1.28\%$ (mean \pm se) of total landings between 1977 and 1990 (landings reported in Table 2.8.2 of Harbo 1997; see also Sloan and Breen 1988). Aggregations have been reported in areas of the GB survey region, such as Nanoose Bay in the Strait of Georgia (Quayle 1971) and William Head in the Sooke region (Wallace 1999), but subsequently, and sometimes rapidly, disappeared (Quayle 1971; Lessard et al. 2007b). Early surveys in Johnstone Strait indicated high densities

up to 10 Abalone/m² in one location, but abalone were scarce at most other locations in 1977 (timed swims, Breen et al. 1978) and only 1.13 Abalone/m² were found in this location in 1986 (Breen Survey Method; Adkins 1996). Breen et al. (1978) also visually estimated densities of 1 Abalone/m² or less, with few juvenile abalone, in Queen Charlotte Strait in 1977. In 2004, Davies et al. (2006) observed only 0.02 Abalone/m² in Johnstone Strait (Breen Survey Method), with almost all individuals at the same location that was surveyed in 1977 and 1986.

5.2 TRANSECT SURVEYS

Transect surveys were conducted near Kitkatla, BC in 2000 and 2016 in areas around Goschen Island, the Prager Islands, and Dolphin Island. The survey areas were selected in consultation with representatives of the Gitxaala Nation, based on Traditional Ecological Knowledge of areas where abalone were most abundant. In October 2000, approximately 100 scouting dives were conducted in the identified areas to find sites that could be suitable for abalone enhancement experiments. Of these, 25 sites with good abalone habitat were selected to be surveyed. The transect survey method (Cripps and Campbell 1998; DFO 2016) was used to survey two transects at each site in 2000 and one transect at each site in 2016 (due to time constraints). Mean abalone density across all transects in each year was based on the density observed on each transect (count of emergent abalone divided by the number of quadrats surveyed). Since shell lengths were only measured at 17 of the 25 sites in 2000 (i.e. size-frequency data available for 17 sites, count data available for 25 sites), only these 17 sites were included when estimating densities by size category in either year. Additionally, only transect number one at each site in 2000 was resurveyed in 2016, so only data from transect one at each site were used to estimate mean abalone density in 2000. The boot package (Davison and Hinkley 1997; Canty and Ripley 2020) in R version 4.0.2 (R Core Team 2020) was used to estimate 95% confidence intervals around the mean densities by size category and year, as well as the overall mean densities (5000 replicates with replacement). Diagnostic plots (histograms and quantile plots) of the bootstrap estimates revealed a normal distribution with some deviation at the tails. Bootstrap CIs were accordingly calculated using the basic (empirical) CI method built into the boot.ci function in the boot package, which is robust to deviations at the tails of the distribution (Canty and Ripley 2020).

Although the differences in methods preclude a direct quantitative comparison of abalone densities in the index site surveys and Transect Surveys, qualitative comparison of trends is possible. Indeed, the transect survey time series shows similar trends to the index site surveys for Northern BC survey regions in recent years, namely an increase in the mean density of total abalone (≥ 20 mm shell length), that is not consistent across all size categories. The largest increase occurred in the juvenile category (≥ 20 mm to < 70 mm shell length), while the adult size category (≥ 70 mm shell length) increased slightly, and the large adult category (≥ 100 mm shell length) declined (Figure 16). These differences in mean densities by size category are reflected by the changing size-frequency detected between the two surveys (Figure 17). In 2000, the survey sites had larger individuals, whereas in 2016 these same sites included few abalone > 100 mm (Figure 17). When all 25 survey sites are included, the count-derived mean density of all abalone observed increased from 0.35 Abalone/m² (95% confidence interval 0.10-0.54 Abalone/m²) in 2000 to 2.27 Abalone/m² (95% confidence interval 1.67-2.83 Abalone/m²) in 2016.

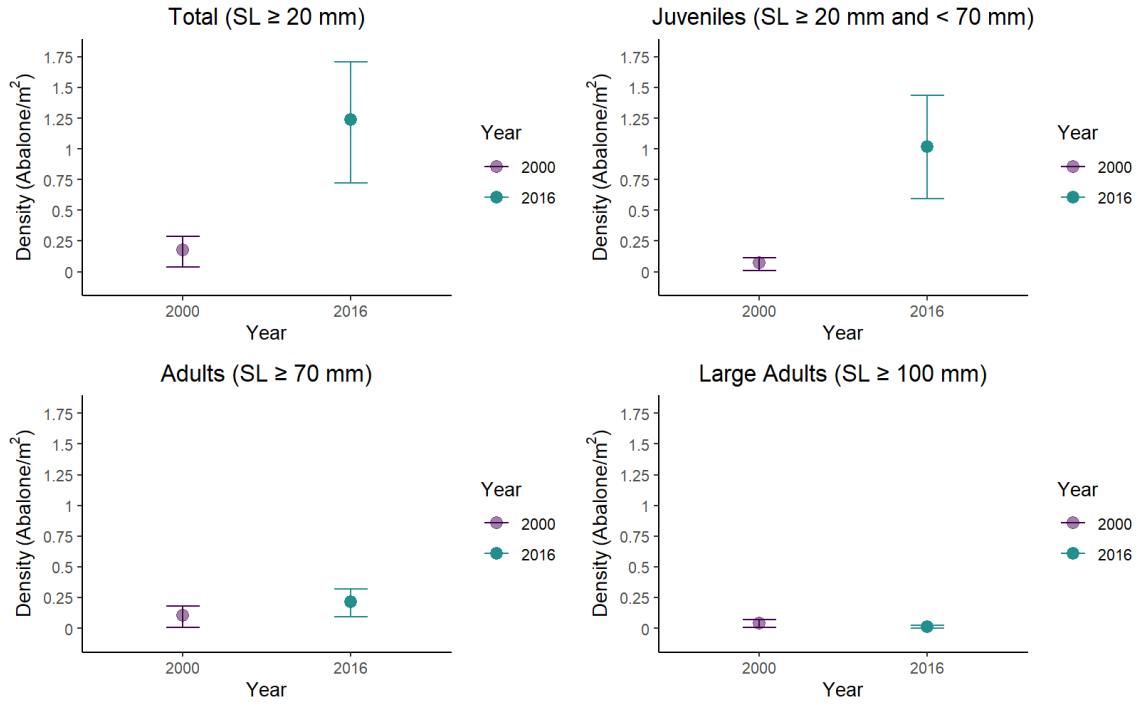


Figure 16. Northern Abalone densities by size category (bootstrapped 95% confidence intervals around the means) over time, derived from transect surveys near Kitkatla, BC ($n = 17$ sites in both 2000 and 2016). The size categories are total (shell length (SL) ≥ 20 mm), juveniles (shell length ≥ 20 mm to < 70 mm), adults (shell length ≥ 70 mm), and large adults (shell length ≥ 100 mm).

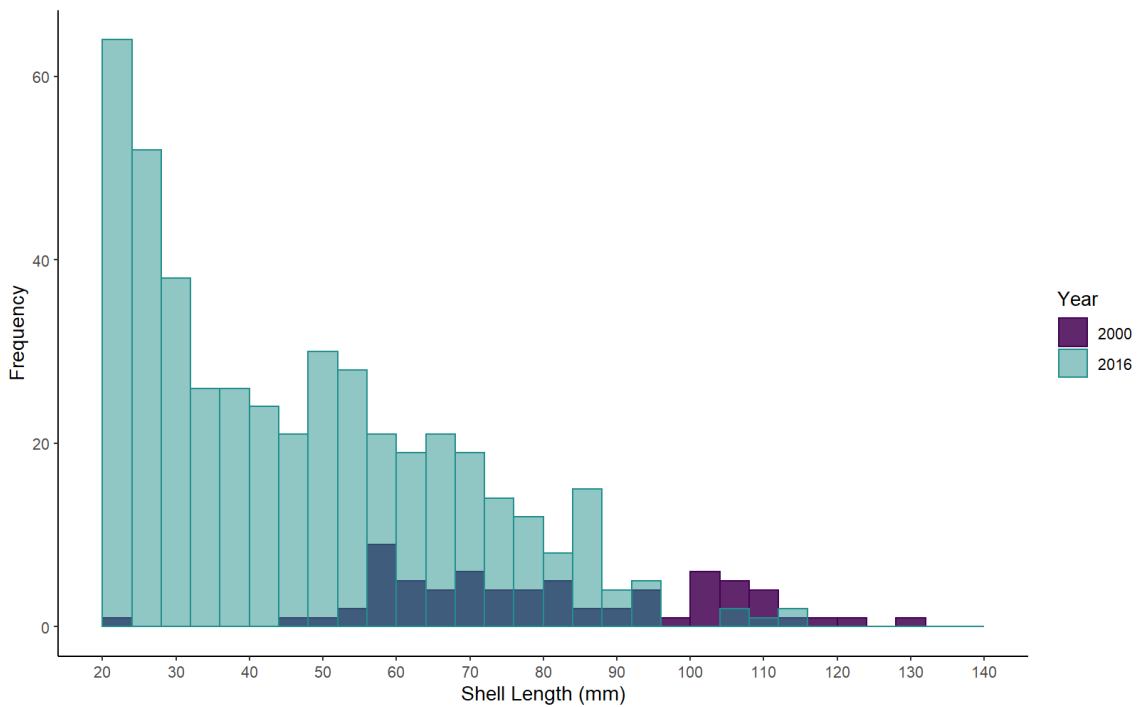


Figure 17. Size-frequency of Northern Abalone measured in transect surveys near Kitkatla, BC, ($n = 17$ sites in both 2000 and 2016).

5.3 POPULATION TRENDS DISCUSSION

The primary purpose of this pre-COSEWIC report is to present a summary of DFO's current state of knowledge on abalone in British Columbia. However, it is important to highlight a few of the important results and trends presented in previous sections in order to provide context. Most notably, in recent years, substantial increases have been observed in the estimated density of small size categories of abalone at certain index sites, particularly in Northern BC. However these increases have not been observed for larger size categories. Given that the estimated density of the small size categories began to increase between one and two abalone generations ago (see Section 2.1), one would expect some correspondence between the small and large size categories.

Recent increases in estimated mean juvenile abalone densities are likely the result of decreased mortality due to large declines in Sunflower Star (*Pycnopodia helianthoides*) abundance from sea star wasting disease (Schultz et al. 2016; Harvell et al. 2019) beginning in 2013, combined with favourable environmental conditions for juvenile settlement and survival. This observation contrasts with the early years of the time series (1978-1980), when searches for cryptic abalone were initiated because so few emergent juvenile abalone were observed and it was becoming obvious that there was a standing stock that wasn't in equilibrium with its current recruitment (P. Breen, Breen Consulting, Wellington, New Zealand, pers. comm., 2018). However, juvenile densities and settlement in this time period also varied from site to site based on depth and habitat, with some observations of high numbers of juveniles (Breen 1986; Sloan and Breen 1988). Care must be taken when interpreting the juvenile abalone time series, due to the difficulty in finding small abalone (Campbell 2000) and because the protocol changed to search more carefully for smaller abalone in about 2004 (Curtis and Zhang 2018). A portion of the increases in estimated mean juvenile densities may be due to this change in surveying behaviour.

With the above caveats in mind, the calculation of mortality and subsequently determining whether juveniles should be recruiting into the adult size class or adults should be remaining in the adult size class is based on densities of juveniles and adults in preceding years. Given recent increased juvenile densities in Northern BC, if the total instantaneous annual mortality (Z) was similar to the pre-2012 (lower mortality) period, adult densities should be increasing. Adult density is not increasing as expected and the estimated total instantaneous annual mortality is high from 2012 on. It is difficult to parse out juvenile and adult mortality from total mortality, particularly as estimates of settlement rates and early post-larval stage recruitment are lacking. Although our estimates of total instantaneous annual mortality are based on densities of adults (≥ 70 mm), these estimates include mortality at the adult stage as well as mortality of juveniles before they reach the adult stage (see Appendix A). It is for these reasons that the mortality rate presented in this report is the total instantaneous annual mortality for abalone, and includes mortality of all sources whether natural or poaching.

One possible explanation for the increase in juvenile density not being reflected in the adult density is that juvenile abalone may have been experiencing disproportionately high mortality associated with intense settlement events prior to the last two sets of surveys. High juvenile mortality would prevent juvenile abalone from recruiting to the adult portion of the population. Although primarily focused on early post-settlement, previous work has shown that intense settlement events can lead to an increase in competitive interactions for resources in abalone species (McShane 1991, 1995) and other benthic marine invertebrates (Gosselin and Qian 1997), resulting in increased density-dependent juvenile mortality. Alternatively, increases in predation (e.g., from Sea Otters) or poaching may be preventing cohorts from reaching larger

size categories, or may be differentially targeting large abalone, causing higher adult mortality. A further confounding factor is that the expansion of Sea Otters is leading to changes in abalone habitat and behaviour that may influence the detectability of larger abalone. Recent studies suggest that even large abalone, formerly thought to adopt an emergent lifestyle, may be sheltering in crevices and in other cryptic spaces when in the presence of Sea Otters (Lee et al. 2016). Finally, it is also possible that changes in environmental conditions, habitat and/or predation pressure are leading to reductions in growth rates, and may accordingly prevent or slow recruitment of abalone into larger size classes. Given the caveats highlighted above, it is important to exercise caution when interpreting recent increases in the estimated juvenile and total densities of abalone in some areas of British Columbia.

6 POPULATION SIZE

Although the estimate of extent of occurrence has been improved (Section 4.1) and the estimates of abalone densities at index sites have been updated (Section 5.1), estimated densities for each region cannot currently be extrapolated to a total number of individuals for several reasons. Firstly, the extent of occurrence represents the potential range or distribution of abalone in BC that has been restricted by certain parameters (e.g., depth). Yet the area of occupancy, namely the part of the coastwide extent of occurrence that is actually occupied by abalone, is unknown (Section 4.1). Furthermore, the primary source of DFO data on abalone densities (index site surveys) is limited to medium and high quality habitat, but abalone can be found across habitats of varying quality. Given that index sites do not represent a random selection of all available habitats, and both the proportion of the area of occurrence that is made up of medium and high quality habitat and the total area itself are unknown, densities cannot currently be scaled up to a population estimate. Therefore, the effective population size reported in Withler et al. (2003) still represents the best available estimate. Withler et al. (2003) estimated the effective population size for abalone to be 370,000 individuals, based on microsatellite data for abalone from 31 locations in BC and one location in Alaska (Section 3). Effective population size is defined as the number of individuals in a population who contribute offspring to the next generation. It is important to note that this estimate is based on data collected from 1998-2002, and the intervening years likely represent more than two abalone generations.

7 HABITAT

The life history of abalone includes both a pelagic larval phase (7-14 days; Strathmann 1987; Sloan and Breen 1988; Pearce et al. 2003) and benthic juvenile and adult phases. Very little is known about the requirements of abalone prior to settlement, but settlement cues are thought to include crustose coralline algae (Roberts 2003). During the benthic stage, abalone develop and undergo ontogenetic shifts in their habitat use. Early studies suggest that as juveniles grow, they shift from deeper habitats dominated by bare rock and crustose corallines to shallower, more emergent habitats with a complement of foliose macroalgae (Breen 1979; Breen and Adkins 1982; Sloan and Breen 1988). More recent observations from various surveys (i.e. not just index site surveys) indicate that juveniles are found across various depths (including shallow habitats) (S. Hankewich, Kitsoo Fisheries Program, Klemtu, British Columbia, pers. comm., 2020; J. Lessard, DFO Science, Nanaimo, British Columbia, pers. comm., 2020). Very small juveniles tend to occupy exposed rock surfaces, whereas larger juveniles generally occupy cryptic habitats, and adults again favour emergent habitats (Sloan and Breen 1988). These shifts in habitat use are thought to be tied to shifts in diet and vulnerability to predation. It is important to note that

these trends are reported from surveys when Sea Otters were largely absent from the coast, and cryptic behaviours are known to be enhanced in the presence of Sea Otters (see Section 2.5; Campbell 1996; Watson 2000; Lee et al. 2016). Despite being relatively sedentary and generally moving less than 50 m in a year, even occasionally occupying home scars, abalone are not thought to have a residence, as defined by SARA (Quayle 1971; Emmett and Jamieson 1988; Sloan and Breen 1988; DFO 2015b). Suitable habitat for the adult stage is described in detail in Lessard and Campbell (2007), DFO (2012) and Nephin et al. (2020). In general, abalone occupy rocky substrates from the low intertidal to shallow subtidal zone (< 10 m) across a range of exposures, in areas with full salinity (> 30 ppt) and good water exchange, and perform well in areas of low-medium exposure with complex substrate and a rich complement of macroalgae such as *Nereocystis leutkeana* and *Macrocystis pyrifera*, as well as articulated and encrusting coralline algae (Sloan and Breen 1988; Lessard and Campbell 2007; COSEWIC 2009; Rogers-Bennett et al. 2011; Lee et al. 2016; Neuman et al. 2018; Carson et al. 2019). In consultation with literature and species experts, abalone habitat parameters (such as depth and salinity) were used to inform and develop a habitat suitability index (HSI) model (Nephin et al. 2020). Predictions from the HSI model informed an updated estimate of extent of occurrence (6,985 m²) for abalone in BC waters (see Section 4.1 and Appendix C). Availability of suitable habitat is not a limiting factor for abalone populations, and as such loss of habitat is not currently considered a major threat (reviewed in DFO 2012). Direct threats to habitat are discussed in DFO (2007), DFO (2012), and DFO (2015a). Furthermore, a possible emerging threat to abalone habitat is loss of macroalgae (e.g., *Nereocystis leutkeana* and *Macrocystis pyrifera*), for example through direct harvest and climate change (Sutherland et al. 2008; Krumhansl et al. 2017; Pfister et al. 2018).

8 THREATS

Threats subsections are arranged in alphabetical order.

8.1 ENVIRONMENTAL CHANGE

Global climate change may pose a threat to abalone, operating under a variety of mechanisms, from seawater temperature increases to ocean acidification, to decreasing salinity and changing upwelling and currents. Changing ocean temperatures have already been loosely implicated in the decrease of abalone in the southern portion of their range (Rogers-Bennett 2007). Sea surface temperatures are increasing (at rates twice the global average in southern BC), particularly during summer months (Amos et al. 2015). Abalone have a broad thermal tolerance (2-24 °C for adults and < 21 °C for larvae) that is not currently being approached by sea surface temperature estimates in the northern part of the range, including BC and Washington (Paul and Paul 1998; Bouma 2007; Amos et al. 2015; Chandler et al. 2018; Neuman et al. 2018; Carson et al. 2019). While the broad thermal tolerances of abalone provide some buffer, the species may be impacted indirectly. For example, increasing temperatures can increase susceptibility to diseases such as withering syndrome, which has proven fatal to abalone held at 17.32 °C in a laboratory setting (Crosson and Friedman 2018). While disease-driven mass mortality of an abalone predator (the Sunflower Star) may benefit abalone, it also has negative implications, freeing urchins from predation pressure and thereby increasing competition for space and food (Burt et al. 2018; Harvell et al. 2019). Another example of a temperature-driven indirect effect is that early life stages of the kelp *Nereocystis leutkeana*, an important habitat former and food source, may not persist at temperatures above 17 °C (Vadas 1972). In fact, climate change

may reduce food availability by numerous mechanisms, as increasing temperatures and altered upwelling regimes could limit nutrient availability and primary production (Chhak and Di Lorenzo 2007; García-Reyes et al. 2015).

As calcifiers, abalone are particularly vulnerable to ocean acidification. Laboratory studies have demonstrated reduced larval survival, reduced shell sizes and increasing shell abnormalities for abalone at pCO₂ levels predicted for this century (IPCC 2007; Crim et al. 2011). It is unknown to what extent abalone may be able to adapt to changing conditions within the time frame of change (Neuman et al. 2018). Other climate change related threats include changes in rainfall and fresh-water intrusions that may reduce salinity, upwelling events that can alter water chemistry and quality, changing ocean currents which may have implications for larval exchange and population connectivity, and increasing storm frequency and intensity that can lead to dislodgement and mortality.

8.2 ILLEGAL HARVEST

Illegal harvest (or poaching) has been an ongoing issue for abalone in BC since all harvest (commercial, recreational, and First Nations) was prohibited in 1990, and is considered to be one of the principal threats to abalone (Campbell 2000; Jubinville 2000; Lessard et al. 2007b). However, it is difficult to quantify the amount of on-going poaching (A. Demsky, DFO Conservation and Protection, Langley, British Columbia, pers. comm., 2019). Poaching of abalone in BC is primarily driven by the high value of this species on the black market (Campbell 2000, A. Demsky, DFO Conservation and Protection, Langley, British Columbia, pers. comm., 2019). Abalone are particularly susceptible to poaching, as their primary habitat (< 10 m depth) is easily accessible to divers, and their tendency to aggregate further increases their vulnerability.

It is currently unknown whether abalone illegal harvests have increased or decreased in the previous decade, as there is no way to track the volume moved on the black market and most cases of poaching go unreported (A. Demsky, DFO Conservation and Protection, Langley, British Columbia, pers. comm., 2019). Based on DFO news releases, there were 43 poaching-related convictions, fines, or recorded poaching events between 1996 and 2014 (L. Convey, DFO Fisheries Management, Nanaimo, British Columbia, pers. comm., 2019). Large abalone seizures, such as the 11,000 seized in Haida Gwaii in 2006, have continued into the current decade. An estimated 7000 abalone were confiscated during a single incident in 2010 (A. Demsky, DFO Conservation and Protection, Langley, British Columbia, pers. comm., 2019) and numerous fines involving seafood buyers have been levied in subsequent years. Lessard et al. (2007b) reported 30 abalone poaching convictions between 1997 and 2006, along with 37 reports of suspected poaching in 2004 and 2005. It is estimated that only 10-20% of all poaching activity is prosecuted (Lessard et al. 2007a), as the vast size of the British Columbia coast makes it impossible for DFO Conservation and Protection to patrol the entire coast all the time (A. Demsky, DFO Conservation and Protection, Langley, British Columbia, pers. comm., 2019).

A large range of sizes are present in seizures of illegally harvested abalone, with 2-42% smaller than 100 mm shell length, which was the former minimum legal size in the commercial fishery prior to its closure (Campbell 2000). Poaching activities tend to disproportionately target the largest individuals, and thus, the most fecund individuals in a population (COSEWIC 2009). Removal of large, mature abalone reduces the reproductive potential of the population and may leave spawning individuals too far apart for successful reproduction, as fertilization success depends on spawning aggregation density (Campbell 2000).

Recent estimates of total instantaneous annual mortality appear to show ongoing illegal harvest of abalone in BC. Total annual mortality rates for abalone in the ECHG (1990-2002) and CC (1993-2001) survey regions estimated by Zhang et al. (2007) were $0.29 \pm 0.05 \text{ y}^{-1}$ ($\pm \text{ se}$) and $0.36 \pm 0.07 \text{ y}^{-1}$, respectively. These mortality rates are greater than those calculated by Breen (1986) for adults in areas where there was no commercial fishery ($0.15\text{-}0.20 \text{ y}^{-1}$), but are within the range estimated for areas where the commercial fishery was operating ($0.21\text{-}0.41 \text{ y}^{-1}$). More recent estimates of total instantaneous annual mortality rates (Curtis and Zhang 2018, Section 2.5), using the methods of Zhang et al. (2007), are also within the range of values in Breen (1986) for areas where the commercial fishery was operating. In Section 2.5, the total instantaneous annual mortality rate for ECHG was estimated as $0.50 \pm 0.04 \text{ y}^{-1}$ (1990-2017) and $0.20 \pm 0.02 \text{ y}^{-1}$ for the CC (1993-2016) in areas where Sea Otters were absent and $0.42 \pm 0.07 \text{ y}^{-1}$ where Sea Otters were present. For areas of the CC survey region where no Sea Otters were present, the estimated total instantaneous annual mortality rate was within the range in Breen (1986) for areas where the commercial fishery was closed. It is unknown how much total instantaneous annual mortality rates are affected by illegal harvest (Section 8.2) and Sea Otter predation (Section 8.4). Additionally, intrinsic differences in the habitat at the index sites where Sea Otters are present and those where Sea Otters are absent may be responsible for some of the difference in these estimates. Index site densities show large variation within the survey regions, and a large number of sites would need to be added to each survey region to reduce the coefficient of variation to at least 0.5 (Hansen et al. 2020, Figures 11-12).

8.3 RECRUITMENT FAILURE

Although not detected in the Northern Abalone stock-recruitment curves of Zhang et al. (2007), studies show that recruitment success in other abalone species, and indeed in Northern Abalone in certain parts of their range, may be limited by reduced fertilization success at low spawning densities (e.g., Shepherd and Partington 1995; Babcock and Keesing 1999; Dowling et al. 2004; Rothaus et al. 2008; Coates and Hovel 2014; Coates et al. 2014), also known as the Allee effect or depensation (Allee et al. 1949; Stephens et al. 1999). Some abalone species in Australia exhibit population collapse or recruitment failure at densities below 0.15 Abalone/m^2 to 0.30 Abalone/m^2 (Shepherd and Partington 1995; Babcock and Keesing 1999). Allee thresholds of $\sim 0.15\text{-}0.3 \text{ Abalone/m}^2$ have been adopted in evaluating densities and conservation concerns in various abalone species, including Northern Abalone (e.g., DFO 2007; Rothaus et al. 2008; Coates et al. 2014; Donnellan and Hebert 2017). Additionally, the long-term absence of small size classes of abalone can be indicative of settlement and/or recruitment failure. Low juvenile Northern Abalone densities have been observed in the San Juan Islands in Washington State (Bouma et al. 2012) and have been attributed to reduced fertilization success (Rothaus et al. 2008; Carson et al. 2019). Northern Abalone aggregate prior to spawning, thereby enhancing reproductive success (Sloan and Breen 1988). For example, Carson and Ulrich (2019) reported that two populations of Northern Abalone with average densities of 0.17 and 0.25 Abalone/m^2 are self-sustaining, but these populations have spawning aggregations at much higher densities (up to 1.2 Abalone/m^2). There is considerable evidence for recruitment failure in Northern Abalone populations in Washington State (Rothaus et al. 2008; Carson et al. 2019). Curtis and Zhang (2018) also suggested that reproductive or settlement failure may have been occurring in the CC survey region (prior to 2006) and in portions of the ECHG survey region (prior to 2007), based on the lack of Northern Abalone $< 40 \text{ mm}$ shell length in all areas.

Estimated mean adult Northern Abalone densities in the most recent surveys in the Northern BC survey regions (CC, ECHG, WCHG) were above 0.30 Abalone/m^2 (Shepherd and Partington

1995; Babcock and Keesing 1999, Figures 11-13, Appendix E, Tables E.1-E.3), but estimated mean adult Northern Abalone densities in all survey regions in Southern BC (QCS, WCVI, GB) were well below 0.15 Abalone/m² in the most recent surveys (Section 5, Figures 14-15, Appendix E, Tables E.4-E.5). Estimated mean juvenile densities in the QCS and WCVI survey regions increased in the most recent survey, despite the low estimated mean adult densities observed during the surveys. Small Northern Abalone (< 40 mm shell length) were found in all recent surveys in the WCVI region (2003-2018), indicating successful settlement (Curtis and Zhang 2018, Appendix F, Figure F.5). However, few Northern Abalone < 40 mm shell length were found in the QCS survey region (Curtis and Zhang 2018, Appendix F, Figure F.4). The GB region, where mean adult Northern Abalone densities were 0.010 Abalone/m² in the Sooke area in 2005 and 0.008 Abalone/m² in the northern Strait of Georgia area in 2009, showed little to no recruitment, although juvenile Northern Abalone were observed in the northern Strait of Georgia in 2009 (Section 5). In 2019, only one Northern Abalone smaller than 40 mm was found in the GB survey region.

Since Northern Abalone are broadcast spawners (Breen and Adkins 1980b), recruitment at an index site may be influenced by connectivity to other Northern Abalone aggregations and broader oceanographic conditions in the region. Zhang et al. (2007) found weak density dependence in the stock-recruitment relationships for the ECHG and CC regions. Assuming a pelagic larval duration around 10-14 days and spawning generally during the spring and summer months (based on Sloan and Breen 1988), Northern Abalone larvae in the oceanic surface layer could be expected to travel at a daily average speed of about 10 cm/s, for a distance of 100-150 km in a northerly direction in the summer months (C. Hannah, DFO Science, Sidney, British Columbia, pers. comm., 2019). Therefore, larval dispersal between spawning aggregations would be expected. Indeed, the percentage of quadrats surveyed during the DFO Northern Abalone Index Sites Surveys that contained at least one Northern Abalone increased in all survey regions (except for QCS) during the 2000s (Curtis and Zhang 2018). Although there is recent evidence of abalone settlement in BC, the prevalence of recruitment failure elsewhere, the sporadic nature of abalone settlement events, and the ongoing low densities of abalone in parts of BC, all indicate that recruitment failure is still a threat.

8.4 SEA OTTER PREDATION

Sea Otters are an abalone predator (Watson 1993, 2000; Lee et al. 2016) whose range has continued to expand since their initial reintroduction to BC in 1969 (Watson 2000; Nichol et al. 2015). Sea Otters are thought to have been extirpated by 1930 as a result of the maritime fur trade on the west coast of North America (Nichol 2015). Reintroduced in three translocations to Checleset Bay on the west coast of Vancouver Island (1969-1972, Bigg and MacAskie 1978), Sea Otters presently occupy areas on the west coast of Vancouver Island, in Queen Charlotte Strait, and on the Central Coast (Figure 18). Sea Otters were first reported on the Central Coast in 1989, in the Goose Island Group, and spread to the northwestern edge of Queen Charlotte Strait from the west coast of Vancouver Island in 2004 (Nichol et al. 2015). Sea Otters have been at or near equilibrium density with their habitat in the Checleset Bay area since the mid-late 1990s (COSEWIC 2007). While population growth in the longest occupied and central areas of these ranges has slowed, BC Sea Otter populations continue to increase and expand (Nichol et al. 2015). Expansion for the west coast of Vancouver Island and Queen Charlotte Strait range is mainly in Queen Charlotte Strait (Nichol et al. 2015). Although the population on the west coast of Vancouver Island is within the range of the maximum population size estimated by Gregr et al.

(2008), the BC coast-wide population is well below the estimated maximum size and is expected to continue to grow and expand its range (Nichol et al. 2015).

Sea Otter increases on the Central Coast occurred after the decline of abalone in the CC survey region (Figure 11) and did not contribute to the decline seen in all regions in Northern BC (Figures 10-12). However, the current population growth and range expansion of Sea Otters in BC may limit the recovery of abalone. Sea Otters prey on benthic invertebrates in intertidal to subtidal areas, with most foraging dives less than 30 m in depth (Riedman and Estes 1990; Bodkin et al. 2004; Lafferty and Tinker 2014). In areas where Sea Otters are established, abalone tend to be more hidden, found in crevices and other cryptic habitat (Watson 1993, 2000; Lee et al. 2016). In a recent study, Lee et al. (2016) found lower densities of exposed abalone (i.e. individuals out in the open and not hidden under rocks/covered by kelp) in sites occupied by Sea Otters for more than 30 years (west coast Vancouver Island), than in sites with shorter (Central Coast) or no Sea Otter occupation (southeast coast of Haida Gwaii). A similar pattern exists based on observations of cryptic abalone (i.e. those found by shifting rocks) for index sites surveyed by the index site surveys in the CC survey region. Abalone were more likely to be cryptic at larger sizes at index sites with Sea Otters present compared to index sites where Sea Otters were absent (Figure 6). This result was consistent across all index sites examined for cryptic abalone in all survey regions with Sea Otters present (Figure 19). Breen et al. (1982) also found smaller, primarily cryptic, abalone at Sea Otter feeding sites on the west coast of Vancouver Island, but lacked observations of abalone at these locations prior to the reintroduction of Sea Otters in BC. In addition, total instantaneous annual mortality rates for the Central Coast (CC survey region, 1993-2016) were 2.2 times higher in areas with Sea Otters present ($0.42 \pm 0.07 \text{ y}^{-1}$ ($\pm \text{sd}$), than in areas where Sea Otters were absent ($0.20 \pm 0.02 \text{ y}^{-1}$ ($\pm \text{sd}$), Figure 8). Index sites show high variation in abalone densities within a survey region and this may reflect local environmental conditions at the index sites that are not well captured in the current Bayesian hurdle model, or differences in illegal harvest or other mortality factors across index sites, and not solely Sea Otter predation. Furthermore, the Sea Otter occupancy variable does not account for the number of Sea Otters present, differences in time spent foraging at the index sites, or differences in the prey available to Sea Otters at an index site, which may all influence the predation pressure on abalone at an index site.

The co-existence of abalone and Sea Otters in areas of the west coast of Vancouver Island for approximately the last 50 years, and throughout BC in the thousands of years prior to the extirpation of Sea Otter, suggests that abalone can persist in Sea Otter occupied areas (Watson 2000). The exact mechanism of abalone survival at low densities in the presence of Sea Otters is unknown, as is the potential and likely varied impact on abalone stock-recruitment relationships and survival at both local and coast-wide scales, across the range of habitats in BC (Lessard et al. 2007b). This uncertain relationship is best shown in the Central Coast region, where index sites in different areas with Sea Otters present show varying trends in abalone densities during the 2000s, with an increase in adult abalone density at index sites in the Simonds Group area and no increase in adult density at index sites in both the Stryker Island and Spider Island areas (Curtis and Zhang 2018). Abalone populations are subject to shifting baselines following European contact (Lee et al. 2019), with the extirpation, reintroduction and expansion of Sea Otter populations, as well as expansion and closure of the abalone fisheries. Interactions between the endangered abalone and its threatened Sea Otter predator present an interesting conservation conundrum that has been explored in other studies (e.g., Chadès et al. 2012; Lee et al. 2016). It is unclear whether current abalone conservation targets are achievable in the presence of Sea Otters (DFO 2007; Chadès et al. 2012). Not only do Sea Otters have

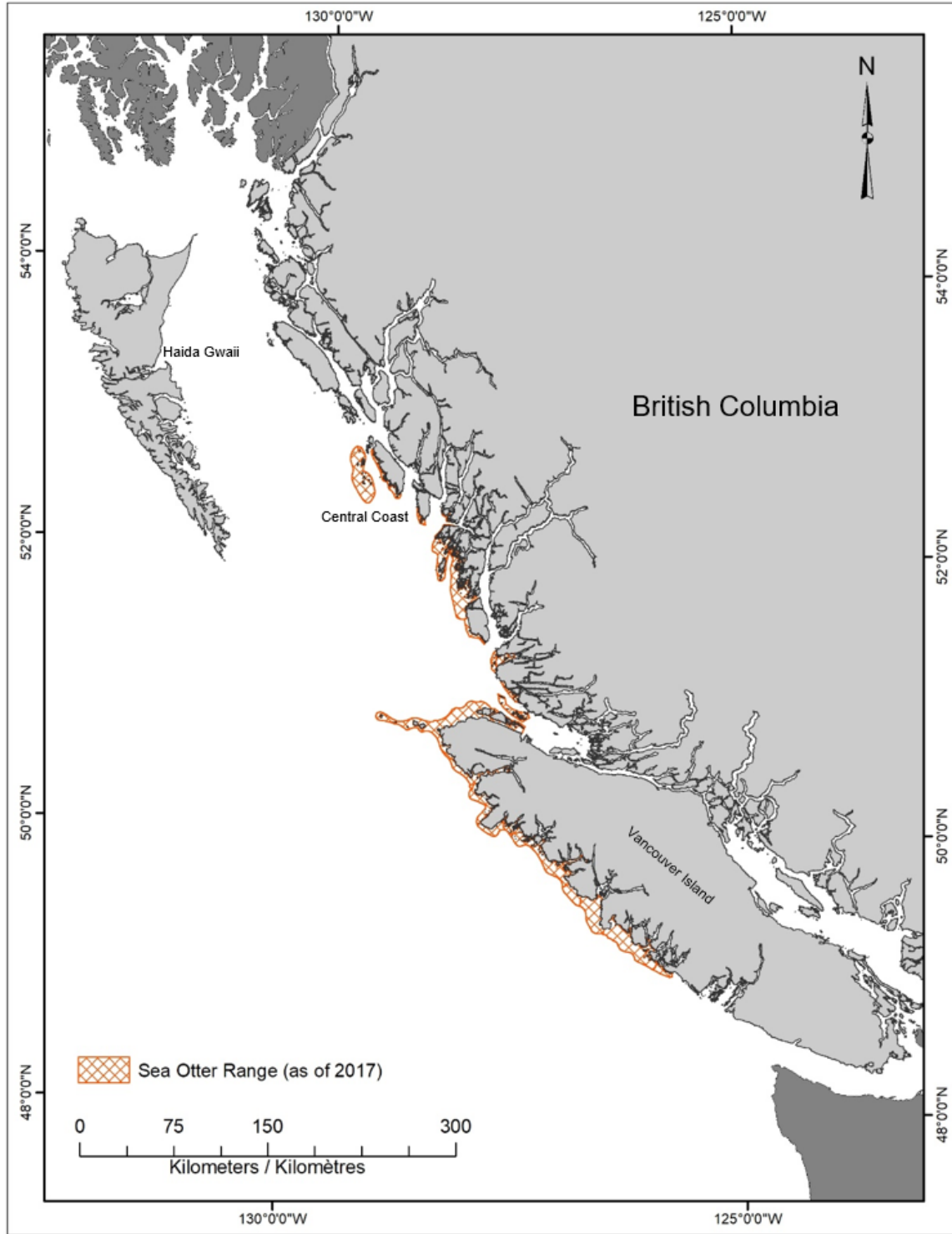


Figure 18. Sea Otter range in BC, as of 2017.

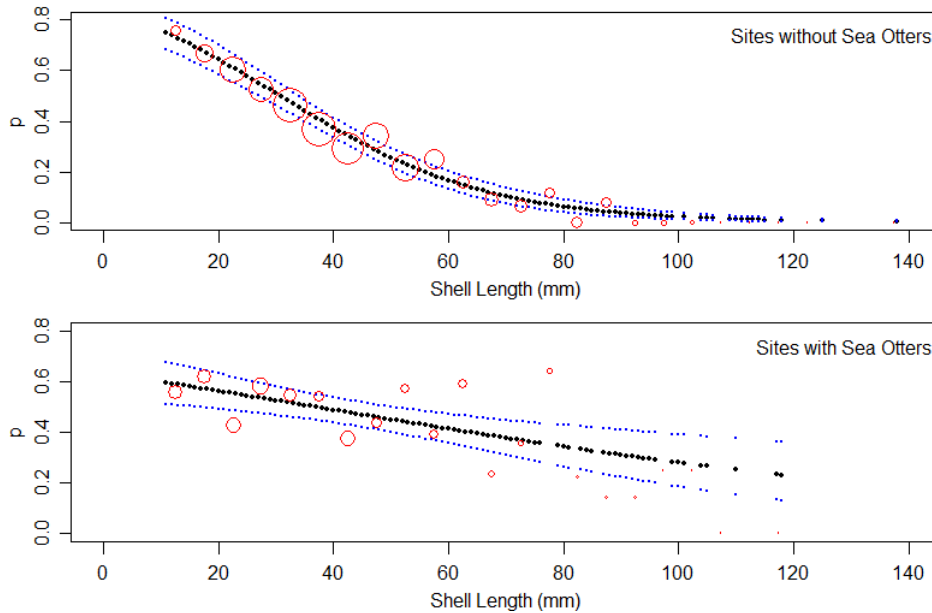


Figure 19. Size-specific probability of a Northern Abalone being cryptic in index sites locations with (lower panel) and without (upper panel) Sea Otters. Data are from all index sites where searches for cryptic Northern Abalone were conducted during DFO Northern Abalone Index Site Surveys in 2004-2018. Red circles are observed data and the size of the circle represents the sample size.

direct effects on abalone through predation, they also have indirect effects, such as altering habitat (e.g., removal of sea urchins and other herbivores facilitates a transition from barrens to kelp forests) and influencing abalone's use of that habitat (Lee et al. 2016).

9 MANIPULATED POPULATIONS

One of the approaches identified in the Recovery Strategy and the Recovery Potential Assessment (Toole et al. 2002; DFO 2007; Lessard et al. 2007b) to assist in meeting recovery objectives for abalone is undertaking research and rebuilding experiments. Recent research on abalone rebuilding approaches in BC are summarized in DFO (2015a), with additional updates here focusing on two rebuilding methods: (1) outplanting hatchery-reared individuals; and (2) aggregating wild adults.

9.1 OUTPLANTING

The Bamfield Huu-ay-aht Community Abalone Project (BHCAP) was the last of the abalone hatcheries in BC to close (R. Govender, DFO Fisheries Management, Vancouver, British Columbia pers. comm., 2019) and it last produced hatchery-spawned abalone in 2011 (DFO 2015a). Abalone hatchery projects and broodstock collections are discussed in Lessard et al. (2002). DFO (2015a) summarizes recent research on outplanting of abalone in BC. In general, outplanting of abalone has been limited by variable but high predator-driven natural mortality (Read et al. 2013; Hansen and Gosselin 2013). Hatchery-reared abalone demonstrate anti-predator behavioural deficits relative to their wild counterparts, which are exacerbated by increasing time spent in the hatchery environment (Hansen and Gosselin 2016). Nevertheless, abalone outplanting attempts have been successful in enhancing densities in some studies. Carson et al.

(2019) found that an average of 3.4% of outplanted juvenile abalone, from successive outplantings at 12 sites (over 15,000 juveniles), survived to adult sizes, which varied by site (range of 0-7.5%). In addition, 8 of the 12 outplanting sites reached densities above the assumed threshold for successful reproduction (> 0.3 Abalone/m², Shepherd and Partington 1995; Babcock and Keesing 1999). Success may be further improved, for example by selecting appropriate size classes and using complex substrates (Griffiths and Gosselin 2008; Read et al. 2012, 2013). Although abalone aquaculture in BC has ceased, abalone outplanting is still ongoing in Washington (Vadopalas and Watson 2014; Carson et al. 2019). Site-level abalone outplanting successes have been much smaller than the widespread increases of juvenile abalone currently seen in the survey regions in Northern BC (Figures 11-13).

9.2 AGGREGATION STUDIES

From 2002 to 2007, DFO conducted a pilot project on aggregating adult abalone in the Broken Group Islands in Barkley Sound. Although this work is currently unpublished, preliminary results show that aggregation was successful in temporarily increasing densities of juvenile abalone at the experimental sites (Lessard et al. 2007b). Haida Nation (2002), Kitasoo/Xai'xais Nation (2004 and 2010) and Metlakatla First Nation (2009) have aggregated abalone at several sites as well (J. Lessard, DFO Science, Nanaimo, British Columbia, pers. comm., 2020). Although moving and aggregating adult abalone is unlikely to result in large-scale increases in juvenile abalone densities, such as those currently seen in Northern BC survey regions, it could help increase local densities and their reproductive potential.

10 FUTURE DIRECTIONS

Future analyses are recommended that could separate the year and region effects in the GAM models through use of annual anomalies in density as the dependent data. These analyses could also address the importance of biological drivers of density rather than trying to standardize the time series through removal of environmental covariates. However, this future work would address a different objective than the GAM modeling conducted in Hansen et al. (2020), which formed the basis of the standardization herein.

Currently we only use mean parameter values for growth models constructed in the past in our estimation of total mortality rates. Multilevel hierarchical growth models may be developed in the future, incorporating all available growth data from various locations. This approach would facilitate incorporation of uncertainties about abalone growth into the mortality estimation, and would be valuable in incorporating better information about abalone growth as it becomes available for different locations.

The convergence diagnostic used in estimating a standardized index of abundance herein (see Appendix D) is the conventional test developed by Brooks and Gelman (1998). Vehtari et al. (2020) recently proposed an improved convergence diagnostic, that we are not yet familiar with. The methodology of Vehtari et al. (2020) could be considered in future work, particularly if it withstands the test of time.

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APPENDIX A. ESTIMATING MORTALITY RATES

A.1 SIZE-SPECIFIC CRYPTIC PROBABILITIES

To estimate current mortality for abalone, it is necessary to account for the cryptic portion of the population that is not detected during the index site surveys, which search primarily for emergent abalone (see methods DFO 2016; Curtis and Zhang 2018; Hansen et al. 2020). Cryptic abalone are those individuals that cannot be seen without shifting rocks. Lessard et al. (2007b), Zhang et al. (2007) and Curtis and Zhang (2018) provide annual mortality estimates based on searches for cryptic abalone conducted in 1984 (Boutillier et al. 1985), 1987 (Carolsfeld et al. 1988), and 1990 (Thomas et al. 1992). As Sea Otter populations become re-established along parts of the BC coastline, the vulnerability and cryptic behaviours of abalone appear to be changing (Campbell 1996; Watson 2000; Lee et al. 2016). This shift in abalone behaviour has led to again surveying cryptic abalone (DFO 2016). In the current index site surveys protocol, a subsample of quadrats (quadrat numbers 2, 4, 6 and 8 of the 16) are searched for both emergent and cryptic abalone, by shifting all rocks that can be manoeuvred. Any cryptic abalone found within those quadrats are counted and measured. New size-specific probabilities of abalone being cryptic were estimated from data collected on index site surveys in 2016 in the CC survey region and in 2017 in the ECHG survey region (see Section 5.1 for survey information). The probability (ρ_i) of an individual abalone, i , being cryptic (C_i) was modelled using the Bernoulli probability distribution:

$$C_i \sim \text{dbern}(\rho_i) \quad (\text{A.1})$$

where ρ is assumed to vary with shell length (mm) of the individual abalone (L_i) and is associated with shell length through a logit link:

$$\text{logit}(\rho_i) = \alpha + \beta \cdot L_i \quad (\text{A.2})$$

where α , and β are model parameters. The value of α determines the level of cryptic probability for very small individuals, and the value of β determines the rate of change in cryptic probability when individuals grow larger. Vague normal distribution priors were assigned to α and β of $\text{dnorm}(0, 100^2)$.

A.2 TOTAL MORTALITY ESTIMATION

Total mortality (Z) is composed of two sources of mortalities on juvenile and adult abalone: natural mortality and poaching mortality. Using the cryptic probability models and the population model of Zhang et al. (2007), total instantaneous annual mortality was estimated by comparing the estimated density of abalone (> 70 mm shell length) in each survey occurrence of the index site surveys in a survey region (either CC or ECHG) to the predicted density of abalone (> 70 mm shell length) estimated from the previous survey occurrence in that survey region, and from the stock-recruitment model (Lessard et al. 2007b; Zhang et al. 2007). The time interval between any two consecutive survey years is either 4 or 5 calendar years. Using the stock-recruitment model allows for new recruits which were not able to be observed in the previous surveys to be included. The predicted density would tend to be higher than the estimated density as mortality is not incorporated in the prediction. As per Lessard et al. (2007b) and Zhang et al. (2007), the estimation procedure for total instantaneous annual mortality is as follows:

1. Select the first survey year;
2. Randomly sample with replacement the number of emergent abalone in each quadrat of each index site in the selected survey year;

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3. Randomly select a pair of values for the parameters (α, β) of the cryptic model from the saved MCMC samples for each survey area in each survey year;
 4. Calculate the number of abalone (emergent and cryptic) for each observed shell length, using the cryptic model with the selected values for α and β ;
 5. Calculate the density (d) of abalone greater than 70 mm in each survey area (e.g., Stryker Island or Carpenter Bay, see Curtis and Zhang (2018) for maps of the surveyed areas within the ECHG and CC survey regions) in the selected survey year;
 6. Predict the shell lengths of abalone at the next survey occurrence based on the observed shell lengths at the current survey year, using the von Bertalanffy growth model with fixed parameter values;
 7. Calculate the density (\tilde{d}) of abalone greater than 70 mm in each survey area at the next survey occurrence based on the estimated density at the current survey year and the predicted length-frequency data for the next survey year with no incorporation of any mortalities;
 8. Calculate the density of spawning biomass in each survey area for the current survey year, using the length-weight model with fixed parameter values;
 9. Calculate the expected density of 4-year-old abalone 4 years later in each survey area, using the stock-recruitment model with fixed parameter values;
 10. Calculate the expected density of 5-year-old abalone 5 years later in each survey area, assuming spawning biomass density remains the same in the year following the current survey year;
 11. Generate densities of 4- and 5-year-old abalone by multiplying the expected densities by e^φ where φ is a deviate randomly generated from the normal distribution $dnorm(0, 0.61^2)$;
 12. Generate densities of 4-year-old ($R4$) and 5-year-old ($R5$) abalone greater than 70 mm assuming shell lengths of 4- and 5-year-old abalone follow a normal distribution with a coefficient of variation of 8%;
 13. Select the next survey year and repeat steps 2-12 until the last survey year has been selected;
 14. Estimate total instantaneous annual mortality rate (Z) using the non-linear least squares approach:

$$d_{y,a} = \tilde{d}_{y,a} \cdot e^{-Z \cdot \omega_y} + R4_{y,a} + R5_{y,a} \cdot e^{-Z} \cdot f_y + \varepsilon \quad (\text{A.3})$$

where ω is the number of years between the previous survey occurrence and this survey occurrence (either 4 or 5 years), f is an identification parameter that is 0 if $\omega = 4$ and 1 if $\omega = 5$, the subscripts y and a refer to survey year and survey area, respectively, and ε is a normal deviate;

15. Repeat steps 1-14 1000 times.

APPENDIX B. ESTIMATING SEA OTTER OCCUPANCY AT THE DFO NORTHERN ABALONE INDEX SITES

Sea Otters are recolonizing parts of their former range in BC, and Sea Otter rafts have been observed in parts of the WCVI, CC and QCS survey regions (see Figures 1 and 18, Nichol et al. 2015). For these three regions, index sites in locations that overlap with the current distribution of Sea Otter in BC were evaluated for the presence/absence of Sea Otter rafts (three or more individuals) and for the length of Sea Otter occupation, as in Hansen et al. (2020). Index sites in all other regions (i.e. ECHG, WCHG, GB) were assigned a code corresponding to absence for Sea Otter occupancy. Sea Otter surveys are not conducted in these regions (Nichol et al. 2015). A GIS-derived index of Sea Otter occupation for abalone index sites was developed using Sea Otter survey data since 2001. Sea Otter raft locations obtained during spring/summer Sea Otter surveys conducted since 2001 (Nichol et al. 2015) were imported as a shape file into ArcMap 10.1.1. Buffers representing a 3 nautical mile (nm) radius were created around each raft site. If an abalone index site fell within the buffer, that index site was considered occupied in the year of that survey. As another check, the abalone index sites were buffered with a 3 nm radius and the raft sightings that intersected with these buffers were identified and the corresponding survey years recorded. Sea Otter rafts tend to form in the same locations over multiple years (Garshelis and Garshelis 1984; Jameson 1989; Nichol et al. 2015), so the presence of a Sea Otter raft in the spring or summer of one year is a strong indication that Sea Otters will be present in subsequent years (Nichol et al. 2015). Raft sightings at other times of the year (e.g., winter) in a previously unoccupied area are not a reliable indicator of consistent occupation (Nichol et al. 2015). As the surveys are conducted in spring/summer, every year after the first year of occupation of the abalone index site (intersection with 3 nm buffer) was considered to be continuously occupied by at least three Sea Otters. Sea Otters were recorded as present at the index site for every year of the index site surveys after the first year of Sea Otter occupation.

For the index sites in the WCVI and QCS regions, the Sea Otter occupancy variable was produced based on the application of expert opinion. On WCVI, Sea Otter surveys started well before 2001, but did not geo-reference the approximate location of all Sea Otters observed on surveys, therefore the GIS-derived method did not readily apply. There has been substantial consistency among years with respect to the Sea Otter survey team on WCVI and thus use of expert opinion to determine when Sea Otters were first observed within the corresponding 3 nm buffer vicinity of the abalone index sites was deemed an appropriate approach. In addition, for abalone index sites that were close to early Sea Otter surveys but not within the 3 nm buffers, expert opinion was used to determine whether the occupation date of the nearest abalone index site could be used.

For the QCS region, the area over which the abalone index sites are distributed is relatively small compared to other regions and the sites are quite close together, often less than 2 nm apart. Application of the GIS-derived method resulted in different Sea Otter presence/absence values for sites that were in close proximity to one another and this seemed biologically unrealistic. Thus, given the time-scale resolution of the Sea Otter survey data, the clusters of abalone index sites and the motility and foraging behaviour of Sea Otters, it was assumed that index sites in close proximity would be more likely to have experienced similar foraging pressure from Sea Otters. Therefore, based on expert opinion, an alternative estimate that assumes these clusters of index sites have been occupied for the same amount of time was used.

In the WCVI survey region, the presence of Sea Otters predates the establishment of the index sites in 2003. The first year of Sea Otter occupancy was estimated as 1977 to 2001 for index sites in the Quatsino Sound, Brooks Bay, Checleset Bay, and Kyuquot Sound areas of the WCVI

survey region (see Curtis and Zhang (2018) for maps of areas within the survey regions), where 100% of index sites were occupied by Sea Otters in 2018. Years of Sea Otter occupancy of the index sites ranged from 18 to 42 years. In the QCS survey region, Sea Otters occupy index sites in both areas surveyed (North Queen Charlotte Strait and Gordon Channel) and the first year of Sea Otter occupancy of the index sites ranges from 2006 to 2013. Sea Otters occupied 52.9% of the index sites in the QCS survey region, as of 2014. For index sites in the CC survey region, Sea Otters are present at sites in the Stryker Island, Simonds Group, and Spider Island areas, in a total of 29.5% of CC survey region index sites in 2016. The first year of Sea Otter occupancy ranges from 2001 to 2011 in the CC survey region. For index sites in the QCS and CC survey regions, the index sites were established prior to Sea Otter occupation of the locations.

APPENDIX C. ESTIMATION OF EXTENT OF OCCURRENCE USING HABITAT SUITABILITY INDEX MODELS

During the development and application of a species distribution modelling framework on Canada's Pacific Coast (Nepkin et al. 2020), a knowledge-based habitat suitability index (HSI) model was developed to predict probability of occurrence for abalone in the North Central Coast (NCC) study area. HSI models rely on literature review and consultation with species experts to develop relationships with environmental predictors. The HSI model for abalone included the following environmental predictors (detail in Table C.1): substrate; mean summer bottom salinity; mean summer tidal current speed; and exposure. Probability of occurrence ranged from 0 to 1. A full description of the NCC HSI model for abalone can be found in Appendix B of Nepkin et al. (2020).

To estimate the extent of occurrence for abalone in BC waters, the NCC HSI model was extrapolated to the rest of the BC Coast. Two adjustments were made to the NCC HSI model to allow extrapolation to the entire coast. First, the range where exposure is fully suitable was shifted from 30-70 (100s of km) to 20-60 (100s of km) to better align with data models developed for the NCC (Nepkin et al. 2020) and with known areas of abalone occurrence. Second, the tidal current speed predictor was removed from the model as it was highly restrictive and predicted low probabilities of occurrence in areas known to have high densities of abalone (e.g., Haida Gwaii).

To estimate an area, probability predictions on a continuous scale from 0 to 1 were converted to a binary scale using a threshold of 0.5. Probabilities ≥ 0.5 were assigned as present, while those < 0.5 were assigned as absent. Following this method, the estimated extent of occurrence (km^2) for abalone in BC waters is 6,985 km^2 .

Table C.1. Environmental predictors used to build the Northern Abalone habitat suitability index (HSI) models in the Pacific Region. *Mean summer tidal speed was used in the model presented in Nephin et al. (2020) developed for the North Central Coast, but not in the updated coastwide model. **Represents total potential exposure based on fetch: sum of fetch from all bearings (0 to 355 in 5 degree increments).

Environmental data type	Predictor layer(s)	Source(s)	Native resolution(s)	Years	Units
Bathymetry	Bathymetry (depth)	Bathymetric elevation models (Davies et al. 2019)	20 m	1930-2012	m
Oceanographic	Mean summer bottom salinity	Regional circulation model of BC (Masson and Fine 2012)	3 km	1998-2007	PSU
	Mean summer bottom temperature				°C
	Mean summer tidal speed*				m·s ⁻¹
Fetch	Sum fetch (proxy for exposure)	Python script (Gregg 2014)	50 m	-	100s of km**
Substrate	Substrate type (rock, mixed, sand, mud)	Background Substrate (Gregg and Haggarty 2017)	20 m, 100 m	-	categorical

APPENDIX D. ESTIMATING A STANDARDIZED INDEX OF ABUNDANCE FOR DFO NORTHERN ABALONE INDEX SITE SURVEYS

Similar to the methods of Curtis and Zhang (2018), a Bayesian hurdle model was used to estimate the annual posterior mean abalone densities and 95% credible intervals for each survey region (i.e. for each of WCHG, ECHG, CC, WCVI, QCS) and for the grouped Northern BC survey regions (ECGH, WCHG, and CC combined). This model is a mixture of two statistical sub-models: binomial and lognormal models. The binomial distribution is used to model probabilities of observing non-zero abalone densities in an index site, while the lognormal distribution is used to model variations of non-zero abalone densities:

$$\begin{cases} W_y \sim \text{dbin}(p_y, T_y) \\ D_{y,j} \sim \text{dlnorm}(\log \hat{D}_{y,j}, \sigma^2) \end{cases} \quad (\text{D.1})$$

where W is the number of index sites with non-zero densities, T is the total number of index sites surveyed, p is the probability of observing at least one abalone (i.e. non-zero density) in an index site, $D_{y,j}$ is the observed non-zero abalone density, $\log \hat{D}$ is the expected non-zero abalone density on the log scale, σ is the standard deviation on the log scale, and the subscripts y and j refer to survey year and index site, respectively.

The probability, p , is assumed to vary in different survey years, and is associated with the year effect through the Logit link function:

$$\text{logit}(p_y) = \kappa + H_y \quad (\text{D.2})$$

where κ is the intercept, and H is the effect of year on p .

The non-zero densities on the log scale ($\log \hat{D}$) were expected to vary by year, but also to vary based on environmental conditions at the index sites. In an exploratory analysis (Hansen et al. 2020), the datasets from the grouped Northern BC survey regions (CC, ECHG, WCHG) and grouped Southern BC survey regions (QCS, WCVI, GB) were analyzed using generalized additive modelling (GAM) to identify environmental covariates that could be used to standardize the time series (1978-2018). The analyses fit GAM models to density data using a group of explanatory variables thought to impact abalone distribution and abundance. The models fit density data with a Tweedie error distribution and a backwards elimination of insignificant covariates. The variables included data collected at the time of the survey (depth, sea star abundance), Sea Otter occupancy (presence/absence, see Appendix B for methods), exposure to wave action estimated for each site, and raster-based variables from compiled seafloor bathymetry (Davies et al. 2019), a substrate model (Gregr and Haggarty 2017), and Regional Ocean Model System (ROMS) model outputs (Masson and Fine 2012). For more detail see Table D.1 and Hansen et al. (2020). For the grouped Northern BC survey regions, several variables, including salinity, exposure of the index site, vector ruggedness index, terrain ruggedness index, topographic position index, substrate type, bathymetry, tidal current speed, and Sea Otter occupancy were significant in the GAM models for the four size categories of abalone (Table D.2, Hansen et al. 2020). For the grouped Southern BC survey regions, mean current speed, Sea Otter occupancy, bathymetry, aspect of the slope, and substrate type were significant in the GAM models for the four size categories of abalone (Table D.2, Hansen et al. 2020).

The expected non-zero log density $\log \hat{D}$, was linked to the year effect and the environmental variables:

$$\log \hat{D}_{y,j} = \pi + G_y + \sum_{i=1}^n \phi \cdot E_{y,j,i} \quad (\text{D.3})$$

where G is the year effect, E is an environmental covariate, and π and ϕ are the model parameters. The subscripts y , j , and i represent year, survey site and the specific environmental covariate, respectively, and n indicates the number of environmental covariates used in the model. Before being used in the model, values of the environmental covariates were standardized by dividing the difference between each value and the mean for that environmental covariate by the standard deviation. All environmental covariates were standardized except for the Sea Otter presence (value of 1) or absence (value of 0) data.

The abalone density index (I) for year y was calculated from the year effect, G , as:

$$I_y = e^{G_y} \cdot p_y \quad (\text{D.4})$$

Abalone density for year y was calculated from the density index, I , as:

$$\hat{D}_y = \frac{I_y}{\bar{I}} \cdot \bar{D} \quad (\text{D.5})$$

where \bar{I} is the mean of the density indices, calculated by dividing the sum of I across the total number of years, N , for the dataset:

$$\bar{I} = \sum_y \frac{I_y}{N} \quad (\text{D.6})$$

and \bar{D} is the mean of the observed abalone densities:

$$\bar{D} = \sum_y \frac{D_y}{N} \quad (\text{D.7})$$

There were missing environmental covariate data for some index sites, due to the lack of GPS positions for some index sites in some years. For these index sites, the environmental variables were model-estimated (predicted) by providing prior distributions:

$$V_{y,j} \sim \text{dnorm}(\mu_V, \sigma_V^2) \quad (\text{D.8})$$

$$\mu_V \sim \text{dunif}(-1, 1) \quad (\text{D.9})$$

$$\sigma_V \sim \text{dunif}(0, 10) \quad (\text{D.10})$$

where $V_{y,j}$ denotes the standardized value of the environmental covariate in year y at index site j . μ_V and σ_V are the mean and standard deviation of the prior distributions, respectively.

Vague priors were provided for all model parameters. Specifically, κ and π were each assigned a normal distribution: $\text{dnorm}(0, 100^2)$. H_y and G_y were, respectively, assigned normal distributions of $\text{dnorm}(0, \sigma_H^2)$ and $\text{dnorm}(0, \sigma_G^2)$, and H_1 and G_1 were set as $-\sum_{y=2}^N H_y$ and $-\sum_{y=2}^N G_y$. The hyper-parameters σ_H and σ_G were each assigned a uniform distribution: $\text{dunif}(0, 10)$. The coefficients, π and ϕ_i , were also each assigned a normal distribution: $\text{dnorm}(0, 100^2)$. The standard deviation of the lognormal distribution, σ , was assigned a uniform distribution: $\text{dunif}(0, 10)$.

The JAGS software program (Plummer 2003) and the R2jags package (Su and Yajima 2020) in R version 4.0.2 (R Core Team 2020) were used for the Bayesian analyses. Two chains were used for each model run. The first 10,000 MCMC samples were treated as a burn-in period and thus discarded. The following 20,000 posterior samples were obtained from the two chains. The Brooks and Gelman method (Brooks and Gelman 1998) was used for convergence diagnoses.

Evidence of convergence was warranted, as the ratio of the pooled posterior variance to the average within-sample variance deviated little from one. Convergence can be assumed when this ratio is smaller than 1.05 (Lunn et al. 2013). The ratios are smaller than 1.01 in our analyses. However, for the large adult size category (≥ 100 mm shell length) for the WCHG and WCVI survey regions, the number of posterior samples was increased to 100,000 after the first 100,000 MCMC samples were discarded as a burn-in period, due to a lack of convergence with fewer iterations. The WCVI survey region model for the large adult size category converged with the increased number of iterations, but the model for the WCHG survey region did not. This is likely due to the short time series (three years), of which one year had zero abalone observed in the large adult size category. Estimated mean densities for large adult abalone in the WCHG survey region should be cautiously interpreted.

Table D.1. Definitions of the environmental covariates used in the Bayesian hurdle model to produce standardized indices of Northern Abalone density, including raster-based variables from compiled seafloor bathymetry (Davies et al. 2019), a substrate model (Gregar and Haggarty 2017), and Regional Ocean Model System (ROMS) model outputs (Masson and Fine 2012). See Hansen et al. (2020) and Appendix B for more details.

Variable	Unit	Definition
Salinity	ppt	Mean summer bottom salinity (1998-2007) from ROMS model outputs
Tidal current speed (Tides)	m-s ⁻¹	Mean summer tidal current speed (1998-2007) from ROMS model outputs
Mean current speed (Currents)	m-s ⁻¹	Mean non-tidal summer current speed (1998-2007) from ROMS model outputs
Bathymetry (Bathy)	m	British Columbia Bathymetric Digital Elevation Model (DEM) from compiled seafloor bathymetry
Terrain ruggedness index (TRI)	–	The mean of the absolute differences between the value of a cell and the values of eight surrounding cells derived from bathymetry
Vector ruggedness index (VRM)	–	Mean difference between the value of a cell and its neighbours, but accounting for differences related to the local slope of the seafloor derived from bathymetry
Topographic position index (TPI)	–	The difference between the value of a cell and the mean value of the eight surrounding cells, indicating the site was on a "hill" or in a "valley" relative to its surroundings, derived from bathymetry
Aspect of the slope (Aspect)	degrees	Direction the seafloor slope is facing, derived from bathymetry
Exposure of site (Fetch)	m	Exposure calculated as the sum of the distance from each site to land in directions around the compass at 30 degree intervals, derived from bathymetry
Substrate type (Substrate)	–	Predicted substrate type (mud, sand, mixed or rock) interpolated to a 20 m by 20 m raster grid, derived from a substrate model
Sea Otter occupancy with expert opinion (Otter PA)	–	Presence/absence of Sea Otters at each index site (includes expert opinion for QCS and WCVI regions)

Table D.2. Environmental variables included in the Bayesian hurdle model for each size class of Northern Abalone: total (≥ 20 mm shell length), juvenile (≥ 20 mm to < 70 mm shell length), adult (≥ 70 mm shell length), and large adult (≥ 100 mm shell length).

Variable	Northern BC				Southern BC			
	Total	Juvenile	Adult	Large Adult	Total	Juvenile	Adult	Large Adult
Salinity	X	X	X	X				
Tides		X	X	X				
Currents					X	X		
Bathy			X			X		
TRI	X	X						
VRM	X	X		X				
TPI				X				
Aspect						X		
Fetch	X	X	X	X				
Substrate		X						X
Otter PA			X		X		X	

APPENDIX E. NORTHERN ABALONE DENSITIES ESTIMATED FROM THE DFO NORTHERN ABALONE INDEX SITE SURVEYS

Table E.1. Posterior mean densities (Abalone/m²) and 95% credible intervals for Northern Abalone by size category (based on shell length) in the Central Coast (CC) survey region estimated using the Bayesian hurdle model standardized by environmental variables at the index sites (see Appendix D). OD is the observed mean density, MED is the estimated posterior mean density, LED is the lower limit of the 95% credible interval (2.5% quantile), UED is the upper limit of the 95% credible interval (97.5% quantile) and n is the number of index sites included. Data are from the DFO Northern Abalone Index Site Surveys 1978-2016.

Year	n	Total (≥ 20 mm)				Juvenile (≥ 20 mm to < 70 mm)				Adult (≥ 70 mm)				Large adult (≥ 100 mm)			
		OD	MED	LED	UED	OD	MED	LED	UED	OD	MED	LED	UED	OD	MED	LED	UED
1978	12	2.40	2.99	1.85	4.48	0.27	0.46	0.22	0.81	2.13	2.38	1.44	3.54	1.10	1.12	0.79	1.46
1979	14	2.86	2.73	1.74	4.01	0.61	0.63	0.38	0.95	2.25	1.93	1.20	2.86	0.60	0.44	0.28	0.63
1980	19	3.01	3.02	1.99	4.23	1.35	1.12	0.74	1.57	1.66	1.64	1.04	2.39	0.26	0.25	0.15	0.38
1983	42	1.57	1.51	1.10	2.01	0.36	0.36	0.25	0.49	1.21	1.22	0.86	1.66	0.24	0.28	0.19	0.38
1985	28	1.49	1.55	1.08	2.13	0.32	0.34	0.22	0.50	1.17	1.22	0.83	1.70	0.33	0.30	0.21	0.42
1989	26	0.56	0.51	0.34	0.74	0.14	0.18	0.09	0.30	0.42	0.48	0.30	0.73	0.11	0.15	0.09	0.23
1993	32	0.46	0.51	0.35	0.71	0.15	0.21	0.14	0.30	0.32	0.36	0.24	0.52	0.08	0.10	0.06	0.16
1997	46	0.42	0.40	0.28	0.54	0.12	0.14	0.08	0.22	0.30	0.28	0.19	0.41	0.10	0.11	0.07	0.17
2001	55	0.27	0.26	0.18	0.36	0.10	0.14	0.09	0.21	0.17	0.19	0.12	0.29	0.04	0.05	0.03	0.09
2006	68	0.39	0.35	0.25	0.47	0.16	0.19	0.13	0.26	0.23	0.25	0.16	0.36	0.02	0.03	0.02	0.06
2011	76	0.90	0.79	0.60	1.01	0.47	0.46	0.35	0.59	0.44	0.40	0.28	0.53	0.07	0.09	0.06	0.14
2016	78	2.02	1.75	1.36	2.22	1.43	1.25	0.99	1.53	0.60	0.54	0.40	0.73	0.08	0.10	0.06	0.14

Table E.2. Posterior mean densities (Abalone/m²) and 95% credible intervals for Northern Abalone by size category (based on shell length) in the East Coast Haida Gwaii (ECHG) survey region estimated using the Bayesian hurdle model standardized by environmental variables at the index sites (see Appendix D). OD is the observed mean density, MED is the estimated posterior mean density, LED is the lower limit of the 95% credible interval (2.5% quantile), UED is the upper limit of the 95% credible interval (97.5% quantile) and n is the number of index sites included. Data are from the DFO Northern Abalone Index Site Surveys 1978-2017.

Year	n	Total (≥ 20 mm)				Juvenile (≥ 20 mm to < 70 mm)				Adult (≥ 70 mm)				Large adult (≥ 100 mm)			
		OD	MED	LED	UED	OD	MED	LED	UED	OD	MED	LED	UED	OD	MED	LED	UED
1978	51	2.53	2.84	2.11	3.64	1.27	1.27	0.95	1.65	1.25	1.45	1.03	1.91	0.29	0.33	0.23	0.44
1979	9	2.46	2.53	1.46	3.98	0.56	0.60	0.32	0.98	1.91	1.50	0.83	2.37	0.67	0.45	0.26	0.69
1984	70	0.52	0.49	0.35	0.64	0.22	0.22	0.15	0.30	0.30	0.34	0.23	0.48	0.09	0.12	0.08	0.17
1987	69	0.64	0.66	0.48	0.86	0.23	0.24	0.17	0.33	0.41	0.43	0.30	0.58	0.20	0.21	0.15	0.28
1990	69	0.46	0.42	0.31	0.56	0.19	0.24	0.16	0.33	0.27	0.28	0.19	0.38	0.10	0.12	0.08	0.17
1994	69	0.29	0.29	0.21	0.38	0.11	0.14	0.10	0.19	0.18	0.19	0.13	0.26	0.06	0.08	0.05	0.11
1998	115	0.56	0.57	0.44	0.72	0.22	0.26	0.20	0.33	0.34	0.35	0.25	0.46	0.11	0.13	0.09	0.17
2002	68	0.33	0.36	0.25	0.50	0.18	0.23	0.15	0.32	0.15	0.20	0.13	0.30	0.04	0.07	0.04	0.11
2007	82	0.41	0.40	0.29	0.52	0.26	0.29	0.21	0.38	0.15	0.17	0.11	0.25	0.03	0.04	0.02	0.07
2012	84	0.83	0.86	0.64	1.10	0.46	0.51	0.39	0.66	0.37	0.40	0.28	0.55	0.05	0.07	0.04	0.11
2017	84	3.02	2.64	2.06	3.24	2.66	2.37	1.98	2.79	0.36	0.37	0.26	0.50	0.05	0.07	0.04	0.10

Table E.3. Posterior mean densities (Abalone/m²) and 95% credible intervals for Northern Abalone by size category (based on shell length) in the West Coast Haida Gwaii (WCHG) survey region estimated using the Bayesian hurdle model standardized by environmental variables at the index sites (see Appendix D). OD is the observed mean density, MED is the estimated posterior mean density, LED is the lower limit of the 95% credible interval (2.5% quantile), UED is the upper limit of the 95% credible interval (97.5% quantile) and n is the number of index sites included. Data are from the DFO Northern Abalone Index Site Surveys 2008-2018.

Year	n	Total (≥ 20 mm)				Juvenile (≥ 20 mm to < 70 mm)				Adult (≥ 70 mm)				Large adult (≥ 100 mm)			
		OD	MED	LED	UED	OD	MED	LED	UED	OD	MED	LED	UED	OD	MED	LED	UED
2008	39	0.69	0.85	0.58	1.16	0.63	0.76	0.51	1.06	0.06	0.10	0.04	0.19	0.00	0.00	0.00	0.05
2013	48	1.03	1.21	0.93	1.51	0.72	0.83	0.60	1.11	0.32	0.33	0.24	0.42	0.02	0.01	0.00	0.03
2018	50	2.21	1.88	1.51	2.24	1.72	1.47	1.14	1.79	0.49	0.44	0.34	0.55	0.04	0.04	0.01	0.05

Table E.4. Posterior mean densities (Abalone/m²) and 95% credible intervals for Northern Abalone by size category (based on shell length) in the Queen Charlotte Strait (QCS) survey region estimated using the Bayesian hurdle model standardized by environmental variables at the index sites (see Appendix D). OD is the observed mean density, MED is the estimated posterior mean density, LED is the lower limit of the 95% credible interval (2.5% quantile), UED is the upper limit of the 95% credible interval (97.5% quantile) and n is the number of index sites included. Data are from the DFO Northern Abalone Index Site Surveys 2004-2014.

Year	n	Total (≥ 20 mm)				Juvenile (≥ 20 mm to < 70 mm)				Adult (≥ 70 mm)				Large adult (≥ 100 mm)			
		OD	MED	LED	UED	OD	MED	LED	UED	OD	MED	LED	UED	OD	MED	LED	UED
2004	19	0.04	0.06	0.02	0.11	0.02	0.02	0.00	0.05	0.02	0.04	0.01	0.06	<0.01	0.01	0.00	0.02
2009	34	0.11	0.10	0.06	0.14	0.04	0.04	0.02	0.06	0.07	0.06	0.04	0.09	0.02	0.02	0.01	0.03
2014	34	0.09	0.08	0.05	0.12	0.04	0.04	0.02	0.06	0.06	0.05	0.03	0.08	0.03	0.02	0.01	0.03

Table E.5. Posterior mean densities (Abalone/m²) and 95% credible intervals for Northern Abalone by size category (based on shell length) in the West Coast Vancouver Island (WCVI) survey region estimated using the Bayesian hurdle model standardized by environmental variables at the index sites (see Appendix D). OD is the observed mean density, MED is the estimated posterior mean density, LED is the lower limit of the 95% credible interval (2.5% quantile), UED is the upper limit of the 95% credible interval (97.5% quantile) and n is the number of index sites included. Data are from the DFO Northern Abalone Index Site Surveys 2003-2018.

Year	n	Total (≥ 20 mm)				Juvenile (≥ 20 mm to < 70 mm)				Adult (≥ 70 mm)				Large adult (≥ 100 mm)			
		OD	MED	LED	UED	OD	MED	LED	UED	OD	MED	LED	UED	OD	MED	LED	UED
2003	18	0.16	0.16	0.08	0.25	0.09	0.09	0.04	0.15	0.07	0.07	0.04	0.10	0.01	0.01	0.00	0.01
2008	23	0.11	0.13	0.08	0.19	0.07	0.09	0.05	0.12	0.04	0.04	0.02	0.07	<0.01	0.00	0.00	0.01
2013	62	0.09	0.11	0.07	0.16	0.07	0.08	0.06	0.11	0.02	0.03	0.01	0.05	0.00	0.00	0.00	0.01
2018	59	0.26	0.21	0.15	0.29	0.16	0.13	0.10	0.18	0.11	0.09	0.06	0.12	0.01	0.00	0.00	0.01

APPENDIX F. NORTHERN ABALONE SIZE-FREQUENCY HISTOGRAMS

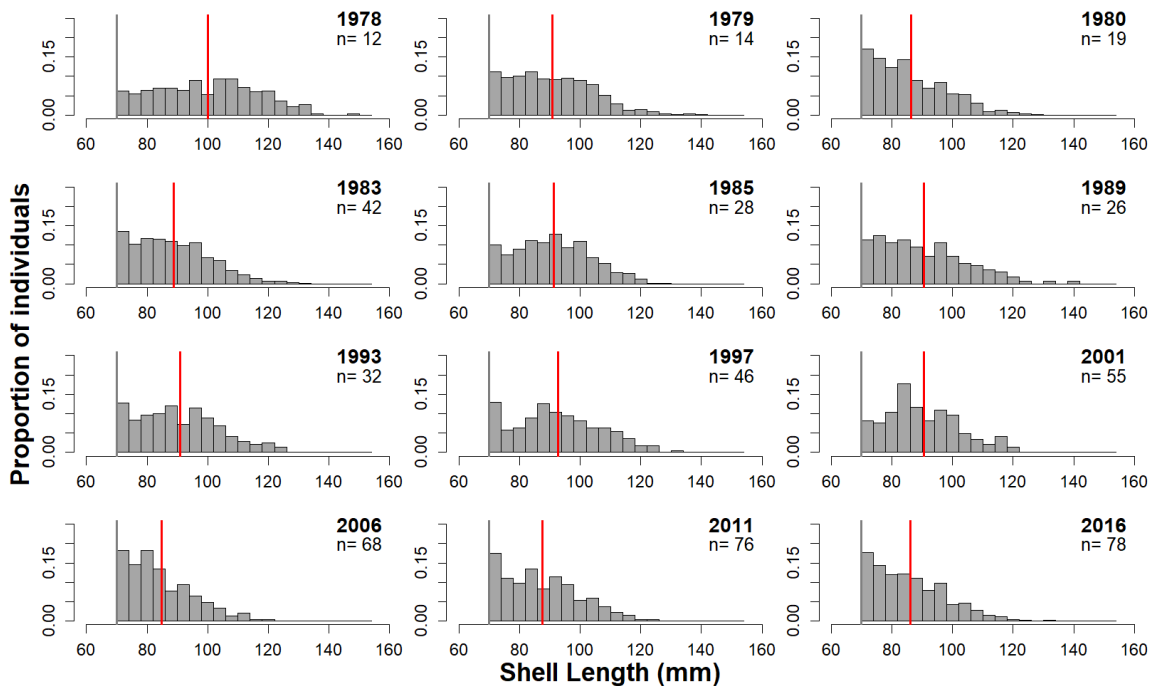
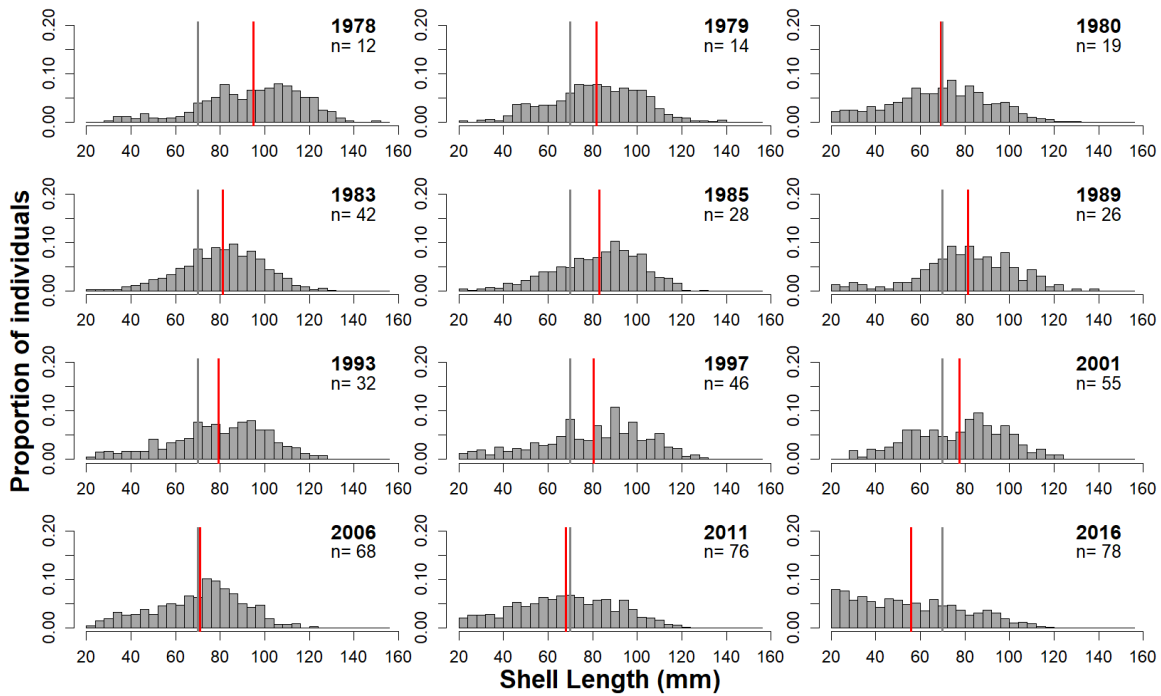


Figure F.1. Size-frequency of total (≥ 20 mm, upper panel) and adult (≥ 70 mm, lower panel) Northern Abalone measured during the DFO Northern Abalone Index Site Surveys in the Central Coast (CC) survey region between 1978-2016, where n is the number of index sites surveyed in each year. The vertical red line is the mean length (mm) for that year. The grey line is the start of the adult size category (≥ 70 mm).

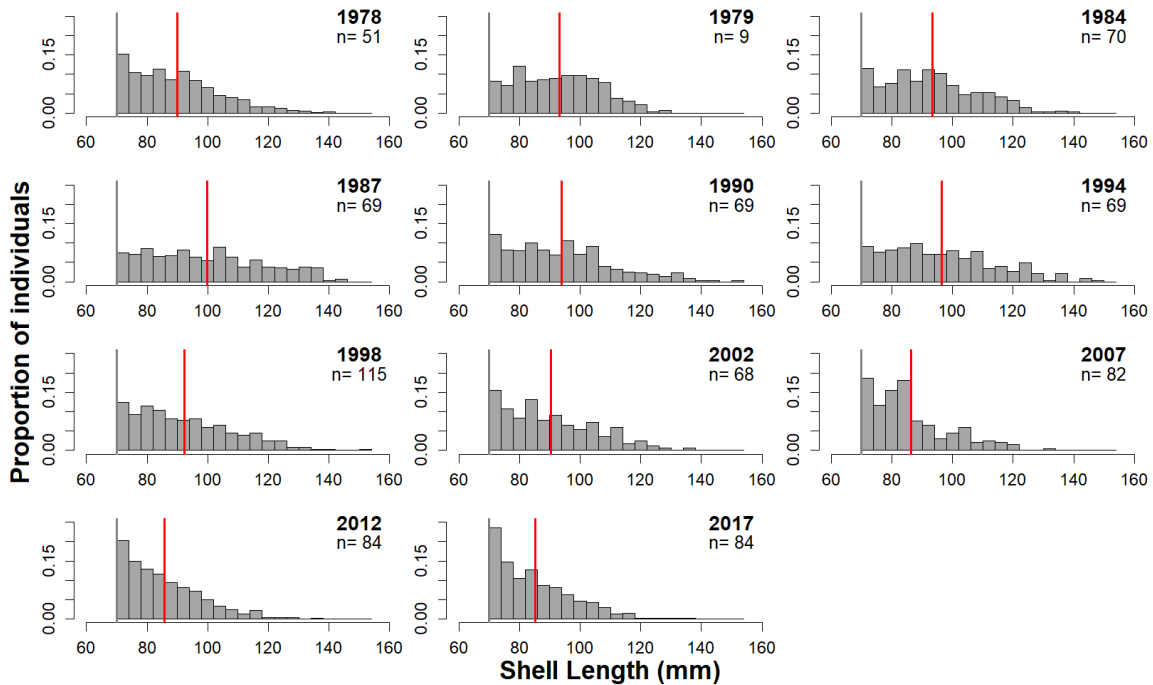
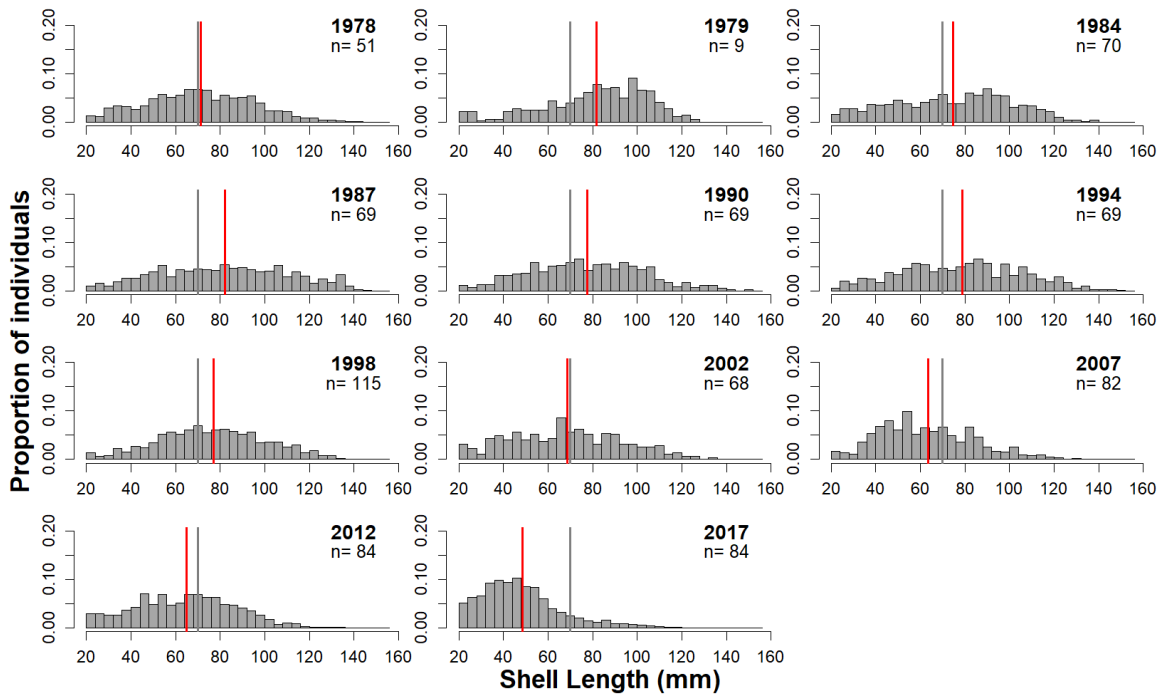


Figure F.2. Size-frequency of total (≥ 20 mm, upper panel) and adult (≥ 70 mm, lower panel) Northern Abalone measured during the DFO Northern Abalone Index Site Surveys in the East Coast Haida Gwaii (ECHG) survey region between 1978-2017, where n is the number of index sites surveyed in each year. The vertical red line is the mean length (mm) for that year. The grey line is the start of the adult size category (≥ 70 mm).

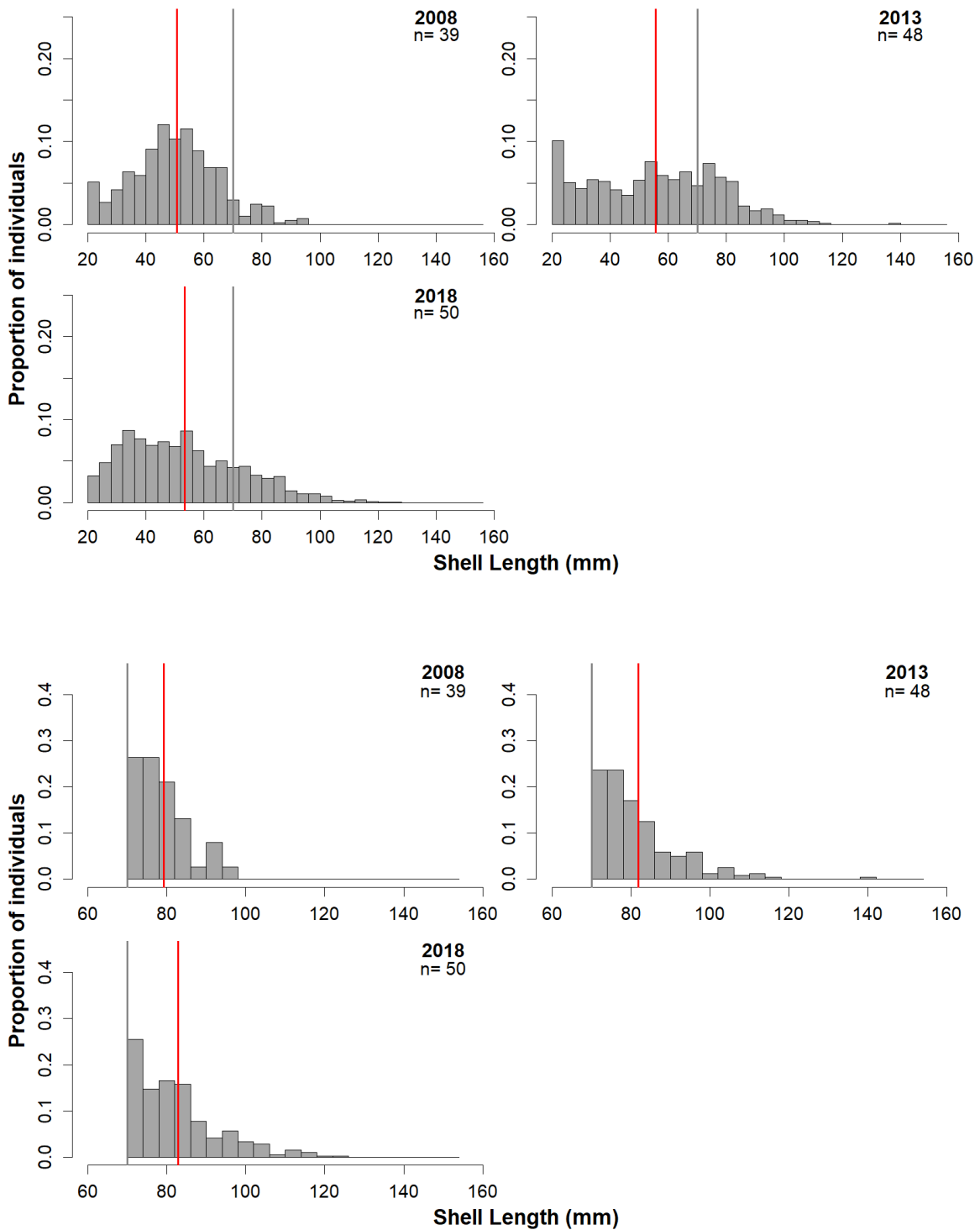


Figure F.3. Size-frequency of total (≥ 20 mm, upper panel) and adult (≥ 70 mm, lower panel) Northern Abalone measured during the DFO Northern Abalone Index Site Surveys in the West Coast Haida Gwaii (WCHG) survey region between 2008-2018, where n is the number of index sites surveyed in each year. The vertical red line is the mean length (mm) for that year. The grey line is the start of the adult size category (≥ 70 mm).

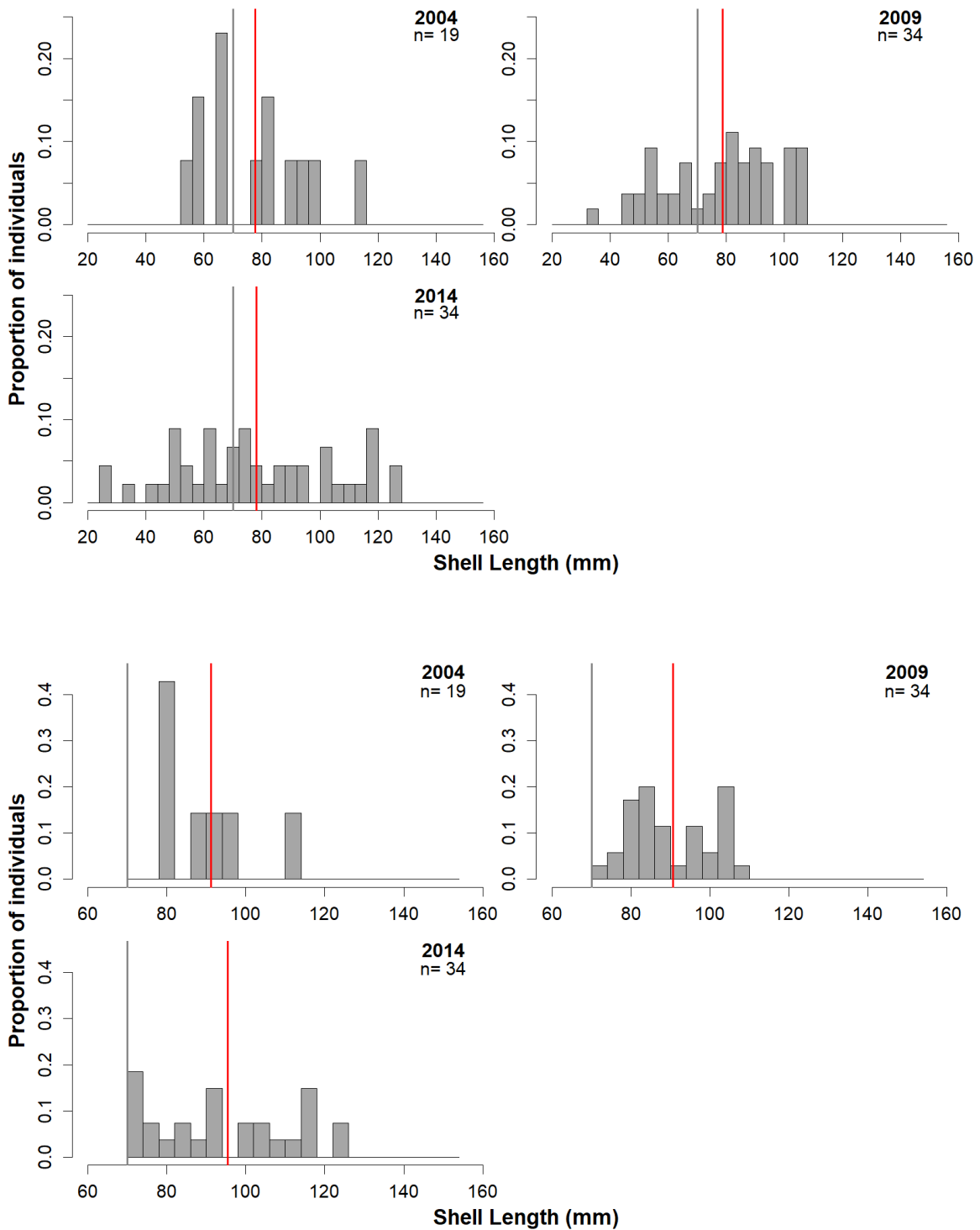


Figure F.4. Size-frequency of total (≥ 20 mm, upper panel) and adult (≥ 70 mm, lower panel) Northern Abalone measured during the DFO Northern Abalone Index Site Surveys in the Queen Charlotte Strait (QCS) survey region between 2004-2014, where n is the number of index sites surveyed in each year. The vertical red line is the mean length (mm) for that year. The grey line is the start of the adult size category (≥ 70 mm).

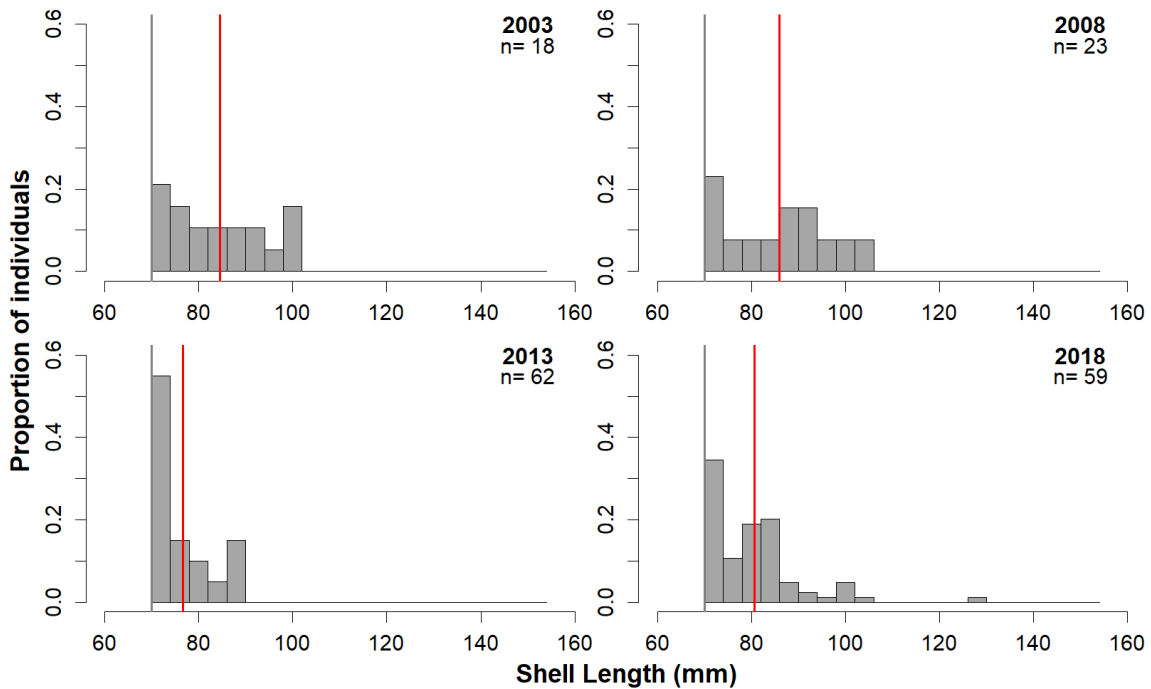
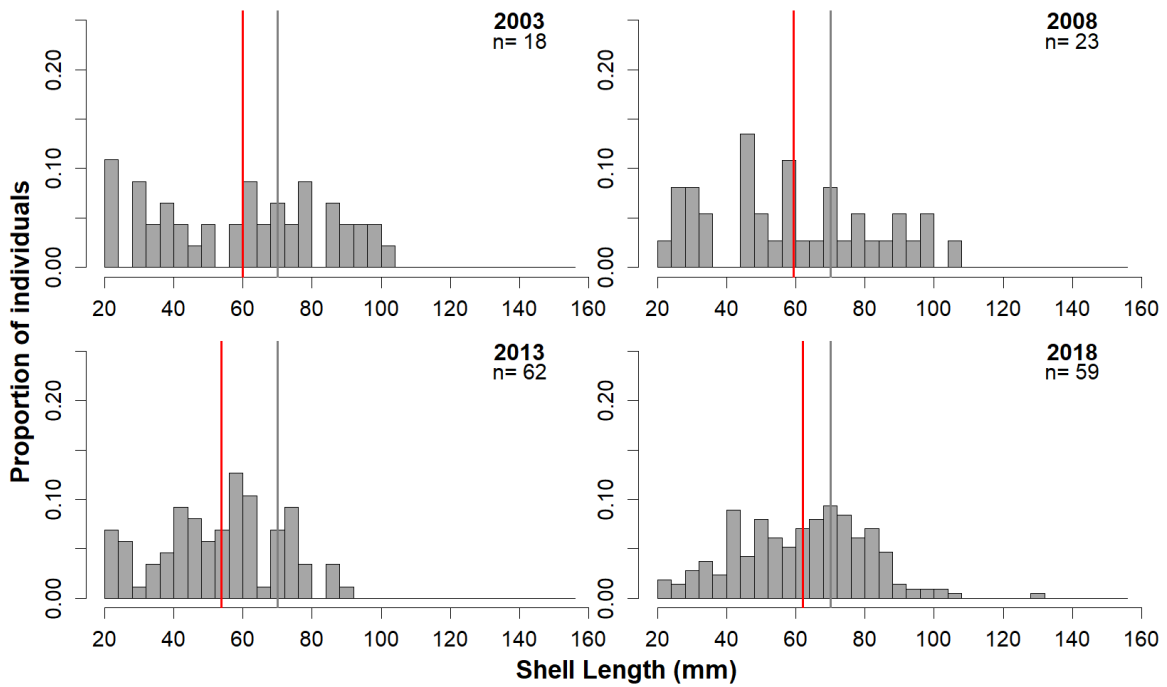


Figure F.5. Size-frequency of total (≥ 20 mm, upper panel) and adult (≥ 70 mm, lower panel) Northern Abalone measured during the DFO Northern Abalone Index Site Surveys in the West Coast Vancouver Island (WCVI) survey region between 2003-2018, where n is the number of index sites surveyed in each year. The vertical red line is the mean length (mm) for that year. The grey line is the start of the adult size category (≥ 70 mm).

APPENDIX G. MATHEMATICAL SYMBOLS USED IN MODELS

Table G.1. Mathematical symbols used in the models and their meanings.

Model	Symbol	Meaning
Cryptic Probability	C_i	State of being cryptic or emergent for individual i
	ρ_i	Probability of being cryptic for individual i
	L_i	Shell length (mm) for individual i
	α	Intercept of the linear model correlating ρ_i on the logit scale to L_i
	β	Regression coefficient of L_i in the linear model correlating ρ_i on the logit scale to L_i
Mortality Estimation	Z	Total instantaneous annual mortality rate (instantaneous annual natural mortality rate + instantaneous annual poaching rate)
	$d_{y,a}$	Observed density (m^{-2}) > 70 mm shell length in survey area a in survey year y
	$\hat{d}_{y,a}$	Predicted density > 70 mm shell length in survey area a in survey year y based on data from the previous survey, assuming no mortality
	ω_y	Number of years between the survey in year y and the previous survey
	φ	Randomly generated normal deviate
	$R4$	Randomly generated density of 4-year-olds > 70 mm shell length (new recruits)
	$R5$	Randomly generated density of 5-year-olds > 70 mm shell length (new recruits)
	f	Identification parameter that is 0 or 1 (based on number of years between two consecutive surveys)
	ε	Normal deviate
	Density Estimation	W_y
T_y		Total number of index sites surveyed in survey year y
p_y		Probability of observing non-zero density in an index site in survey year y
H_y		Effect of survey year y on p_y on the logit scale
κ		Intercept of the linear model correlating p_y on the logit scale to H_y
D_{yj}		Observed non-zero density (m^{-2}) in index site j in survey year y
$\log \hat{D}_{yj}$		Expected non-zero density (m^{-2}) on the log scale in index site j in survey year y
σ		Standard deviation on the log scale for the lognormal distribution of D_{yj}
G_y		Effect of survey year y on $\log \hat{D}_{yj}$
E_{yji}		Environmental covariate i for index site j in survey year y
π		Intercept of the linear model correlating $\log \hat{D}_{yj}$ to G_y and E_{yji}
ϕ_i		Regression coefficient on environmental covariate i in the linear model correlating $\log \hat{D}_{yj}$ to G_y and E_{yji}
I_y		Density index for survey year y
\hat{D}_y		Estimated density for survey year y
N		Number of years in the dataset
\bar{D}		Mean observed density over the survey years
\bar{I}		Mean density index over the survey years
V_{yj}		Standardized value of an environmental covariate in year y at index site j
μ_V		Mean of the prior distribution on environmental covariate V
σ_V		Standard deviation of the prior distribution on environmental covariate V
σ_G	Standard deviation of the prior distribution on year effect G_y	
σ_H	Standard deviation of the prior distribution on year effect H_y	