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Research paper

Implementing a model for data-poor fisheries based on steepness of the stock-recruitment relationship, natural mortality and local perception of population depletion. The case of the kelp *Lessonia berteroana* on coasts of north-central Chile



Cristian M. Canales^{a,*}, Claudia Hurtado^b, Carlos Techeira^b

- a Laboratory of Marine Population Dynamics and Statistical Modelling (DIMARE), Escuela de Ciencias del Mar, Pontificia Universidad Católica de Valparaíso, Chile
- ^b División de Investigación Pesquera, Instituto de Fomento Pesquero (IFOP), Chile

ARTICLE INFO

Handled by A.E. Punt Keywords: Kelp population model Data-poor fishery Stock assessment Depletion rate Steepness Beached seaweed

ABSTRACT

Over the past decade, it has become increasingly important to develop and utilize specific methods for modeling fisheries with limited data. The sustainable development of aquatic resources and fisheries management requires an understanding of species exploitation despite limited knowledge or poor data. Many data-limited assessment methods are based on catch data and assumptions, with little consideration given the biological aspects of the species under study. Herein, a population depletion model is reparametrized to simplify biological reference point estimates related to a maximum sustainable yield. This model includes biological aspects (parameter probability distributions), the fishery history, and levels of population depletion as perceived by the fishers. This approach was used with landings data (2000–2014) for *Lessonia berteroana*, a brown kelp harvested off north-central Chile (25°17′S–29°30′S). Management of this kelp is in its early stages, with no formal procedures established for assessment. We estimated population variables and reference points for three zones and considered beached seaweed to represent biomass mortality due to natural causes. The results, which accounted for uncertainty in resilience (steepness of the stock-recruitment relationship), natural mortality, process error, and minimum proportions of beached kelp, contributed to our understanding of this fishery and allowed us to propose an assessment tool for fisheries with poor or limited data.

1. Introduction

Limited knowledge and low-quality data hinder our understanding of species exploitation and the creation of sustainable fisheries management practices, resulting in an important challenge for countries wishing to generate economic benefits from aquatic resources. Because the status of many fish stocks remain unknown, the development and implementation of fisheries management in the face of limited or poor data have gained importance over the past decade. For example, 70% of allowable biological catches for several species (504 stock units in 2014) exploited in the USA are calculated based on limited or poor data (Newman et al., 2015).

When data are limited, management models may be based on: (1) recent catch statistics (e.g., Restrepo et al., 1998; Gabriel and Mace, 1999; MacCall, 2009), (2) depletion models parameterized in terms of catch series (e.g., Kimura et al., 1984; Dick and MacCall, 2011; Martell and Froese, 2013; Sabater and Kleiber, 2014), or (3) the most recent

reliable estimates of abundance from surveys; these methods were compiled by Carruthers et al. (2014) and Newman et al. (2015). Dick and MacCall's (2011) hybrid method allows for more flexibility in the latent production function proposed by Mangel et al. (2010), explicitly incorporating the Beverton-Holt stock-recruitment relationship (BHSRR). In this model, population dynamics are expressed as a function of four variables or critical parameters as a priori distributions: biomass depletion or the point at which the maximum sustainable yield (MSY) is reached relative to the virgin biomass (B_{msv}/B_0) , natural mortality rate (M), fishing mortality rate or the point at which the MSY is achieved relative to M (F_{msy}/M), and the level of biomass depletion assumed for a particular year (e.g., Dick and MacCall, 2011; Cope, 2013). The model is then fitted using Monte Carlo methods that ignore possible correlations between, for example, M and F_{msy}/M . We reparameterized the Mangel et al. (2010) and Dick and MacCall (2011) models to propose an approximation that would reduce the number of parameters and incorporate more relative knowledge of population

E-mail addresses: cristian.canales.r@pucv.cl, cristiancanal@gmail.com (C.M. Canales).

^{*} Corresponding author.

parameters. For this, we considered the latent production function in terms of M, the degree of resilience defined by the steepness (h) of the stock-recruitment relationship, and virgin biomass (B_0).

We applied this approximation to the landing statistics for *Lessonia berteroana*, a brown kelp known locally as "huiro negro" (ex *Lessonia nigrescens*, González et al., 2012). The main area of exploitation (40% of national landings) is located off north-central Chile (25°–30°S). This artisanal fishery has experienced a major increase ($\gg > 7$ times) in landings over the past 15 years in response to greater demand from international markets (Vásquez et al., 2012).

L. berteroana is the kelp species of greatest commercial interest in Chile. Annual landings reach ~50,000 tons (SERNAPESCA, 2015), or ≫ > 75% of all brown seaweed (Macrocystis spp, L. trabeculata, L. spicata, L. berteroana) harvested in Chile (Vásquez, 2008; Vásquez et al.,2012). L. berteroana has been described as a fast-growing, highly productive species (Santelices and Ojeda, 1984; Tala and Edding, 2007), with high natural mortality (Santelices and Ojeda, 1984; González et al., 2002). Its population structure is semi-closed (Tellier et al., 2009, 2011). The species inhabits rocky substrates, and adult plants appear to control recruitment by saturating the available space (Santelices and Ojeda, 1984). The same has been reported for Macrocystis pyrifera (Dean et al., 1989) and Alaria marginata (McConnico and Foster, 2005).

As a species of the order Laminariales, *L. berteroana* plays an important ecological role in structuring marine ecosystems and serves as an area of reproduction and refuge for a number of marine invertebrates and vertebrates (e.g., Jones et al., 1994; Paine, 1994; Castilla, 2000; Thiel et al., 2007). In this sense, *L. berteroana* helps maintain biological and genetic diversity within the local marine community (Graham et al., 2007; Vega et al., 2016). This kelp consequently has economic, social, and ecological importance. Its fisheries are managed based on regional-scale plans. However, given the lack of monitoring programs for important variables and the paucity of research on population dynamics, assessment methodologies must be developed and implemented for the *L. berteroana* fishery.

To create a population dynamics model able to account for uncertainty, we integrated knowledge of the species' biology off Chile, its fishery, landings statistics, and the perception of population depletion (δ) within the fishing community. This allowed us to generate initial estimates of reference variables (related to MSY) that could be useful for management of the L. berteroana fishery. We evaluated structural uncertainty related to population and fishery parameters, thereby contributing to a better understanding of stock dynamics. This also allowed us to propose a model that might be useful for the management of other data-poor fisheries.

2. Materials and methods

2.1. Fisheries and data

L. berteroana landings statistics (2000-2014) were taken from the free access zones off the Atacama Region, north-central Chile (25°17'S-29°30'S). This information was provided by the National Fisheries Service (SERNAPESCA) for the three main ports where this kelp is landed: Chañaral (26°20'S), Caldera (27°S), and Huasco (28° 27'S) (Fig. 1). Moreover, 118 artisanal fishers from the region (61% of the total), averaging 20 years of experience in the fishery, were interviewed to generate information regarding L. berteroana population depletion, a parameter that is often assumed (e.g., Dick and MacCall, 2011; Martell and Froese, 2013). Interviews were performed by personnel from the Fisheries Development Institute (Instituto de Fomento Pesquero, IFOP), from 12 to 16 December 2016. The random design covered 19 fishing areas located on isolated beaches around the aforementioned landing ports (46% near Caldera, 12% near Chañaral, 42% near Huasco). Taking into account the fisher's years of experience, the main question posed was: What biomass proportion do you believe is left at sea?. The accuracy of the information gathered was poor (subjective perception), so data were tabulated into three discrete intervals: (\ll 0.4, 0.4–0.6, \gg > 0.6). Later, the frequency of these empirical results (Fig. 2) was considered to be a source of variability (Section 2.3).

2.2. Depletion model

Our approximation was based on the simple delay-difference model proposed by Mangel et al. (2010) and Dick and MacCall (2011):

$$B_{y} = (B_{y-1} - H_{y-1}) + P_{y}$$
(1)

where B_y is the biomass of all mature and fully recruited individuals (exploitable stock), H_y is the effective harvest of fully recruited individuals in year y, and P_y is the function of latent annual production:

$$P_{y} = \frac{\alpha B_{y-d}}{\beta + B_{y-d}} - mB_{y-d} \tag{2}$$

The first term of this function is the biomass of new recruits to the exploitable stock generated by existing biomass (with d years of lag, assumed to be 1) defined by the BHSRR. The second term is the combined effects of somatic growth and adult natural mortality. The BHSRR represents kelp dynamics considering that the asymptotic segment is determined by density dependence. This is motivated by intraspecific competition for substrate between adults, juveniles, and post-settlement recruits, i.e., permanent replacement of individuals among the population occurs given limited substrate (recruitments vs natural death). $m = (1 - e^{-M})$, where M is the instantaneous natural mortality rate. The parameters α and β of the BHSRR may be represented as a function of the steepness (h) of the stock-recruitment relationship and the virgin biomass (B_0) (Mace and Doonan, 1988; Francis, 1992). The latent productivity of a population is null (P = 0) in an unfished virgin state (i.e., B_0 , R_0). Thus, it can be deduced from Eq. (2) that the original recruitment is $R_0 = mB_0 = (1 - e^{-M})B_0$ and that the parameters of BHSRR are a known function of h, m, and B_0 . On the other hand, if the derivative of the function P (Eq. (2)) is equal to 0 with respect to the biomass, it may be demonstrated (See Appendix A) that B_{msy} is a function of m, h, and B_0 :

$$B_{msy} = -\beta + \sqrt{\frac{\alpha\beta}{m}} = B_0 \frac{(h-1+2\sqrt{h(1-h)})}{5h-1}$$
 (3)

Substituting Eq. (3) into Eq. (2) leads to an equation for MSY:

$$MSY = \alpha + m\beta - 2\sqrt{\alpha\beta m} = mB_0 \frac{(3h + 1 - 4\sqrt{h(1 - h)})}{5h - 1}$$
 (4)

 F_{msy} is the ratio between MSY and B_{msy} . All of these biological reference points are now expressed in terms of B_0 , h, and M.

2.3. Modeling for kelp fisheries

Kelp landing statistics for north-central Chile are composed of two components: harvested specimens (i.e., manually extracted) and those gleaned from the beach after natural detachment. This second component is uncertain and likely varies among years. Moreover, field experience indicates that the relative contribution of gleaned kelp is important at the start of the fishery when commercial demand is low (as was the case in recent years) and following partial depletion of $L.\ berteroana$ in the intertidal belt (i.e., beached kelp comes from less accessible stocks). For practical purposes and based on this information, we assumed that the annual proportion of beached kelp (π) was inversely proportional to the total landings (D), as:

$$\pi_{y,z} = 1 - (1 - \rho_z) \left(1 - \frac{D_{y,z}}{max\{D_{y,z}\}} \right)$$
 (5)

where ρ_z is an assumed minimum historical proportion of beached kelp

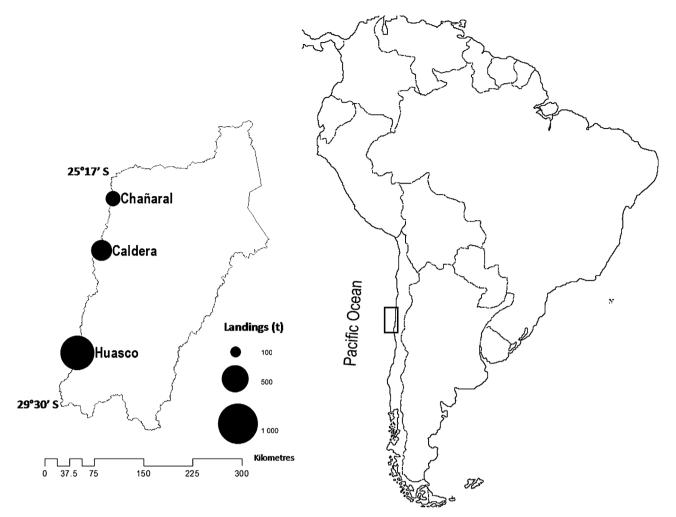


Fig. 1. Area of study represented by a rectangle over South America map, and the three main ports of Lessonia berteroana fishery in central north Chile. Landing magnitude in each port are represented by circles size.

in the z^{th} zone. Thus, the effective harvest (H) used in the population dynamics model (Eq. (1)) comes from multiplying the factor $(1-\pi_{y,z})$ by the annual landing statistics $(D_{y,z})$ such that the product $\pi_{y,z}D_{y,z}$ (seaweed gleaned from the beach) is less than $mB_{y,z}$ (biomass of seaweed that died due to natural causes). This reduces the problem to calculating the virgin biomass B_0 , which reproduces the value of population depletion (δ) in recent years, considering scenarios of h, ρ , M, and the official landing statistics.

2.4. Sources of uncertainty

Each parameter was considered to be uncertain: steepness (h) was assumed to be Beta distributed (Shertzer and Conn, 2012) with parameters (a=15.1, b=4.3) corresponding to a 95% confidence interval (CI95%) of [0.6, 0.9], i.e., moderate to high resilience. Authors such as Vásquez (2008) and Thomas et al. (2016) have indicated empirical survival rates (in biomass) of adult plants between 66% and 74% after a year's monitoring. Consequently, $M=0.3 {\rm yr}^{-1}$ was considered to be a mean value of a lognormal distribution with a standard error of 0.2, i.e., a CI95% between 0.2 ${\rm yr}^{-1}$ and 0.4 ${\rm yr}^{-1}$. In the same way, and based on the information generated in the field survey, the minimum beached kelp proportion (ρ) was assumed to be uniformly distributed within a range of [0.1–0.3] (Fig. 3).

A Monte Carlo procedure, with 5000 random samples taken from probability distributions of h, M, and ρ by zone, was used to characterize uncertainty. In addition, a process error term was also included

when determining latent production. This term was assumed to be normally distributed $\varepsilon \sim N(0,\sigma^2)$, with $\sigma=0.3$ (Fig. 3). Two alternatives were considered regarding process error: either the main environmental perturbation occurred on recruitment (Eq. (6)a) or natural mortality had the most important effect on the function of annual latent productivity (Eq. (6)b), i.e.:

$$P_{y} = \begin{cases} \frac{\alpha B_{y-d}}{\beta + B_{y-d}} e^{\varepsilon_{y} + 0.5\sigma^{2}} - mB_{y-1} & (a) \\ \frac{\alpha B_{y-d}}{\beta + B_{y-d}} - mB_{y-1} e^{\varepsilon_{y} + 0.5\sigma^{2}} & (b) \end{cases}$$
(6)

For each port, a population depletion value was randomly sampled from its empirical distribution and converted to a continuous variable based on a uniform distribution delimited by the sample value. The rationale for this approach was that estimates of depletion made by artisanal fishers varied within a range. In order to analyze these results, different intervals (or scenarios) of steepness and natural mortality as well as minimum beached kelp proportions were considered. For each scenario, we recorded the median and standard deviation of the main performance variables: B_0 , B_{msy} , current biomass relative to $B_{msy} - B/B_{msy}$ k, F/F_{msy} , and MSY. In addition, the greatest amount of kelp gleaned from the beach was also estimated. For this, we assumed that all biomass lost to natural mortality ($m B_{msy}$) was at the upper limit. The model's code for calculation was written with Scilab 5.5.2 (Scilab, 2012) and the Simplex algorithm was used as a root-finding algorithm.

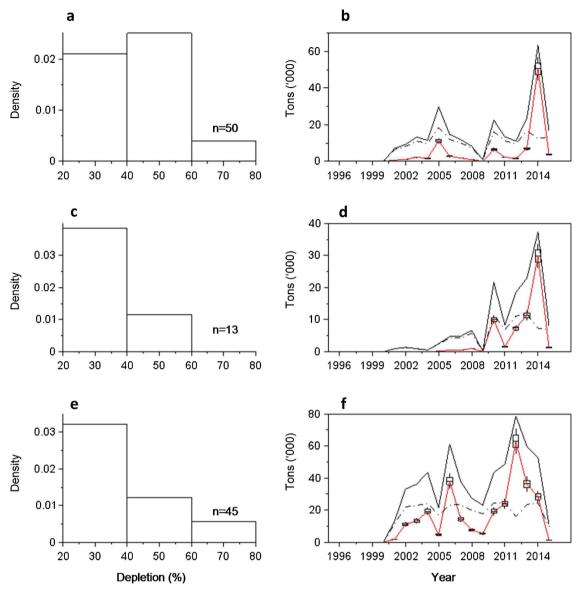


Fig. 2. Empirical distribution of Lessonia berteroana depletion perceived by artisanal fishers (n) by port: Caldera (a), Chañaral (b) and Huasco (c). Landings (black lines), effective catch (red line and boxplot) and proportion of beached seaweed (segmented line) by port and year: Caldera (d), Chañaral (e) and Huasco (f). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3. Results

3.1. Exploration of the model under equilibrium conditions

By exploring and parameterizing the model described by Mangel et al. (2010), we were able to understand the relationship between natural mortality, steepness (h), and productivity (Fig. 4a), as well as the decrease in B_{msy} given increased F_{msy} (Fig. 4b). In a similar way to Mangel et al. (2010), our results showed that MSY may exceed B_{msy} , depending on the values of h and M. Species with high natural mortality rates (M) were more productive for the same value of steepness (h) (Fig. 4c), indicating that latent productivity was very high and may have constituted the greatest part of the annual population biomass. The production curve was asymmetric, so MSY was not necessarily obtained at 50% of the virgin biomass, as it was in Schaefer's model. Under scenarios of high resilience in recruitment, for example, when $h \gg > 0.8$, the model generated values of $B_{msv} \ll 0.2B_0$ and values of $F_{msy} \gg 2 M$ (Fig. 4b). When steepness was moderate, as in this study (h = 0.6–0.8), B_{msy} fell between 0.2 and 0.3 B_0 , MSY was greater than or equal to 0.5 B_{msy} , and F_{msy} reached values as high as 0.9–1.9 M.

3.2. Model application in kelp fisheries

By applying the model to *L. berteroana* by zone, we were able to evaluate its behavior with respect to the characteristics of the data and assumptions about process error. Despite its limitations, the model generated useful reference values for fishery management. The results showed that both the scale and annual trajectory of biomass at all zones/ports depended on the process error scenario. If process error mainly affected recruitment, the biomass trajectory (median) showed slight growth until exploitation began and a smaller population scale in general. However, when process error affected mainly natural mortality, biomass error bands were significantly larger for all areas (Fig. 5, Table 1).

The results of the model indicated that the biomass of *L. berteroana*'s around Caldera declined primarily after 2014, when 50,000 mt of kelp were removed (Fig. 5a, b). Likewise, around Chañaral, the biomass reduction began in 2010 and intensified after 2012, when the harvest reached 30,000 mt (Fig. 5c, d). Biomass around Huasco, with its more extensive history of kelp exploitation, began to decline in 2005, but then increased after intense exploitation (63,000 mt) in 2011 (Fig. 5e,

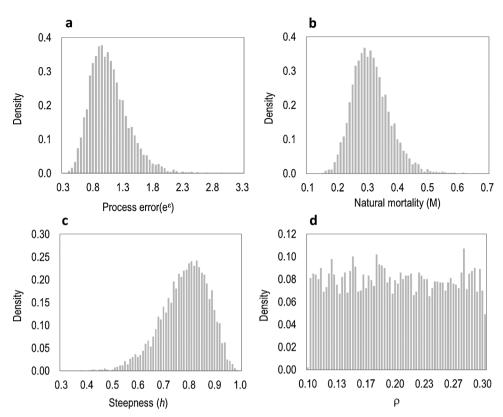


Fig. 3. Probability distributions considered as stochastic variability sources in the model's simulations. Process error (a), Natural mortality (b), Steepness (c) and minimum beached seaweed proportion (p) (d).

f). At all three ports, biomass reduction could be explained by removal levels that exceeded the MSY (Fig. 5) over many years without dropping the population below the target biomass, B_{msy} . More recent lower landings were explained by smaller harvests caused by low abundances.

MSY / B_{msy}

2.00

1.50

1.00 0.50

0.00

0.8 1.0

1.2

0.4

0.6

8.0

1.0

The model showed that, in recent years, the fishery was supported mainly by beached kelp.

An expected linear relationship between population depletion as perceived by fishers and estimates of virgin biomass (B_0) was not

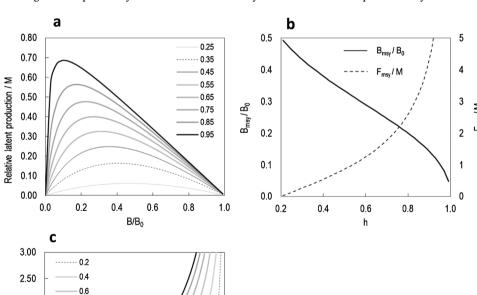


Fig. 4. Equilibrium analysis of the depletion model based on steepness and natural mortality. a) Biomass depletion ratio vs relative latent production (to M) for different steepness (lines) values. b) Steepnes (h) values vs optimal depletion ratio (B_{msy}/B_0) and ratio of F_{msy}/M . c) Steepnes (h) values vs Relative Maximum Sustainible Yield (MSY/B_{msy}) for different instantaneous natural mortality rates (represented by each line).

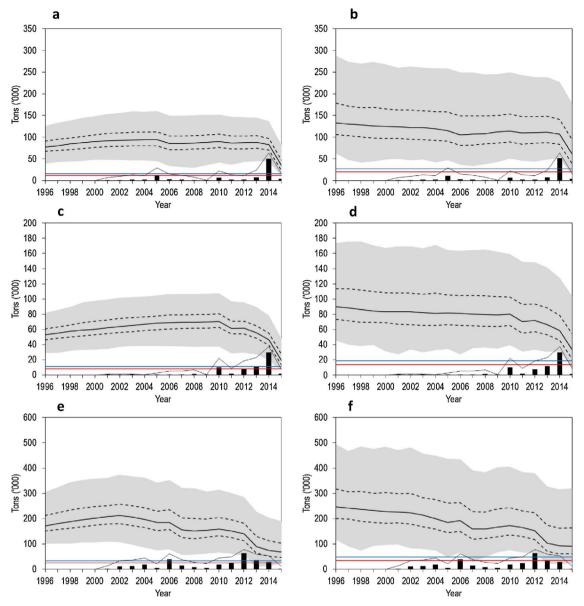


Fig. 5. Biomass, landings and harvest of Lessonia berteroana biomass by year for two process error types: in recruitment (left panels) and natural variations in mortality (rigth panels): Caldera (a, b), Chañaral (c, d), Huasco (e, f). Gray shaded area represents the maximum and minimum values. Dotted lines are the interquartile range and solid line the median. Black bar is the harvest and black thin line is the total landing (harvest plus beached seaweed). Horizontal red and blue lines are median values of B_{msy} and MSY, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

observed, particularly when process errors affected natural mortality (Fig. 6a, b, c), and for B_0 , B_{msy} , and MSY (Table 1). The scatter plot between the depletion level vs B_0 suggested a non-linear relationship, especially when natural mortality was subject to process error (Fig. 6d, e, f). In the same way, but considering relative biomass vs relative fishing mortality in 2014 (B/B_{msy} and F/F_{msy}), the results showed that, on average, fishing mortality at all ports was below F_{msy} . The probability of this occurring depended on the process error scenario. The probability of overfishing ($F \gg > F_{msy}$) was estimated at 0.31 (Caldera), 0.37 (Chañaral), and 0.12 (Huasco), if process error affected recruitment (Fig. 7a, b, c). These probabilities fell to 0.21, 0.23, and 0.07, respectively, when process error affected mainly natural mortality (Fig. 7d, e, f).

A different result was obtained from the analysis based on effective harvest (H) relative to MSY from 2014. The distribution of B/B_{msy} vs H/MSY showed, on the one hand, greater dispersion along both axes compared to B/B_{msy} vs F/F_{msy} (Fig. 8). On the other hand, the risk of that year's harvest exceeding MSY was estimated to be close to 100%. In

fact, the risk of overfishing by harvest (i.e., $p(H/MSY \gg > 1)$) was 1.0 around Caldera and Chañaral and 0.49 around Huasco if we considered process error to only affect recruits (Fig. 8a, b, c). This risk decreased to 0.96 (Caldera), 0.98 (Chañaral), and 0.25 (Huasco) when the process error affected natural mortality. On the other hand and despite the larger B_{msy} , H/MSY for the harvests around Caldera and Chañaral should have been reduced to 78% and 74%, respectively, whereas exploitation around Huasco seemed to be close to MSY (Table 1).

Some of the results were explained by the fact that B_0 , B_{msy} , and MSY were greater when process error affected M than when it affected recruitment (Table 1). Moreover, this last source of error seemed to be more important than variations in the minimum ratio of beached kelp (ρ) and the steepness (h) value. When comparing point estimates of B_0 , B_{msy} , and MSY between scenarios of ρ and h, a coherent pattern was only apparent around Huasco, where increments in the latter two parameters led to the expected decline of B_0 , B_{msy} , and MSY. In other words, the highest resilience (h) led to a lower B_{msy} value, although estimates of these variables were always imprecise $(CV) \gg 0.35$;

Table 1
Median of virgin biomass (B_0), target biomass at MSY (B_{msy}) an ratios related to Maximum Sustainable Yield (MSY), Fishing mortality (F), harvest (F), harvest (F), and F0. between a gathered on beach (F0, by zone. Coefficients of variation are in parentheses. Biomass measures are given in thousands tons. F1 represents the joint probability calculated as a ratio of conditioned events by F1 and F2. Population indicators are related to 2014.

Source	error	Process error in recruitment									Process error in natural mortality							
Zone	ρ	h	Р	B_0	B/B _{msy}	F/F _{msy}	MSY	B_{msy}	H/MSY	GA_{msy}	B_0	B/B _{msy}	F/F _{msy}	MSY	B_{msy}	H/MSY	GA_{msy}	
Caldera	0.1-0.2	<0.75	0.17	76.3 (0.23)	5.25 (0.27)	0.83 (0.49)	11.9 (0.28)	15.6 (0.34)	4.23 (0.29)	4.0 (0.38)	133.1 (1.14)	3.94 (0.29)	0.61 (0.7)	19.9 (1.13)	27.4 (1.28)	2.55 (0.44)	7.1 (1.31)	
		0.75-0.85	0.20	78.9	5.31	0.80	11.9	15.4	4.36	4.0	135.4	3.98	0.58	20.4	27.8	2.44	7.1	
	0.2-0.3	> O OF	0.13	(0.25) 73.5	(0.30) 5.27	(0.49) 0.84	(0.36) 10.8	(0.37) 15.6	(0.3) 4.59	(0.43) 3.8	(2.5) 126.9	(0.30) 3.68	(0.72) 0.72	(1.57) 18.1	(4.36) 27.0	(0.48) 2.81	(3.58) 6.9	
		>0.85	0.13	(0.25) 78.2	(0.30) 5.18	(0.63) 0.83	(0.36) 11.7	(0.32) 16.0	(0.34) 4.26	(0.36) 4.2	(1.04) 135.5	(0.28) 3.80	(0.6) 0.65	(1.04) 20.0	(1.15) 27.8	(0.4) 2.5	(1.15) 7.3	
		<0.75		(0.25)	(0.28)	(0.49)	(0.31)	(0.35)	(0.31)	(0.34)	(2.56)	(0.33)	(0.69)	(3.03)	(2.33)	(0.45)	(2.47)	
		0.75-0.85		77.1 (0.25)	5.22 (0.28)	0.83 (0.62)	11.3 (0.34)	15.8 (0.34)	4.49 (0.33)	4.0 (0.40)	132.4 (0.72)	3.91 (0.36)	0.62 (0.62)	20.4 (0.81)	27.5 (0.8)	2.57 (0.4)	7.0 (0.9)	
		>0.85	0.13	78.7 (0.25)	5.11 (0.26)	0.82 (0.48)	11.6 (0.31)	16.3 (0.35)	24.36 (0.28)	4.3 (0.32)	131.9 (0.56)	3.54 (0.34)	0.63 (0.71)	20.0 (0.69)	27.1 (0.64)	2.52 (0.42)	7.1 (0.77)	
		Total		77.1	5.22	0.83	11.5	15.8	4.38	4.0	132.5	3.81	0.63	19.8	27.4	2.57	7.1	
		Total		(0.25)	(0.28)	(0.53)	(0.33) 7.9	(0.34)	(0.31)	(0.37)	(1.42)	(0.32)	(0.67)	(1.38)	(1.76)	(0.43)	(1.70)	
Chañaral	0.1-0.2	<0.75	0.17	(0.21)	4.22 (0.32)	0.84 (0.64)	(0.32)	10.8 (0.28)	3.81 (0.32)	2.7 (0.34)	91.6 (0.51)	3.06 (0.3)	0.67 (0.58)	13.3 (0.62)	19.2 (0.56)	2.17 (0.35)	5.1 (0.56)	
		0.75-0.85	0.20	52.5 (0.22)	4.19 (0.3)	0.89 (0.51)	7.8 (0.32)	11.2 (0.31)	3.89 (0.27)	2.8 (0.36)	88.7 (0.60)	3.29 (0.34)	0.65 (0.78)	13.8 (0.66)	19.1 (0.61)	2.13 (0.42)	5.0 (0.60)	
		>0.85	>0.85 0.13	54.6 (0.21)	4.23 (0.3)	0.90 (0.52)	7.9 (0.31)	11.5 (0.29)	3.64 (0.29)	2.8 (0.34)	90.5 (0.5)	3.32 (0.37)	0.58 (0.65)	14.0 (0.47)	17.8 (0.65)	2.07 (0.36)	4.9 (0.63)	
	0.2-0.3	<0.75	0.18	53.4	4.33	0.85	8.2	10.6	3.60	2.8	87.7	3.18	0.71	12.8	18.4	2.32	4.6	
		0.75-0.85	0.19	(0.2) 53.3	(0.31) 4.25	(0.6) 0.88	(0.27) 7.7	(0.33) 11.1	(0.3) 3.78	(0.33) 2.8	(0.94) 92.0	(0.27) 3.11	(0.63) 0.67	(1.07) 13.8	(1.16) 18.6	(0.39) 2.11	(1.46) 4.7	
				(0.22) 50.3	(0.29) 4.26	(0.5) 0.90	(0.29) 7.9	(0.33) 10.5	(0.27) 3.88	(0.36) 2.7	(1.65) 88.4	(0.35) 3.15	(0.64) 0.72	(1.78) 13.6	(2.22) 18.0	(0.38) 2.15	(3.10) 4.7	
		>0.85	0.13	(0.24)	(0.28)	(0.47)	(0.33)	(0.36)	(0.27)	(0.40)	(0.58)	(0.43)	(0.55)	(0.65)	(0.66)	(0.38)	(0.65)	
		Total		52.6 (0.22)	4.24 (0.30)	0.88 (0.54)	7.9 (0.31)	10.9 (0.32)	3.77 (0.29)	2.8 (0.36)	89.8 (0.80)	3.18 (0.34)	0.67 (0.64)	13.5 (0.88)	18.5 (0.98)	2.16 (0.38)	4.8 (1.17)	
Huasco	0.1-0.2	<0.75	0.17	198.1 (0.27)	1.70 (0.36)	0.75 (0.56)	23.6 (0.30)	49.5 (0.34)	1.25 (0.25)	12.3 (0.36)	279.8 (1.07)	1.59 (0.35)	0.59 (0.64)	33.0 (1.49)	73.8 (1.02)	0.91 (0.32)	19.2 (1.31)	
		0.75-0.85	0.20	182.5 (0.38)	2.05 (0.41)	0.55 (0.55)	28.2 (0.46)	36.4 (0.38)	1.06 (0.27)	9.4 (0.44)	250.7 (0.7)	1.92	0.43 (0.57)	37.9 (0.70)	49.1 (0.70)	0.78 (0.30)	12.4	
		>0.85	0.13	174.2 (0.36)	2.90 (0.5)	0.32 (0.8)	32.0 (0.38)	26.9 (0.36)	0.94 (0.25)	7.0 (0.4)	242.8	2.61 (0.42)	0.28	44.1 (0.65)	37.9 (0.73)	0.68	9.4 (0.73)	
	0.2-0.3	<0.75 0.75-0.85	0.18	161.8	1.64	0.77	20.9	42.0	1.28	10.9	254.2	1.57	0.55	30.3	62.9	0.87	16.2	
				(0.3) 165.4	(0.34)	(0.6) 0.45	(0.26)	(0.39)	1.05	(0.33)	(0.5)	(0.35)	0.43	(0.62)	(0.55)	(0.31)	(0.65)	
		>0.85	0.13	(0.33) 162.5	(0.35) 3.00	(0.66) 0.30	(0.30) 29.5	(0.36) 25.0	(0.23) 0.91	(0.35) 6.3	(1.21) 197.3	(0.39) 2.39	(0.61) 0.32	(1.25) 35.3	(1.21) 30.0	(0.31) 0.75	(1.24) 7.8	
			0.13	(0.4) 174.1	(0.39)	(0.74) 0.52	(0.36)	(0.43)	(0.26) 1.08	9.0	(1.29) 240.5	(0.52)	(0.66)	(1.10) 35.7	(1.27) 49.5	(0.30)	(1.04) 12.7	
		Total		(0.34)	(0.39)	(0.65)	(0.34)	(0.38)	(0.25)	(0.38)	(0.91)	(0.40)	(0.62)	(0.97)	(0.92)	(0.31)	(0.94)	

Table 1). The results also showed that kelp gleaned from the beach corresponded, on average, to 35% of the MSY, assuming that the all seaweed detached by natural causes eventually ended up on the beach.

Finally, considering all sources of uncertainty for the parameters and given a scenario of process error in the recruitment of L. berteroana, the exploitable biomass reference, B_{msy} , was estimated to be $\sim 16,800$ mt around Caldera, $\sim 11,700$ mt around Chañaral, and $\sim 38,800$ mt around Huasco. On the other hand, when process error mainly affected natural mortality, these biomass estimates were higher and could reach 24,900 mt, 16,800 mt, and 48,3000 mt, respectively (Table 1). In all cases, MSY was determined by h and M and was estimated to be close to 0.74 B_{msy} (Fig. 4, Table 1).

4. Discussion

We parameterized a population model for data-poor fisheries considering the steepness of the stock-recruitment relationship, natural mortality rates, the proportion of beached kelp, and the perception of fishers with regards to the level of population depletion. We set out to incorporate the perception of fishers with scientific information since

key variables for fishery management such as MSY and B_{msy} are often primarily deduced from landings statistics and assumptions made about some operational parameters (e.g., Dick and MacCall, 2011; Cope, 2013; Martell and Froese, 2013). One advantage of this type of parameterization is that values for MSY and B_{msy} may be calculated directly using independent values for virgin biomass generated, for example, from surveys in unexploited or protected areas or from recruitment estimates by direct methods tied to a per recruit analysis. Unlike the formulations of Mangel et al. (2010) and Dick and MacCall (2011), we used the instantaneous rate of natural mortality (M) in a function of the proportion of natural death (m). Thus, the model could be extended to species with short lifespans ($M \gg > 1$). This parameter, together with the landing statistics, determined the population scale and is often considered to be fixed (hypothesis) as part of a structural uncertainty analysis (e.g., Brodziak et al., 2011; Andrew and Mangel, 2012).

Assessments of data-poor fisheries, particularly of sedentary resources, often rely on assumptions about parameters and processes. We assumed that the short dispersion time of spores implied closed kelp populations. In this case, population depletion could be perceived by fishers, either due to interruptions in the continuity of the kelp forest or

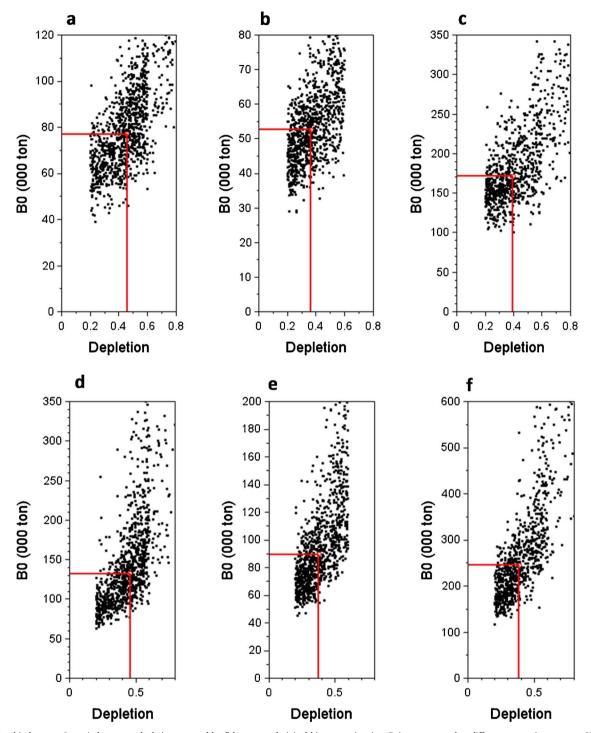


Fig. 6. Relationship between *Lessonia berteroana* depletion reported by fishermen and viginal biomass estimation. Points correspond to different uncertainty sources: Upper graphics represent situation when the process error is included in recruitments, while lower figures represent the situation when the process error is included in natural variation of mortality (beached). Each graphics column represents the zones: Caldera (a, d), Chañaral (b, e) and Huasco (c, f). Red lines are related to median values. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

in the systematic contraction of the population's latitudinal extension. In either case, population dynamics could be represented by a model in which density dependence was relaxed even more by increasing the steepness of the stock-recruitment relationship. Specifically, the small area in which this process occurred could lead to a continuous dispersal of spores by plants located nearby. Further study of this matter is required, specifically to identify fragmented habitats that would allow a representation of the geographical limits of more discrete population units.

The model was applied with parameter uncertainty to determine population variables for L. berteroana. These variables were estimated considering harvest levels deduced from landing statistics as well as the perception of artisanal fishers. In general terms and considering an average steepness (h = 0.8), the MSY value was $0.75~B_{msy}$. This high exploitation rate could be explained by the fact that productivity in species with high growth rates (e.g., L. berteroana) is determined mainly by the somatic growth of recruits (Kindsvater et al., 2016). Under such conditions, the biomass remaining after harvest may be similar to that

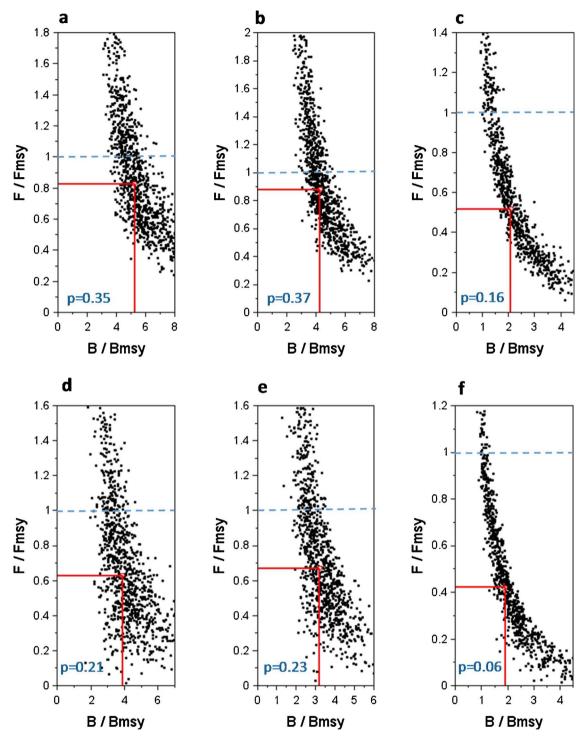


Fig. 7. Relationship between Lessonia berteroana relative biomass vs fishing mortality (F) related to MSY. Points correspond to different uncertainty sources: Upper graphics represent situation when the process error is included in recruitments, while lower figures represent the situation when the process error is included in natural variation of mortality (beached). Blue dotted lines represent the overfishing limit. Each graphics column represents the zones: Caldera (a, d), Chañaral (b, e) and Huasco (c, f), respectively. Median values of each axis are represented by red lines while blue lines correspond overfishing limits. Blue text is the overfishing probability calculated as a ratio of conditional events. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

harvested, but sustainable over time. In the same sense and theoretically, estimates of the proportion B_{msy}/B_0 decreased with increased h: in analyses of exploited populations, the values of h that were typically used reached up to 0.2 (e.g., Myers, 2001; Mangel et al., 2010; Shertzer and Conn, 2012).

Although latent population production was determined in the model by the balance between recruitment in weight of the exploitable stock and loss by natural mortality, somatic growth was included implicitly in both natural mortality and the magnitude of recruitment. Growth of L. berteroana from settling on the rocky substrate to reaching commercial size (exploitable stock) occurred over 7–9 months, and coincided with reaching maturity (Correa et al., 2006; González et al., 2012). In other words, if resilience (or steepness) was high, the contribution of recruitment to biomass tended to be constant and was explained mostly by somatic growth and less by changes in the parent population.

Although estimates of B_{msy} and F_{msy} were consistent with

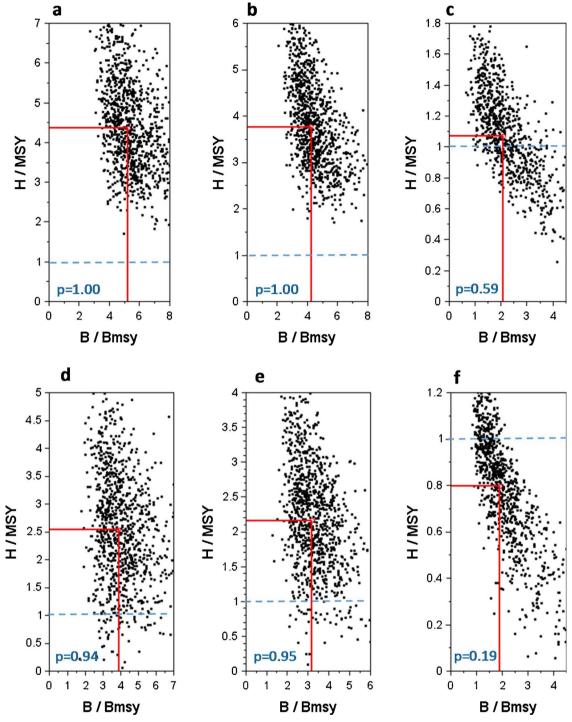


Fig. 8. Relationship between Lessonia berteroana relative biomass vs relative harvest (H) related to MSY. Points correspond to different uncertainty sources: Upper graphics represent the situation when the process error is included in recruitments, while lower figures represent situation when the process error is included in natural variation of mortality (beached). Each graphics column represents the zones: Caldera (a, d), Chañaral (b, e) and Huasco (c, f), respectively. Median values of each axis are represented by red lines while blue lines correspond overfishing limits. Blue text is the overfishing probability by harvest calculated as a ratio of conditional events. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

assumptions of harvested data, the lack of precision regarding proportions of beached vs harvested kelp and the lack of abundance indices and fishing effort measures led to major uncertainty in our estimates of population variables. In this sense, considering the volatility of the studied system, biological parameter uncertainty and process error assumptions were considered to evaluate their impact on population estimates and fisheries management measures. The results showed that process error was more influential on population variables when lower

harvest levels determined a fishery, but that greater variability and biomass levels were obtained when process error was assumed to affect mainly natural mortality.

Resilience levels and assumptions of process error were important. For example, despite the low abundances that followed periods of overfishing, the growth rate of *L. berteroana* allowed for quick recovery in overfished or depleted zones. Notwithstanding, although *L. berteroana* populations may have high resilience expressed in a low level of

critical biomass (B_{msy}/B_0), the species' limited tolerance to changes in abiotic factors (e.g., temperature) should be considered. Some reports have indicated that large areas of this kelp off the coast of northern Chile (23°S) have been affected by warmer sea surface temperatures due to El Niño (Camus, 1994; Martínez et al., 2003). On the other hand and independently of the biomass situation, fisheries management should always be based on biological reference points. In this sense and for Chilean kelp fisheries, recommendations should consider landing values based on the sum of MSY and the greatest amount of kelp gleaned from the beach (estimated to be $\sim 35\%$ over the MSY).

This study set out to propose an approach that could be used given limited knowledge of a population status. We recommend establishing transitory scientific agreements among experts about key parameters to use in the model. For this species, improving the function of the proportion of beached kelp should be addressed in the short term. Moreover, data collection programs, such as abundance indices from surveys (e.g., Stekoll et al., 2006; Bell et al., 2015), field monitoring, and environmental information related to population changes (e.g., Jackson, 1987; Yoshimori et al., 1998; Wernberg and Goldberg, 2008; Gorman et al., 2013), could be developed to reduce uncertainty in estimates of exploitation reference variables.

Finally, to achieve sustainable exploitation rates for resources like *L. berteroana* and other brown seaweeds (e.g., *Macrocystissp, Lessonia trabeculata, Lessonia spicata*), some ecosystem elements should be considered. Thus, the role of fishing organizations could be included in the management of local fisheries, as mentioned by Hannesson (1988), Kurien (1988), FAO (2003), Purcel (2010), and Stratoudakisa et al. (2015). The opinions of fishers should be considered to be a key element in field collection data (e.g., Freire, 2005; Ainsworth and Pitcher, 2005), which should lead to greater commitment from users, transparency in making decisions, and restricted solution space or improved parametrical ways of use in stock assessment models given data-poor scenarios.

Acknowledgments

The authors thank the Fisheries Development Institute of Chile (IFOP) for supporting field data collection and Mr. Mauricio Mardones (IFOP) for recommendations given during the initial stage of this research. Also, we appreciate discussions with, time bestowed by, and comments of Professor (MSc) Exequiel González of the Pontificia Universidad Católica de Valparaíso, Chile.

Appendix A

 B_{msy} is obtained by taking the derivative of the latent production function (Eq. (2)) respect to biomass, setting it equal to zero and obtaining the positive solution of the resulting quadratic equation.

$$\frac{d}{dB} \left(\frac{\alpha B}{\beta + B} - mB \right) = 0$$

$$\frac{\alpha (\beta + B_{msy}) - \alpha B_{msy}}{(\beta + B_{msy})^2} - m = 0$$

$$mB_{msy}^2 + 2\beta mB_{msy} + (m\beta^2 - \alpha\beta) = 0$$

$$B_{msy} = \frac{2\beta m + \sqrt{4m^2\beta^2 - 4m(m\beta^2 - \alpha\beta)}}{2m}$$

$$B_{msy} = -\beta + \sqrt{\frac{\alpha\beta}{m}}$$

Substituting the equation for B_{msy} into Eq. (2) gives:

$$MSY = \frac{\alpha B_{msy}}{\beta + B_{msy}} - mB_{msy}$$

$$MSY = \frac{\alpha \left(-\beta + \sqrt{\frac{\alpha \beta}{m}}\right)}{\beta + \left(-\beta + \sqrt{\frac{\alpha \beta}{m}}\right)} - m\left(-\beta + \sqrt{\frac{\alpha \beta}{m}}\right)$$

$$MSY = \alpha + m\beta - 2\sqrt{\alpha m\beta}$$

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