Post-harvest recovery of a co-managed First Nations' gooseneck barnacle fishery

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Abstract

Small-scale fisheries are culturally significant and provide coastal communities with economic opportunities. On the west coast of Vancouver Island, British Columbia, five First Nations co-manage a small-scale commercial fishery for gooseneck barnacles (Pollicipes polymerus). To inform the sustainable expansion of this fishery, I conducted an experimental harvest to estimate post-harvest recovery of gooseneck barnacles, the biotic matrix (i.e., acorn and thatched barnacles and mussels), and bycatch of mussels. After 14 months, mean matrix recovery was 74% of its initial cover, while gooseneck barnacle biomass recovery was only 12%. Both were highly variable and none of the variables tested was able to predict recovery of the matrix or of gooseneck barnacles. These results suggest that other factors, such as space, larval supply, and a longer time period, might contribute to both matrix and gooseneck barnacle recovery. Bycatch of mussels, in terms of biomass, increased by 2% with each 1% increase in biomass of gooseneck barnacle harvested, and this effect increased with matrix depth. These findings can inform management, suggesting that if harvest effort increases, the 6-month rotational closure should be re-visited, and that bycatch can be addressed through simple management measures.

Keywords: gooseneck barnacle; fishery; Pacific; recovery; bycatch

I would like to dedicate my thesis to Ivy Martin and her late husband Marcel Martin. My love for this fishery was stoked by your passion and dedication to your family, your community, and your culture.

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Introduction

Small-scale fisheries are thought to provide 90% of employment in the global marine fisheries sector, therefore representing an essential source of income and nutrition in diverse harvests around the world (World Bank 2012). They can also have strong cultural significance while supporting communities with limited options for alternative sources of income and food (Béné 2006; Bennett et al. 2018; FAO 2020). A common challenge in small-scale fisheries is a lack of information about catch and sustainability. To ensure the sustainability of small-scale fisheries, there have been many calls for governments to move towards systems of co-management (Gelcich et al. 2010; Folke et al. 2016). Co-management is a collaboration between government and Indigenous Nations, local communities, or fishing cooperatives, which increases adaptiveness to changes in the environment and encourages sustainable fishery and management practices (Pinkerton 1989; Costanza et al. 1998; Berkes 2008).

There is a current resurgence of Indigenous participation in economic fisheries in Canada. Processes such as modern treaty agreements (Morgan et al. 2018), reconciliation settlements (Brown 2019), and litigation (Kirchner 2010; Gauvreau et al. 2017) are likely contributing factors. A landmark example of the latter is the rights-based fishery resulting from an 11-year court proceeding between five Nuu-chah-nulth Nations from the west coast of Vancouver Island (WCVI), British Columbia, Canada (Ahousaht, Ehattesaht/Chinehkint, Hesquiaht, Mowachaht/Muchalaht, and Tla-o-qui-aht - hereafter referred to as the Five Nations) and the government of Canada (Kirchner 2010). The result of this court case affirmed the Nations' rights to harvest and sell commercially all species in their territories, with the exception of geoduck (Kirchner 2010). The Five Nations manage their fisheries in a co-management framework with the Department of Fisheries and Oceans Canada (DFO), with access to multiple species.

A unique aspect of the Five Nations' fishing rights is the exclusive economic access to gooseneck barnacles (*Pollicipes polymerus*) in their territories, located on the west coast of Vancouver Island, British Columbia. This gooseneck barnacle harvest may be the only one of its kind in North America. In Nuu-chah-nulth gooseneck barnacles are called Ca?inwa (meaning 'playing in the waves'). Gooseneck barnacles are an important traditional food source. The Nuu-chah-nulth people have a long history of harvesting

resources in their territory, with archeological evidence of gooseneck harvest in some areas dating back roughly 5,000 years ago (McMillan and St. Claire 2012). Certain families were responsible for taking care of the gooseneck barnacle beds and managing them by harvesting just enough to ensure the bed was productive (I. Martin, harvester, pers. comm.).

In more recent times, a gooseneck fishery on the WCVI took place between 1978 and 1999 by both Indigenous and non-Indigenous people, but the fishery was closed by DFO due to a perceived lack of information on gooseneck barnacle abundance, lifehistory, and appropriate management controls, as well as a mis-match between recorded landings and exports (Lauzier 1999). An experimental fishery from 2003-2005 was set up in a co-management framework bringing together harvesters, DFO, the provincial government of British Columbia, buyers, and processers; it closed in 2005 due to lack of funding and markets (Day et al. 2012). During this fishery local ecological knowledge (LEK) was collected for each harvest rock to inform harvest limits and regrowth. In 2016, the gooseneck barnacle bed assessment framework was updated by the Five Nations and DFO and it identified research priorities to improve the economic viability of the fishery while maintaining its sustainability (Gagne et al. 2016). This is important to the harvesters because until these research gaps are addressed, the fishery remains restricted to a small geographic area, which limits the participation to two of the Five Nations' territories, and a small available quota that makes it difficult to attract buyers (C. Picco, Ha'oom Biologist, pers. comm.). LEK data from Day et al. (2012) in conjunction with the updated assessment framework from Gagne et. al. (2016) inform management of the fishery today.

In this study, I conducted an experiment to improve our understanding of the post-harvest recovery of gooseneck barnacles and bycatch of mussels, two of the key information gaps identified by Lauzier (1999), Day et al. (2012), and Gagne et al. (2016) that impede the development of this fishery. Gooseneck barnacles grow on wave-swept rocks. They attach directly to rock or biotic substrata, such as adult gooseneck barnacles, acorn or thatched barnacles, and mussels that can grow in a matrix of variable depth (Austin 1987; Bernard 1988; Hoffman 1989). My experiment examined the relationships between harvest plot size, depth of the mussel matrix, plot recovery time, and bycatch. I predicted that smaller harvest plots from a deeper mussel matrix would recover more quickly than larger plots with a thinner matrix. In small, deep plots,

the surrounding mussels, which are overgrown by gooseneck barnacles, can move into the cleared space soon after harvest and attract gooseneck barnacle larvae, which prefer to settle on adult conspecifics as opposed to bare rock (Hoffman 1989). I also predicted that larger, deeper harvest plots would result in a greater amount of bycatch. This work complements the wealth of traditional ecological knowledge held by the Five Nations and other Nuu-chah-nulth Nations on the WCVI.

Methods

Description of the Fishery and Study Area

In Canada, gooseneck barnacles are commonly harvested by hand at low tide, using a flat metal bar called a 'goose gun'. This bar is used to pry the matrix species (mussels Mytilus spp., acorn barnacles Balanus glandula, or thatched barnacles Semibalanus cariosus) from the rock, leaving the gooseneck barnacles' fleshy peduncles intact. Time and safety permitting, the gooseneck barnacles are separated from the live matrix at the harvest site. The product is then validated by a dockside observer who weighs the catch and collects the harvester's log and issues a sales slip. Then the product is sold live to bulk buyers at the dock or delivered directly to local restaurants. Marketable barnacles have a rostral-carinal (RC) length, which is the length of the shell along the aperture, of 15-30 mm and a peduncle length of 20-80 mm (Jamieson et al. 2001) (Figure 1). The harvest occurs on various islands, large islets, and rocks located within Clayoquot Sound, on the west coast of Vancouver Island, BC. Most harvest sites are only accessible by boat and all are only accessible at low tide (Gagne et al. 2016). Harvesters are active year-round, which requires them to harvest in the dark during the winter months. At present, management of the 52 harvest rocks is done through rotating closures, which are informed by Local Ecological Knowledge (Day et al. 2012). Once a management limit for a rock is met, i.e., 7.5% of marketable biomass removed, that rock will be closed to harvest for a period of six months.

I conducted the experiment on six harvest rocks in Clayoquot Sound (Figure 2) over a 14-month period. Sites were selected because they were accessible at low tide during most weather conditions. All sites are within the traditional territory of the Ahousaht and Tla-o-qui-aht First Nations and have been harvested by Indigenous fishers for thousands of years (McMillan and St. Claire 2012).

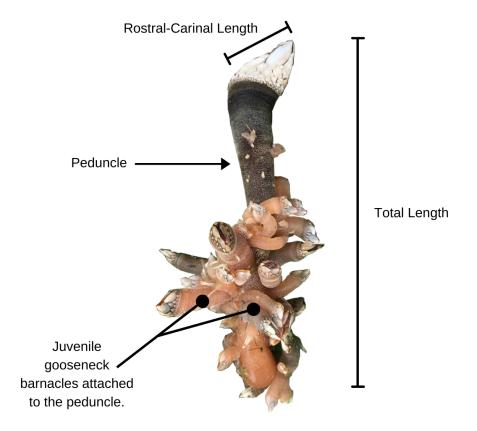


Figure 1. Gooseneck barnacle, with rostral-carinal length (RC length), total length (TL), and peduncle identified. Also shown are juvenile barnacles attached to the adult peduncle.

Field Sampling

To test the effect of plot size and mussel matrix depth on matrix recovery, gooseneck barnacle recovery, and bycatch, I harvested gooseneck barnacles and all biotic substrates from a range of plot areas and depths in May 2018 (Figure 2). On each of the six harvest rocks, six to 10 plots were chosen haphazardly in the intertidal range where gooseneck barnacles occurred (between 0.8 m - 4.3 m above the mean lowest low tide). I cleared plots ranging in size from $0.1 - 0.28 \text{ m}^2$ down to the bare rock with a goose-gun. Harvester methods normally yield harvested patches that can range from fist-sized clumps to areas measuring ~1 m across. Experimental plots were more than 1 m apart.

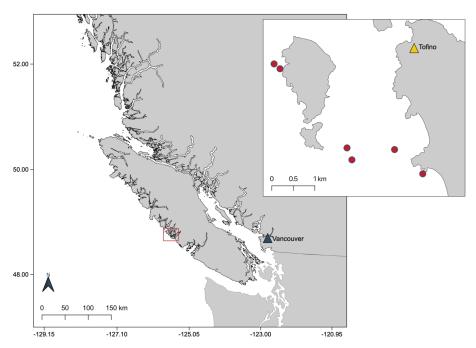


Figure 2. Study area (red square) on the west coast of Vancouver Island, British Columbia, Canada. Inset: Study rock locations (n = 6) located near Tofino are represented by circles (OpenStreetMap contributors 2015a, 2015b).

I collected and bagged all mussels and gooseneck barnacles removed from each plot. I then marked the location of each plot with bolts at the outer corners and recorded each plot's position using a GPS. For each plot, I recorded the height of the plot relative to mean lowest low tide (MLLW), aspect (direction of exposure), and which matrix species was dominant (acorn or thatched barnacles or mussels). I also measured the matrix depth at the midpoint of all four sides of the plot to calculate average matrix depth. A photograph with a scale was taken from directly above (~1.5 m high) to measure size of the harvested plot and to provide a starting reference for mussel movement throughout the experiment.

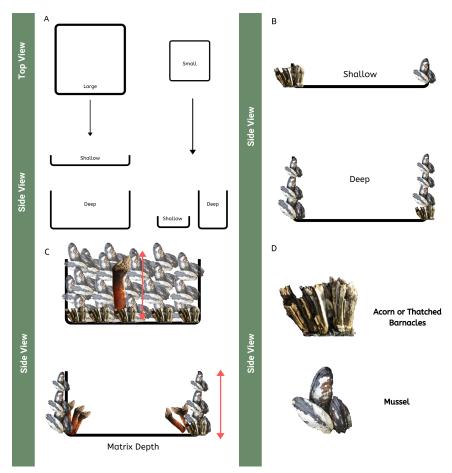


Figure 3. Experimental design and diagram of growing matrix depth for gooseneck barnacles. A) Range of sizes and depths of cleared harvest plots; B) Matrix makeup for shallow plots (i.e. large acorn barnacles or small acorn barnacles with mussels on top) and deep plots (i.e., deep layer of mussels on top of acorn barnacles); C) Measurement of matrix depth (i.e., rock substrate to top mussel layer) and matrix depth (i.e., rock substrate to top mussel layer at edge of a cleared plot). D) Main matrix species, acorn and thatched barnacles (Balanus glandula and Semibalanus cariosus) and mussels (Mytilus californianus).

To estimate the biomass retrieved from each cleared plot, I counted and weighed all gooseneck barnacles and mussels from each plot. I selected 20 gooseneck barnacles from each plot (representing the range of sizes in each plot, Figure 3) and recorded total length (TL), rostral-carinal length (RC), and weight for each individual. I also counted and weighed all individual mussels. Most plots had a layer of acorn and thatched barnacles attached to rock at the bottom of the plot, but I was not able to quantify their

number or biomass. To minimize weight loss from desiccation, I placed samples in sea water during processing.

Plots were revisited on five occasions through the summers of 2018 and 2019. A photograph was taken of each plot to track mussel movement and recovery. In summer 2019, I counted all gooseneck barnacles in each plot and scored each gooseneck barnacle as growing either along the edge of the plot or inside the plot. The edge of a plot was defined as any gooseneck barnacles growing at the plot edge. The inside of a plot was defined by any goosenecks growing independent of the plot edge. A few plots unintentionally had acorn barnacles left in the plot after harvest; those plots were marked as 'seeded' to account for the preference of juvenile gooseneck barnacles for settling on or near acorn barnacles (Bernard 1988). I measured the RC length of all accessible gooseneck barnacles (> 7 mm RC) within each plot.

I measured matrix recovery by comparing the area of each harvested plot at the end of the experiment to its area after initial clearing. The dominant species at the end of the experiment was also noted. Bare rock within plots was measured using Image J (Version 1.53a).

Data Analysis

All analyses were done using R (version 3.5.1; R Project for Statistical Computing, Vienna, Austria). Variance inflation factors (VIF) for all model parameters were less than 2, which confirms that multicollinearity was not an issue in the models (Zuur et al. 2010). A model selection approach (i.e., Akaike Information Criterion corrected for small sample sizes, AICc) was used to evaluate models in candidate sets. I identified the best-supported model as that with the lowest AICc value, although models that differed in AICc values by less than two units were considered equally well supported by the data (Burnham and Anderson 2002).

To test how matrix recovery was affected by matrix depth, harvest plot area, plot height above MLLW (mean lowest low water), and whether the dominant species was mussels or acorn/thatched barnacles I used generalized linear models (GLM). Mean matrix recovery, i.e. the proportion of harvest plot area at the end of the experiment divided by the plot area at the beginning of the experiment, Y_i, for plot, i, was a

continuous proportion between 0 and 1 and was modelled using a beta-distribution. I constructed 16 candidate models using the following global model:

$$\begin{split} Y_{ij} \sim Beta(\mu_i \,, \delta), \\ \mu_i &= 1 - \frac{plot \, area \, final_i}{plot \, area \, initial_i}, \\ logit(\mu_i) &= \beta_o + \beta_1 matrix \, depth_i + \beta_2 plot \, area_i + \beta_3 plot \, height_i \\ &\quad + \beta_4 dominant \, species_i + \, \varepsilon_i, \, \text{ for plot } i = 1, ..., n \end{split}$$

$$\varepsilon_i \sim N(0, \sigma^2), \eta_j \sim N(0, \sigma^2) \end{split}$$

Mean matrix recovery, μ_i , was modelled as a function of the relevant predictors using a logit link function. The random effect was removed due to near zero variance between harvest rocks (eq. 1). Homogeneity of residual variance and lack of correlations between the explanatory variables were confirmed, and AICc was used to identify the best-supported model(s).

To estimate gooseneck barnacle biomass from the RC lengths measured in the field during the last surveys, I examined the relationship between RC length and matrix depth on gooseneck barnacle wet weight obtained in the initial plot clearing. Wet weight was a positive continuous variable. Thus, wet weight Y_i , of plot, i, was modeled with a normal distribution. I constructed five candidate linear mixed-effects models (LMMs) to represent all possible main and interactive effects of these explanatory variables (Table 1), using the following global model:

$$\begin{split} Y_{ij} &\sim N(wet\ weight_{ij},\sigma^2) \\ log(wet\ weight_{ij}) &= \alpha_{j[i]} + \beta_o + \beta_1 log\left(RC\ length_{ij}\right) + \beta_2 log\left(matrix\ depth_{ij}\right) + \\ &\beta_3 log\left(RC\ length_{ij}*\ matrix\ depth_{ij}\right) + \varepsilon_i, \quad \text{for barnacle}\ i = 1, \dots, n \\ \\ \alpha_j &= a + \eta_j, \quad \text{for harvest plots}\ j = 1, \dots, j \\ \\ \varepsilon_{ij} &\sim N\left(0,\sigma^2\right), \eta_j \sim N(0,\sigma^2) \end{split}$$

where the mean wet weight was modeled as a function of the log-transformed relevant predictors. To account for non-independence of barnacles sampled within plots, I included plot, j, as a random effect in all models. Predictors were centred to allow the interpretation of the effect sizes relative to each other (eq. 2). Visual examination of the residuals confirmed that the assumption of homogeneity of residual variance was met. To visualize the relationships, I plotted predicted values of wet weight using the top model identified with AICc analysis.

I then converted the RC length of each gooseneck barnacle measured in post-harvest surveys to wet weight using the best-supported model. Based on published growth rates and the maximum size of gooseneck barnacles that settled into the centre of the experimental plots, individuals that had RC lengths greater than 21 mm were too large to have settled into the plots after clearing and they were likely carried into the plot with the leaning mussels (Lewis and Chia 1981; Bernard 1988). Therefore, they were excluded from this analysis. Most plots had some gooseneck barnacles that could not be measured because they were growing in tight spaces. To account for this, I estimated wet weight by using the average RC length from those individuals that I could measure for each plot. Wet weights of all gooseneck barnacles within a plot were then summed to obtain an estimate of biomass for each plot after 14 months of recovery.

I used generalized linear models (GLM) to test how gooseneck barnacle recovery was affected by the recovery of the matrix, matrix depth, harvest plot area, plot height above MLLW (mean lowest low water), and whether the plot was seeded or not (seeded denotes a plot where accidentally a shell or acorn barnacle was left after the plot was cleared). Gooseneck barnacle recovery was measured as biomass at the end of the experiment, B_t, divided by the starting biomass, B_o, and was a continuous proportion between 0 and 1. Thus, gooseneck barnacle recovery, Y_i, of plot, i, was modelled using a beta distribution. I constructed 32 candidate models using the following global model:

$$Y_i \sim Beta(\mu_i, \delta)$$

$$\mu_i = (\frac{B_{ti}}{B_{oi}})$$

$$\begin{split} logit(\mu_i) &= \beta_o + \beta_1 matrix \, recovery_i + \beta_2 matrix \, depth_i + \beta_3 plot \, area_i \, + \\ \beta_4 plot \, height_i + \beta_5 seeded_i + \varepsilon_{ij} \, , \end{split}$$

$$\varepsilon_i \sim N(0, \sigma^2), \eta_j \sim N(0, \sigma^2)$$

(3)

where the mean gooseneck recovery, μ_i , was modelled as a function of the relevant predictors using a logit link. The random effect was removed due to near zero variance between rocks (eq. 3). Homogeneity of residual variance and lack of correlations between the explanatory variables were confirmed, and AICc was used to identify the best-supported model(s).

Bycatch of mussels, measured as weight of mussels in each plot, was a continuous positive variable. Bycatch, Y_i , of plot, i, was modeled using a log-transformed linear model. I constructed eight candidate models using the following global model:

$$Y_{ij} \sim bycatch$$
,

 $log(bycatch_i) = \beta_o + \beta_1 log(gooseneck harvest_i) + \beta_2 log(matrix depth_i) + \beta_3 log(plot height_i) + \varepsilon_i),$

$$\varepsilon_{ij} \sim N(0, \sigma^2)$$

(4)

Mean bycatch was modelled as a function of relevant predictors. The random effect was removed due to near zero variance between rocks (eq. 4).

Results

I removed 87 kgs, 11,913 individual gooseneck barnacles and a total of 270 kg or 10,253 individual mussels from 42 plots on six harvest rocks. I weighed and took additional measurements of 820 individual gooseneck barnacles. All top model summaries provided in the appendix (Table A1 – A4).

Matrix Recovery

After 14 months, matrix recovery due to mussels leaning into harvested plots or acorn and thatched barnacle settlement was highly variable, ranging from 4.7% - 100% (mean \pm 1 SE: 71.4% \pm 10.6%; Figure 4). Four models were equally well supported, i.e. within 2 AICc units of each other (Table 1). The top model included only matrix depth (22% support), followed by the model including matrix depth and plot area (13% support), the null model (13% support), and a model including plot area alone (10% support). The dominant matrix species and plot height did not appear in the top models. The top models that included predictor variables explained 9-21% of the variance in matrix recovery (Table 1).

Table 1. Models to predict matrix recovery based on the dominant matrix species (mussels or acorn barnacles), plot area, matrix depth, and plot height. K is the number of parameters in each model; \triangle AlCc is the difference in AlCc value between the focal model and the model with the lowest AlCc; Akaike weight w_i is interpreted as the probability that model i is the best model of the candidate set given the data at hand; R^2 (conditional) is amount of variance explained by the model. Models in bold are the best-supported models.

Model	K	Log-likelihood	AICc	$\Delta AICc$	Wi	R^2
matrix depth	3	11.57	-16.29	0.00	0.22	0.15
matrix depth + plot area	4	12.33	-15.18	1.11	0.13	0.21
null	2	9.79	-15.17	1.12	0.13	-
plot area	3	10.79	-14.71	1.57	0.10	0.09
matrix depth + plot height	4	11.81	-14.13	2.16	0.08	0.16
dominant species + matrix depth	4	11.58	-13.67	2.61	0.06	0.15
plot height	3	10.09	-13.33	2.96	0.05	0.02
dominant species	3	9.85	-12.85	3.44	0.04	0
matrix depth + plot area + plot height	5	12.56	-12.81	3.48	0.04	0.21
plot area + plot height	4	11.07	-12.66	3.63	0.04	0.1
dominant species + plot area	5	12.34	-12.37	3.92	0.03	0.09
dominant species +matrix depth + plot area	4	10.84	-12.20	4.09	0.03	0.21
dominant species + matrix depth + plot height	5	11.81	-11.31	4.97	0.02	0.16
dominant species + plot height	4	10.14	-10.81	5.48	0.01	0.02
dominant species + plot area + plot height	5	11.12	-9.93	6.36	0.01	0.11
dominant species + matrix depth + plot area + plot height	6	12.57	-9.77	6.52	0.01	0.21

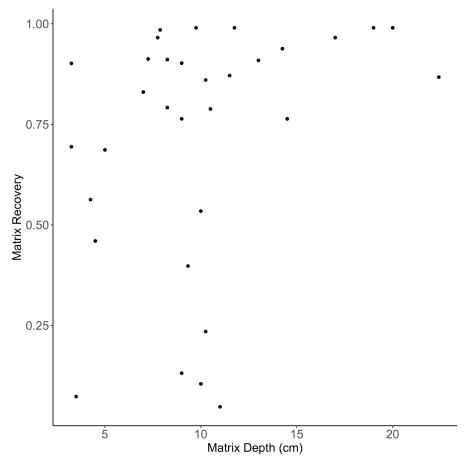


Figure 4. Matrix recovery (% cover of original cleared space) after 14 months in relation to matrix depth (cm). Points represent individual plots.

Gooseneck Barnacle Recovery

The best-supported model to predict gooseneck barnacle wet weight included RC length, growing depth, and the interaction between the two (Table 2). Wet weight increased with RC length and, to a lesser extent, with growing depth (Figure 4). The interaction between growing depth and RC length also affected wet weight such that small gooseneck barnacles in all matrix depths have, on average, similar weight, whereas large gooseneck barnacles are heavier, on average, as growing depth increases (Figure 5). The strong positive coefficient for RC Length indicates that it is the best predictor of wet weight; however, both growing depth and the interaction of RC length and growing depth also have a positive effect on wet weight. I used the best-

supported model to convert RC lengths of gooseneck barnacles observed at the end of the experiment into wet weights, and ultimately calculate plot-level biomass (Figure 6).

Results of AIC model selection analysis of five candidate linear mixed-effects models describing gooseneck barnacle wet weight in terms of rostral-carinal (RC) length, matrix growing depth, and the interaction between the two. Harvest plot was included as a random factor in all models. K is the number of parameters in each model; ΔAICc is the difference in AICc value between the focal model and the model with the lowest AICc; Akaike weight w_i is interpreted as the probability that model is the best model of the candidate set given the data at hand; R² (conditional) is the amount of variance explained by the model. The model in bold is the best-supported model.

Model	K	Log-likelihood	AICc	ΔAICc	\mathbf{W}_{i}	R ²
RC length + growing depth + RC length: growing depth	6	-207.89	427.87	0.00	1.00	0.93
RC length + growing depth	5	-216.38	442.83	14.95	0.00	0.93
RC length	4	-226.44	460.94	33.06	0.00	0.93
growing depth	4	-1241.25	2490.54	2062.67	0.00	0.12
null	3	-1244.14	2494.30	2066.43	0.00	0.12

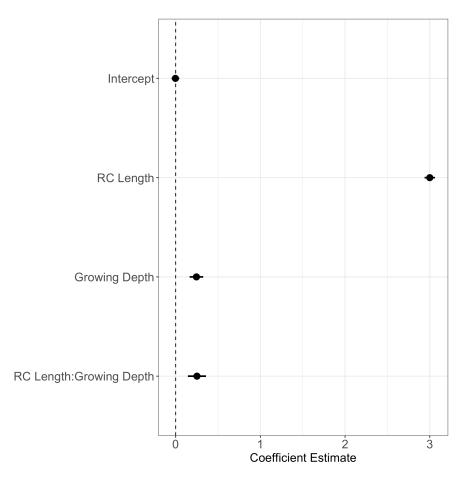


Figure 5. Coefficient estimates (log-transformed and centred) with 95% confidence intervals of the relationships between rostral-carinal length, growing depth, and their interaction and wet weight of gooseneck barnacles. The estimates are derived from the top model shown in Table 1.

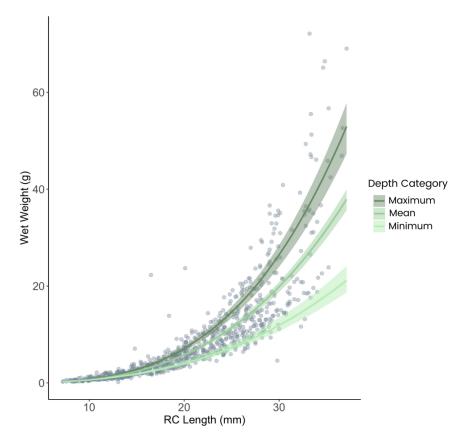


Figure 6. Model predictions for gooseneck wet weight (g) as a function of rostral-carinal length (mm) and growing depth (cm). Maximum, mean, and minimum depth categories are 2.25cm, 9.74 cm, and 22.40 cm, respectively; these categories are representative of the data. Shaded areas represent 95% confidence intervals.

Gooseneck barnacle biomass recovery was also highly variable, ranging from 0-82% (Figure 7) of the original gooseneck barnacle biomass (mean \pm SE: 11.5% \pm 4.5%, Figure 6). None of the variables tested (matrix depth, plot area, plot height above mean lowest low tide, whether the plot was seeded or not and the interaction of matrix depth and plot area), explained the variation in gooseneck barnacle recovery rate (Table 3). The best-supported model was the null model (39% support), followed by a model including matrix recovery (13% support, $R^2 = 0.05$).

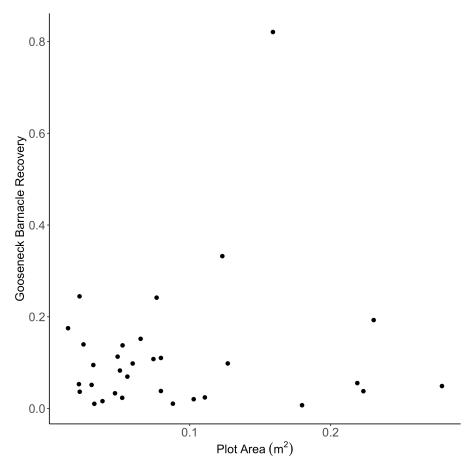


Figure 7. Gooseneck barnacle biomass recovery (proportion of initial biomass) after 14 months in relation to harvest plot area (m2). Points represent individual plots.

Table 3. Models to predict gooseneck barnacle biomass recovery based on matrix recovery, matrix depth, plot area, plot height, the interaction of matrix depth and plot area, and whether or not the plot was seeded, i.e. some acorn barnacles remained in the plot after harvest. K is the number of parameters in each model; ΔAICc is the difference in AICc value between the focal model and the model with the lowest AICc; Akaike weight w_i is interpreted as the probability that model i is the best model of the candidate set given the data at hand; R² (conditional) is the amount of variance explained by the model. Models in bold are the best-supported models.

Model	K	Log-likelihood	AICc	∆AlCc	wi	R2
null	2	33.90	-63.40	0.00	0.23	-
matrix recovery	3	34.55	-62.24	1.16	0.13	0.05
seeded	3	33.94	-61.03	2.36	0.07	0.00
plot area	3	33.91	-60.97	2.43	0.07	0.00
matrix depth	3	33.90	-60.95	2.44	0.07	0.00
plot height	3	33.90	-60.95	2.44	0.07	0.00
matrix recovery + seeded	4	34.68	-59.88	3.51	0.04	0.06
matrix recovery + plot area	4	34.63	-59.79	3.61	0.04	0.06
matrix recovery + matrix depth	4	34.60	-59.72	3.67	0.04	0.06
matrix recovery + plot height	4	34.59	-59.70	3.69	0.04	0.06
matrix depth + seeded	4	33.95	-58.42	4.97	0.02	0.00
plot area + seeded	4	33.95	-58.41	4.99	0.02	0.00
plot height + seeded	4	33.94	-58.41	4.99	0.02	0.00
matrix depth + plot area	4	33.91	-58.35	5.05	0.02	0.00
plot area + plot height	4	33.91	-58.34	5.05	0.02	0.00
matrix depth + plot height	4	33.90	-58.33	5.07	0.02	0.00
matrix recovery + plot area + seeded	5	34.73	-57.15	6.24	0.01	0.06
matrix recovery + plot height + seeded	5	34.73	-57.15	6.24	0.01	0.06
matrix recovery + matrix depth + seeded	5	34.70	-57.09	6.30	0.01	0.06
matrix recovery + plot area + plot height	5	34.70	-57.08	6.31	0.01	0.06
matrix recovery + matrix depth + plot area	5	34.67	-57.04	6.36	0.01	0.06
matrix recovery + matrix depth + plot height	5	34.64	-56.98	6.42	0.01	0.06
matrix depth + plot area + seeded	5	33.95	-55.60	7.80	0.00	0.00
matrix depth + plot height + seeded	5	33.95	-55.60	7.80	0.00	0.00

Model	K	Log-likelihood	AlCc	∆AlCc	wi	R2
plot area + plot height + seeded	5	33.95	-55.58	7.81	0.00	0.00
matrix depth + plot area + plot height	5	33.91	-55.52	7.88	0.00	0.00
matrix recovery + plot area + plot height + seeded	6	34.79	-54.22	9.18	0.00	0.07
matrix recovery + matrix depth + plot area + seeded	6	34.74	-54.13	9.27	0.00	0.07
matrix recovery + matrix depth + plot height + seeded	6	34.74	-54.13	9.27	0.00	0.07
matrix recovery + matrix depth + plot area + plot height	6	34.73	-54.09	9.31	0.00	0.07
matrix depth + plot area + plot height + seeded	6	33.95	-52.55	10.85	0.00	0.00
matrix recovery + matrix depth + plot area + plot height + seeded	7	34.80	-50.93	12.47	0.00	0.07

Mussel Bycatch

Finally, bycatch of mussels was best predicted by matrix depth and gooseneck harvest (69% support, R^2 = 0.76) (Table 4, Figure 7) as well as by the full model, which included matrix depth, gooseneck harvest, and plot height (31% support, R^2 = 0.76) (Table 4). Mussel bycatch increased with the biomass of gooseneck barnacles harvested and this effect became more marked with increasing matrix depth (Figure 8).

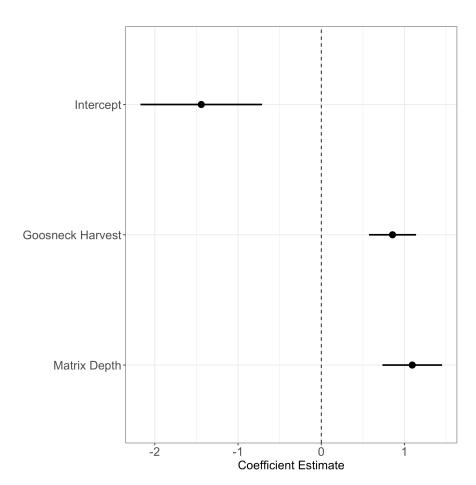


Figure 8. Coefficient estimates (log-transformed) with 95% confidence intervals of the effects of gooseneck harvest (kg) and matrix depth (cm) on bycatch of mussels. The estimates are derived from the top model shown in Table 4.

Table 4. Models to predict mussel bycatch based on the matrix depth, gooseneck harvest (kg), and plot height. *K* is the number of parameters in each model; △AICc is the difference in AICc value between the focal model and the model with the lowest AICc; Akaike weight w_i is interpreted as the probability that model i is the best model of the candidate set given the data at hand; R² (adjusted) is the amount of variance explained by the model. Models in bold are the best-supported models.

Model	K	Log-likelihood	AICc	ΔAICc	Wi	R^2
matrix depth + gooseneck harvest	4	-32.19	73.52	0.00	0.69	0.76
matrix depth + gooseneck harvest + plot height	5	-31.69	75.15	1.63	0.31	0.76
plot depth	3	-45.54	97.75	24.23	0.00	0.55
gooseneck harvest	3	-45.71	98.09	24.58	0.00	0.55
matrix depth + plot height	4	-45.01	99.16	25.64	0.00	0.55
gooseneck harvest + plot height	4	-45.52	100.19	26.67	0.00	0.54
null	2	-62.23	128.78	55.26	0.00	-
plot height	3	-61.95	130.56	57.04	0.00	-0.01

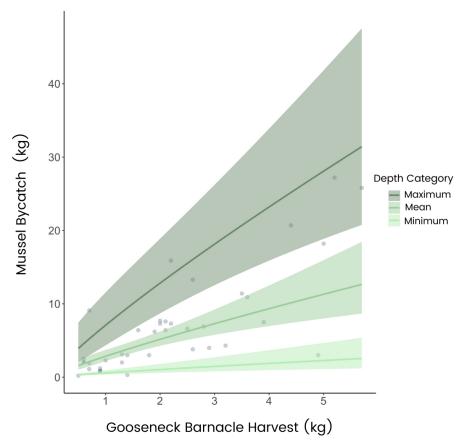


Figure 9. Mussel bycatch as a function of biomass of gooseneck barnacles harvested and matrix depth. Maximum, mean, and minimum depth categories are 2.25cm, 9.74 cm, and 22.40 cm, respectively; these categories are representative of the data.

Discussion

The speed of recovery of gooseneck barnacles after harvest is a key knowledge gap in understanding the best management practices that prioritize conservation of this unique small-scale fishery. I found that the matrix of other barnacle species and mussels recovered faster than of the gooseneck barnacles; however, none of the variables I tested predict well the recovery of the matrix. Unexpectedly, gooseneck barnacles did not recover more quickly in small plots with deep matrices, and none of the other variables I tested predicted recovery either. I also found an effect of matrix depth on the bycatch of mussels. Below I explore the reasons for these findings and the implications for the management of this fishery.

Recruitment of sessile marine invertebrates is influenced to a great extent by the substratum (Paine 1966, 1974; Dayton 1971). This is the case for gooseneck barnacles, which prefer to settle on living substrates (Jamieson et al. 2001). I found that plots recovered by 74.1%, on average, in large part due to mussels 'leaning in' or to acorn or thatched barnacle settlement. This is supported by the LEK and observations by managers during the experimental fishery in 2003-2005, where harvested patches were nearly indistinguishable from non-harvested areas after six months (Day et al. 2012). However, neither of these mechanisms nor any other variables tested predicted matrix recovery in this study. More work is required to get a better understanding of what is driving the recovery of the matrix and what effect, if any, this has on the recovery of gooseneck barnacles themselves. Recovery of the matrix before gooseneck barnacle settlement is important to the fishery because gooseneck barnacles that have settled onto bare rock cannot be harvested for commercial sale due to breakage of the peduncle when scraped from rock.

Despite relatively good recovery of the biotic matrix, there was highly variable and low overall recovery of gooseneck barnacles, which returned to only ~12%, on average, of their initial biomass after 14 months. This could be due to complex factors affecting recruitment and post-recruitment processes. Recruitment can be low when sea surface temperature increases, local currents change, and during upwelling events (Connolly and Roughgarden 1999; Menge et al. 2010; Rivera et al. 2015). In 2015, a temperature anomaly called 'the blob' occurred in the northeast Pacific Ocean. This

ocean warming continued into late 2018, finally tailing off around March 2019 (Freeland and Ross 2019). The higher temperatures and strong winter wave action that characterized the study period could have influenced recruitment into the cleared plots. Conducting this study over multiple years would allow a better understanding of the interannual variation in recruitment and how much this is mediated by factors such as temperature and exposure.

I expected rapid gooseneck barnacle recovery in smaller plots. This was not the case. There is evidence that the recovery of intertidal species can vary inconsistently with plot size after a disturbance (Paine and Levin 1981; Farrell 1991). For example, in intertidal areas in southern California, increasing disturbance size slowed recovery rates of Mytilus californianus, but had the opposite effect on Chthamalus dalli/fissus (Conway-Cranos 2012), potentially due to different species responding differently to edge effects. Mussels respond positively to edge effects as they settle on the byssus of adult mussels (Petersen 1984; McGrath et al. 1988), while barnacles will settle on bare rock. There is also evidence in Semibalanus spp. that a certain distance from conspecifics is required to counteract the negative effects of crowding (Raimondi 1990; Hooper and Eichhorn 2016). Two-thirds of the plots showed recruitment only at the edges; however, one-third of plots showed recruitment in both the edges and the centre of the plot. Some of this unexpected pattern of settlement could have been due to some plots being 'seeded' (where accidentally an acorn or thatched barnacle shell remained in the plot), but not all plots with settlement in the centre were seeded. Experienced harvesters prefer to harvest from areas with a deeper matrix and, if the matrix is sufficiently deep, they do not need to harvest right to the bare rock; however, when the presence of multiple harvesters increase fishing pressure, as it was in the past, harvesters are not always able to selectively harvest only in areas with deep matrix, and plots are cleared to the bare rock (B.George, harvester, pers.comm.)

I found that gooseneck barnacles were heavier, on average, when their rostral-carinal (RC) length is greater. Bernard (1988) observed the same relationship but also noted that it could vary with site, intertidal height, and wave exposure. Later, Jamieson et. al. (2001) found a moderate correlation between wet weight and matrix depth. I found that the RC length – weight relationship is moderated by the matrix depth (Figure 3). A deeper matrix depth results in heavier gooseneck barnacles, on average, than a barnacle with the same RC length growing in a shallower matrix. This is likely a function

of the gooseneck barnacle's filter feeding strategy. In a deeper matrix, gooseneck barnacles must have a longer peduncle to be able to extend beyond the mussel matrix and filter feed in the extreme wave action. The length-weight relationship I provide, with the mediating effect of matrix depth, will allow for more accurate, non-destructive biomass estimates.

Bycatch is an important consideration in any fishery, especially when taking an ecosystem-based approach to management (Parsons 1992; Alverson et al. 1994; Casey and Myers 1998). Although the gooseneck barnacle fishery is currently operating with low effort, information on bycatch is critical to ensure that the mussel populations in the harvest area are not unduly impacted as the fishery grows. It was not possible during this study to quantify acorn or thatched barnacle bycatch or discards of non-marketable barnacles. I found that for every 1% increase of gooseneck barnacles harvested, there was a 2% increase in bycatch of mussels. Anecdotally, I observed mortality in the mussel bycatch to be low. Mussels that are removed and replaced onto the substratum can secrete new byssus threads to secure their position. Studies have shown that in one hour mussels produced ~ 2 attachment threads and in four hours they had produced ~ 5 threads, and the rate of byssus production can increase when mussels are in high flow environments (Young 1985; Côté 1995). I suggest that because of the observed low mussel mortality and their ability to reattach to the substratum, placing bycatch mussels back in harvest plots can minimize the collateral impacts from this fishery.

Although my predictions of gooseneck barnacle recovery were not supported, they do offer insight into management strategies for the growth of this fishery. Currently, the fishery is managed based on rotating closures. A quantitative relationship between gooseneck barnacle bed area and local ecological knowledge of harvestable biomass was established by Gagne et al. (2016) to provide a total rock biomass for gooseneck barnacles. This allows managers to set a very precautionary harvest threshold for each rock, 7.5 per cent of the estimated total rock biomass. When the target harvest amount is reached, that rock is closed for a period of six months, based on LEK. My results show that after intensive clearing of harvest plots during peak recruitment times, recovery was variable and low over a period of 14 months. If these findings are typical and not the result of unusually low gooseneck barnacle recruitment or survival, my study suggests that the rotational closure period may need to be lengthened to allow harvested areas on a rock to recover if harvesters return to the very same areas. Due to the quick recovery

of the typical small divots created by harvesters, previously harvested areas may appear 'recovered' due to the matrix closing and the harvest plot disappearing, encouraging repeat harvest of the same areas. However, if the current biomass quota set for each rock leaves a large proportion of gooseneck barnacles untouched and harvesters can exploit different areas on each visit, the effective closure period for any given harvested patch is in fact longer than 6 months, and perhaps long enough to permit adequate recovery. Longer-term studies of gooseneck barnacle recruitment are needed to shed more light on post-harvest recovery. Additionally, my study found that matrix depth was an important component to harvest plot recovery, which is known by the harvesters since they prefer to harvest in the deeper matrix. This could become more important if harvest effort increases and harvesters begin to harvest in the shallow matrix more frequently. Finally, this work suggests that while bycatch of mussels is high, mortality is low and mussels are able to re-attach, so I recommend that harvesters clean their barnacles on site when possible and deposit those discarded mussels back into the harvest plots to minimize bycatch.

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Appendix

Table A1. Estimated regression parameters, standard errors, z values, and Pr (>|z|) value for the top Beta GLMs from eq 1. Model numbers denote rank in AIC table 1.

Model	Parameter	Estimate	Std. Error	z value	Pr (> z)
1	intercept	-0.01416	0.46505	-0.030	0.976
	matrix depth	0.07934	0.04235	1.873	0.061
2	intercept	-0.23941	0.49730	-0.481	0.630
	matrix depth	0.07260	0.04257	1.705	0.088
	plot area	3.30806	2.84013	1.165	0.244
3	intercept	0.7736	0.2179	3.55	0.000
4	intercept	0.4377	0.3246	1.348	0.178
	plot area	3.8272	2.8623	1.337	0.181

Table A2. Estimated regression parameters, standard errors, and t values for the top LMM from eq 2. Model numbers denote rank in AIC table 2.

Model	Parameter	Estimate	Std. Error	t value
1	intercept	-0.003114	0.023125	-0.135
	rc length	3.000103	0.031382	95.600
	matrix depth	0.244918	0.040784	6.005
	rc length : matrix depth	0.250906	0.054448	4.608

Table A3. Estimated regression parameters, standard errors, z values, and Pr (>|z|) value for the top Beta GLM from eq 3. Model numbers denote rank in AIC table 3.

Model	Parameter	Estimate	Std. Error	z value	Pr (> z)	
1	intercept	-1.9073	0.1961	-9.728	<2e-16	
2	intercept	-1.4700	0.4007	-3.668	0.000	
	matrix recovery	-0.6312	0.5191	-1.216	0.224	

Table A4. Estimated regression parameters, standard errors, z values, and Pr (>|z|) value for the top log transformed LM from eq 4. Model numbers denote rank in AIC table 4.

Model	Parameter	Estimate	Std. Error	t value	Pr (> z)
1	intercept	-1.4416	0.3729	-3.866	0.00
	matrix depth	0.8561	0.1444	5.928	7.86e-07
	gooseneck harvest	1.0933	0.1828	5.980	6.67e-07
2	intercept	-1.29136	0.40555	-3.184	0.00
	matrix depth	0.84615	0.14499	5.836	1.15e-06
	gooseneck harvest	1.09659	0.18308	5.990	7.18e-07
	plot height	-0.04610	0.04856	-0.949	0.349