North Pacific Fisheries Commission

NPFC-2025-SSC BFME06-WP18

Depletion model analysis for North Pacific armorhead in the Southern Emperor–Northern Hawaiian Ridge seamounts

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1. Introduction

Estimating fish population abundance is a central objective in fisheries science and management. Reliable abundance estimates are essential to evaluate stock status, assess the effects of exploitation, and develop sustainable harvest strategies. In the absence of direct estimates of population size, such as those obtained from fishery-independent surveys, stock assessment models provide a valuable alternative for estimating relative or absolute abundance from fishery-dependent information.

For North Pacific armorhead (NPA; *Pentaceros wheeleri*), depletion models have been suggested as an approach to estimate stock abundance, particularly given the challenges associated with traditional assessment methods. NPA has been the major target species of demersal fisheries operating on the Southern Emperor–Northern Hawaiian Ridge (SE–NHR) seamounts since the 1960s. The species exhibits episodic and often large recruitment events, followed by several years of weak recruitment, which results in pronounced fluctuations in stock biomass and catch levels. These recruitment pulses, coupled with difficulties in age determination and uncertainties in early fishery data, have limited the application of conventional age-structured or surplus production models for this species (Kiyota et al. 2014).

Depletion models, originally developed by Leslie and Davis (1939) and later adapted for a variety of fisheries, are based on the principle that catch per unit effort (CPUE) declines as the population is progressively removed by fishing in a specific fishing period. By relating cumulative catch to changes in CPUE, these models allow estimation of initial abundance and catchability under the assumption of a closed population during the fishing period. The simplicity of depletion models makes them particularly useful for assessing short-lived, or spatially isolated fisheries, such as those targeting aggregations on seamounts—conditions that characterize the NPA fishery.

Previous assessments presented to the Preparatory Conference of the North Pacific Fisheries Commission (NPFC) Scientific Working Group have applied depletion models to Japanese trawl data to estimate recruitment biomass and harvest rates (Kiyota et al., 2013). These analyses revealed high exploitation rates during recruitment pulses, with estimates suggesting that only a small fraction of recruits survive until their first spawning season. Building on these findings, further analyses integrating Japanese and Korean commercial fishery data were performed by Kiyota et al. (2014) finding similar results.

In this study, we apply depletion models to more recent fishery data (from 2010 to 2024) from the SE–NHR seamounts to estimate recruitment biomass and exploitation rates of NPA across multiple years. Our objectives are to (1) estimate initial stock size and (2) harvest rate for each year and seamount, to support ongoing NPFC management discussions.

2. Methods

2.1. Data sources

Catch and effort data for the NPA fishery were compiled from Japanese and Korean commercial operations conducted on the SE–NHR seamounts between 2010 and 2024. The dataset included records from both trawl and gillnet gears, with information on catch (kg), fishing effort (hours or number of nets), date, seamount of operation and intended target species (only for the Japanese data). For the analyses we only used the information coming from the trawl fishery, the most representative in terms of catch and data availability (**Figure 1**). In addition, because information on the intended target species was not available for the Korean fishery data, the depletion analysis, for both fisheries combined, was conducted without accounting for targeting behavior and restricted to positive catch sets only. All depletion analyses were carried out for four of the seven seamounts in the study area—Colahan, Koko, Kammu, and Yuryaku—with the latter two belonging to the Milwaukee seamount chain. This selection was based on data availability and continuity across years (**Table 1**).

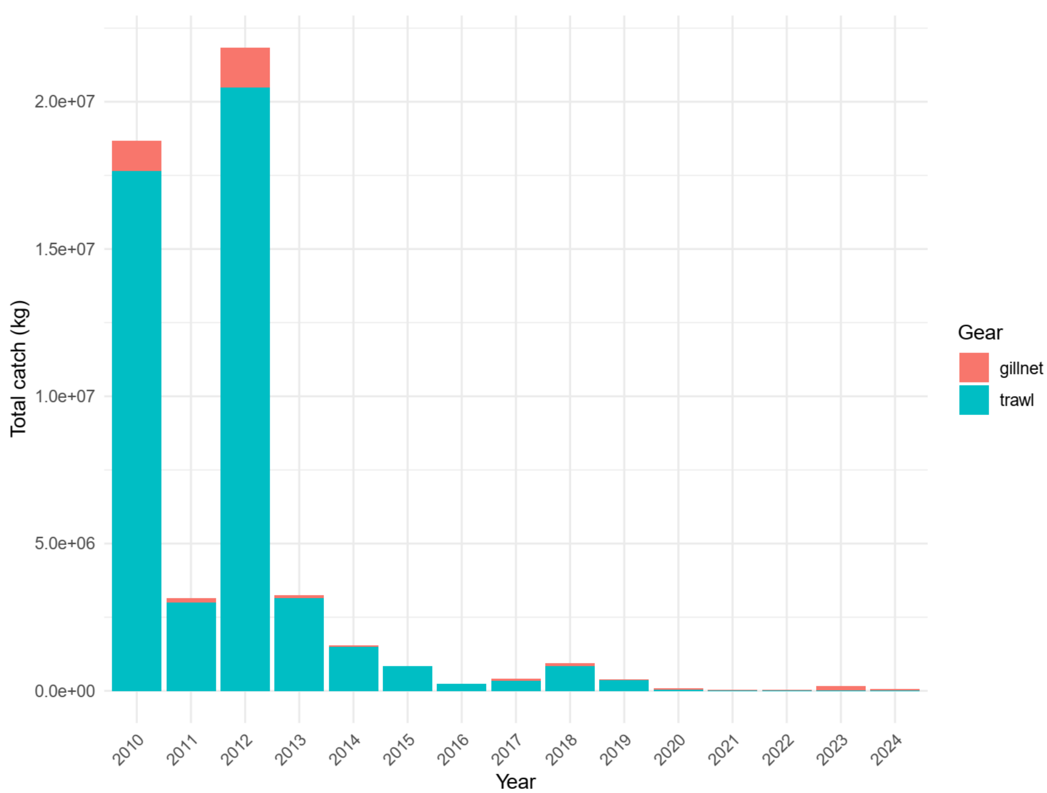

Figure 1. Catch (in kg) of NPA by fishing gear (trawl and gillnet) from 2010 to 2024.

Table 1. Number of CPUE records (accumulated by 10 days intervals) for each year and seamount.

Year	Colahan	Kammu	Koko	Yuryaku	Kinmei	North Koko	Hancock
2010	24	30	26	17	0	0	0
2011	14	29	28	21	3	1	0
2012	20	31	25	17	0	1	0
2013	15	30	27	24	0	0	3
2014	12	28	30	29	0	0	0
2015	22	31	25	27	1	0	0
2016	7	27	19	15	1	0	0
2017	11	29	18	30	0	0	0
2018	20	28	21	28	0	0	0
2019	18	30	19	32	2	1	0
2020	6	15	11	8	0	0	0
2021	10	12	3	4	0	0	0
2022	5	5	7	10	0	0	0
2023	3	7	8	7	0	0	0
2024	4	10	7	9	0	0	0

2.2. Data aggregation and CPUE calculation

Catch per unit effort (CPUE) was calculated for each fishing set as the ratio of catch to the corresponding measure of effort (trawling hours). CPUE and cumulative catch were aggregated by 10-day intervals within each seamount and year. This temporal resolution provided sufficient detail to detect declines in CPUE associated with progressive stock depletion while maintaining an adequate number of observations per stratum (Kiyota et al. 2013).

2.3. Identification of depletion periods

For each seamount, the annual CPUE peak was identified as the maximum CPUE observed within each year. Only the descending portion of the CPUE–catch trajectory following the identified peak was used in depletion model analyses to ensure that observations reflected progressive removals from a single cohort or aggregation.

2.4. Depletion model and statistical analyses

Depletion relationships were analyzed using linear regression models based on the classical Leslie–DeLury formulation (DeLury 1947), which assumes a linear decline in CPUE with cumulative catch under constant catchability and a closed population. For each seamount-year combination, the following model was fitted:

$$CPUE = a - b\ C$$

where *CPUE* is the catch per unit effort, *C* is the cumulative catch, *a* is the intercept (proportional to initial abundance and catchability), and *b* is the slope representing the rate of depletion. The analysis was performed separately for each year, assuming independence among years.

To account for variability among seamounts and improve parameter estimation, we also fitted a linear mixed-effects model with random slopes by seamount, allowing the rate of CPUE decline to vary spatially while estimating an overall mean depletion trend. The model was expressed as:

$$CPUE_s = a - b_S\, C$$

where s represents the random effect on slopes which is normally distributed as:

$$b_s \sim N(\bar{b}\ \sigma_b^2)$$

where $\bar{b}$ is the mean slope across seamounts and σ_b^2 is the variance of slopes across seamounts. As we did with the simple regression, the analysis was performed separately for each year, assuming independence among years.

2.5. Model fitting and diagnostics

All analyses were conducted in R (R Core Team, 2025). Linear regressions were fitted using the base *lm* function, and mixed-effects models were implemented using *RTMB* (Kristensen, 2025). For each seamount and year, estimated slopes and intercepts were used to derive relative depletion rates and initial abundance indices.

To ensure numerical stability and avoid estimation problems in variance components, the RTMB implementation included the following scaling steps, which do not change the biological interpretation of the model:

1. Within each year, CPUE values were centered by subtracting the annual mean of that seamount in the year.

$$CPUE_{c,is} = CPUE_{i,s} - \widetilde{CPUE}_s$$

2. Similarly, the cumulative catch (C) was also centered by its seamount-specific mean

$$C_{c,is} = C_{i,s} - \widetilde{C_s}$$

Although estimation was performed on centered variables, the model internally transformed:

- slopes b_s,
- intercepts a_s,

back to the original CPUE and cumulative catch scales using algebraic relationships. All results are therefore presented and interpreted on the original biological scale.

2.6. Derived quantities

Under the Leslie–DeLury depletion formulation CPUE is expressed as:

$$CPUE_t = qB_t = q(B_t - C_t) = a - b\, C_t$$

where q is catchability, $a = q\ B_t$ and $b = q$. From the fitted regression we therefore obtain the initial biomass as:

$$B_t = -\ a/b$$

The harvest rate (H) over the depletion period (from the peak to the final t) is define as:

$$H_t = C_t/B_t$$

where C_t is the cumulative catch at the end of the depletion period (for a given seamount–year).

The uncertainty for the linear regression approach was calculated using the delta method. For a single seamount–year regression we have estimated parameters $\hat{\theta} = \ (\hat{a}, \hat{b})$ with variance–covariance matrix:

$$V_\theta = \begin{pmatrix} Var(\hat{a}) & Cov\ (\hat{a}, \hat{b}) \\ Cov\ (\hat{a}, \hat{b}) & Var\ (\hat{b}) \end{pmatrix}$$

For $\hat{B} = -\ \hat{a}/\hat{b}$:

$$\frac{\partial g_1}{\partial a} = \frac{1}{b}, \quad \frac{\partial g_1}{\partial b} = \frac{a}{b^2}$$

For $\hat{H} = -\ C\ \hat{b}/\hat{a}$:

$$\frac{\partial g_2}{\partial a} = -\ C\frac{b}{a^2}, \quad \frac{\partial g_2}{\partial b} = \frac{C}{a}$$

The by the Delta method:

$$Var(\hat{B}) \approx\ \nabla\ g_1(\hat{\theta})\ V_\theta\ \nabla\ g_1(\hat{\theta})$$

$$Var(\hat{H}) \approx\ \nabla\ g_2(\hat{\theta})\ V_\theta\ \nabla\ g_2(\hat{\theta})$$

For the mixed effects model uncertainty for all quantities (including derived quantities like $B_{0,s}$ and H_s) was obtained using **ADREPORT**, which uses automatic differentiation and the joint precision matrix to propagate uncertainty from fixed effects, random effects, and hyperparameters. This provides likelihood-based standard errors that correctly reflect uncertainty in the hierarchical depletion model.

For both models the confidence intervals were formed using approximate normality $\pm$ 1.96 $\sqrt{Var(\hat{B})}$ and $\pm$ 1.96 $\sqrt{Var(\hat{H})}$.

3. Results

3.1. Simple regression models

Figure 2 shows the fitted regression lines using the simple regression models between average CPUE and cumulative catch for NPA at the four seamounts considered (Colahan, Kammu, Koko, and Yuryaku) for each year. Negative slopes indicate the expected depletion pattern, where CPUE declines as cumulative catch increases, consistent with localized stock depletion over the fishing season. Years or seamounts displaying positive slopes are not considered informative, as they likely reflect years with low catch levels or recruitment pulses. A positive slope was only registered in the Colahan seamount in 2017 (**Figure 2**).

Similarly, cases where the maximum CPUE occurred at the end of the season were excluded, as they indicate that the local population was not fully exploited before fishing ceased. This pattern was observed in Kammu 2020 and in Colahan 2016, 2020, 2023, and 2024 (**Figure 2**). The absence of a clear declining CPUE trend in these cases may be related to the limited number of observations per year–seamount combination, which ranged from only 3 to 7 (**Table 1**).

Overall, the majority of valid fits (negative slopes with early-season CPUE peaks) show a clear declining trend within years and seamounts, supporting the assumption that within-season declines in CPUE reflect local depletion of NPA aggregations (**Figure 2)**.

Estimated biomass at the beginning of the fishing season (B, left panel in **Figure 3**) were generally higher in the early 2010s, particularly at Kammu and Koko, and declined sharply in subsequent years, suggesting a reduction in the initial biomass available at the start of the fishing season. In contrast, harvest rates (H, right panel in **Figure 3**) remained relatively consistent among years and seamounts, typically between 0.5 and 1.0, indicating that most of the available biomass was removed within each season. Occasional spikes in B and H reflect years with higher model uncertainty or limited data.

Overall, the depletion model results indicate that NPA biomass has declined over time, while the fishery continues to harvest nearly all of the biomass available each year (**Figure 4**). The size of NPA aggregations has decreased substantially over the past decade.

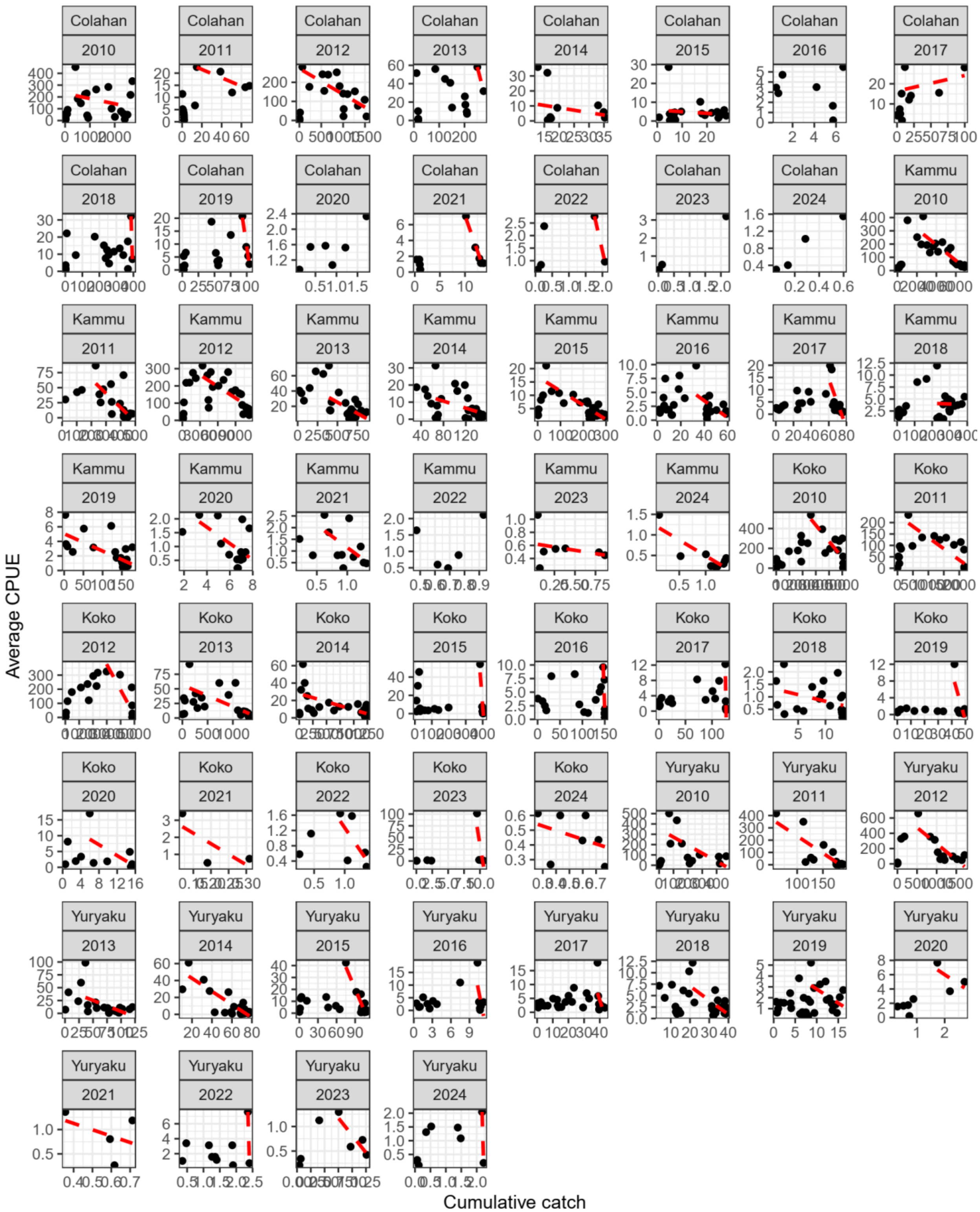

Figure 2. Relationship between average CPUE and cumulative catch for NPA at the four seamounts considered (Colahan, Kammu, Koko, and Yuryaku) across individual fishing years. Each panel represents a single year–seamount combination. The black points indicate observed average CPUE values from 10-day fishing periods, and the red lines show fitted regressions from the simple regression models.

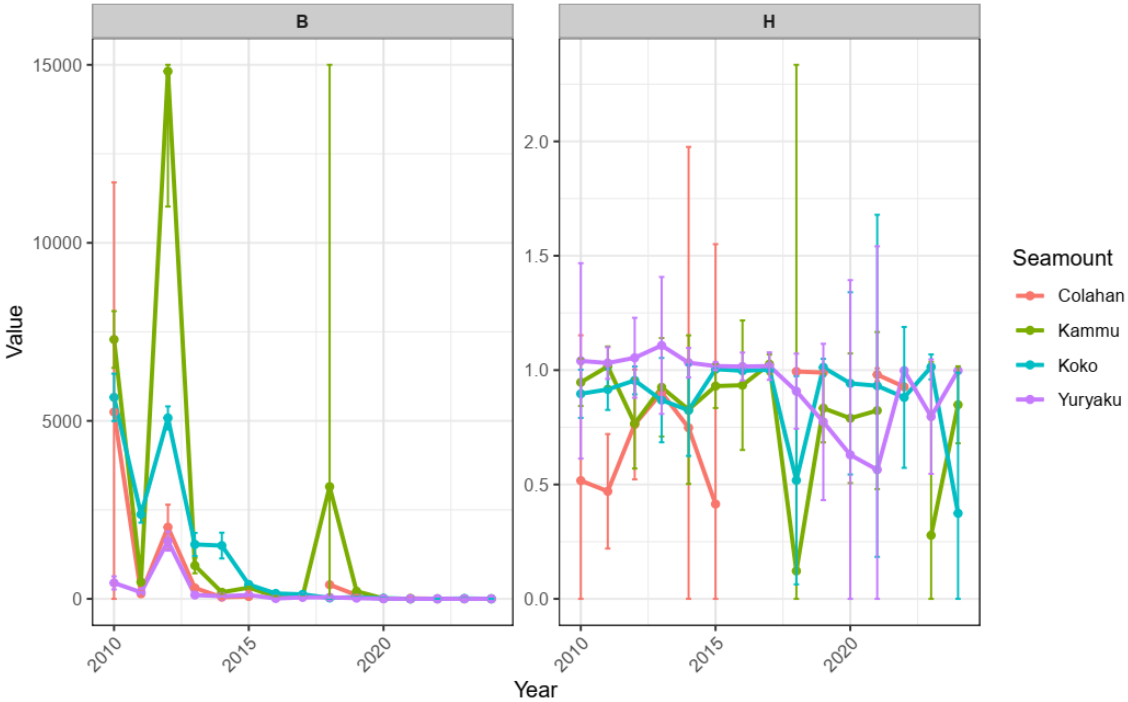

Figure 3. Estimated biomass at the beginning of the fishing season (B) and harvest rate (H) derived from depletion model fits with simple regression for NPA at the four seamounts considered (Colahan, Kammu, Koko, and Yuryaku) between 2010 and 2024. Each vertical line represents annual estimates with 95% confidence intervals for each seamount.

Figure 4. Estimated biomass at the beginning of the fishing season (B) and harvest rate (H) derived from depletion model fits with simple regression for NPA between 2010 and 2024 for all seamounts combined. Each vertical line represents annual estimates with 95% confidence intervals for each year.

3.2. Mixed-effect regression models

Figure 5 shows the fitted regression lines using the mixed effects models (using random slopes for each seamount) between average CPUE and cumulative catch for NPA for each year and seamount. As for the simple regression models, negative slopes indicate the expected depletion pattern, where CPUE declines as cumulative catch increases were excluded.

The patterns of both the estimated biomass at the beginning of the fishing season and the harvest rates were very similar to those obtained from the simple regression model for each seamount (**Figure 6**). The overall trends in B and H also closely matched the estimates from the simple regression model, indicating that NPA biomass has declined over time while harvest rates have remained high throughout the entire period (**Figure 7**).

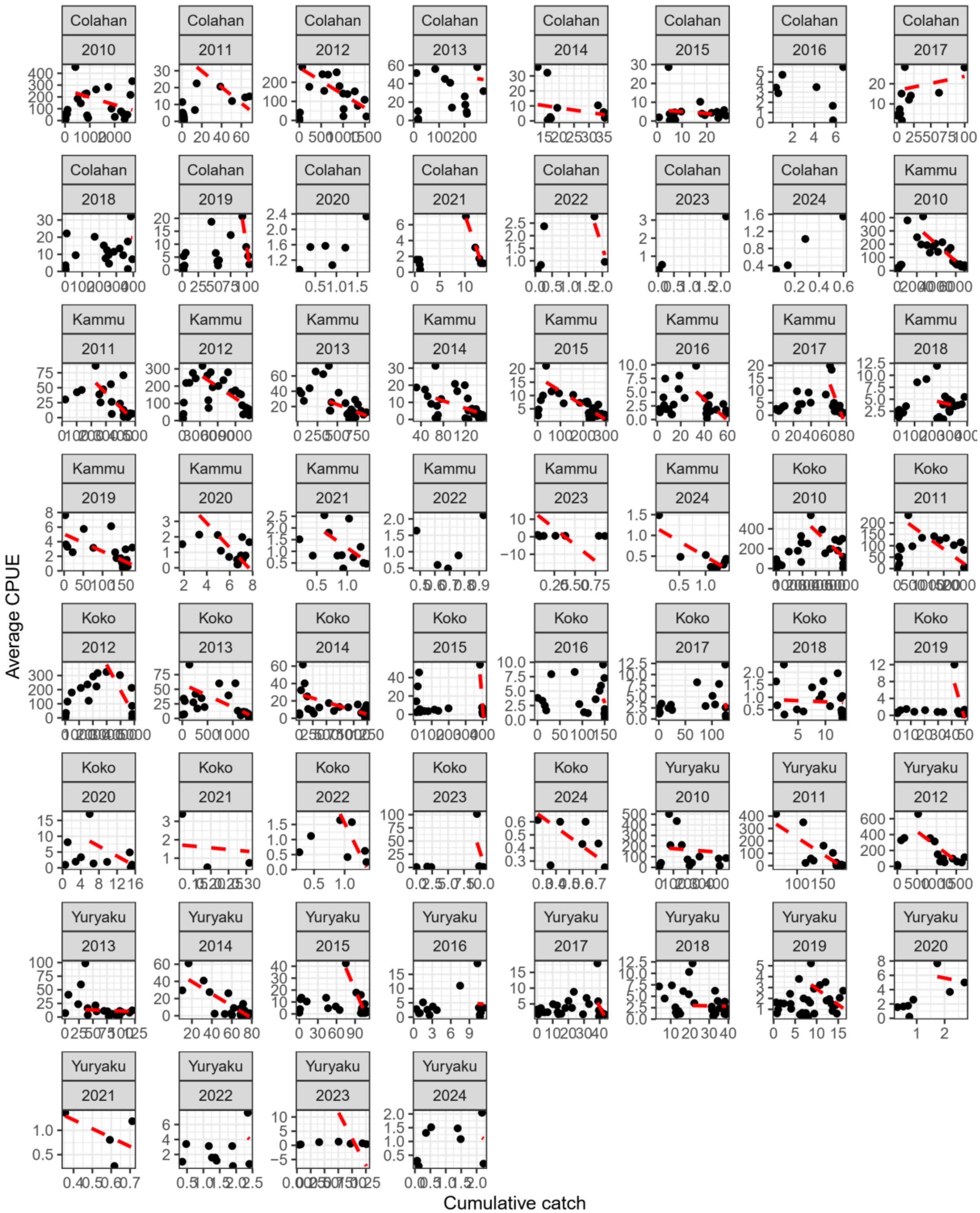

Figure 5. Relationship between average CPUE and cumulative catch for NPA at the four seamounts considered (Colahan, Kammu, Koko, and Yuryaku) across individual fishing years. Each panel represents a single year–seamount combination. The black points indicate observed average CPUE values from 10-day fishing periods, and the red lines show fitted regressions from the mixed effects models with random seamounts slopes.

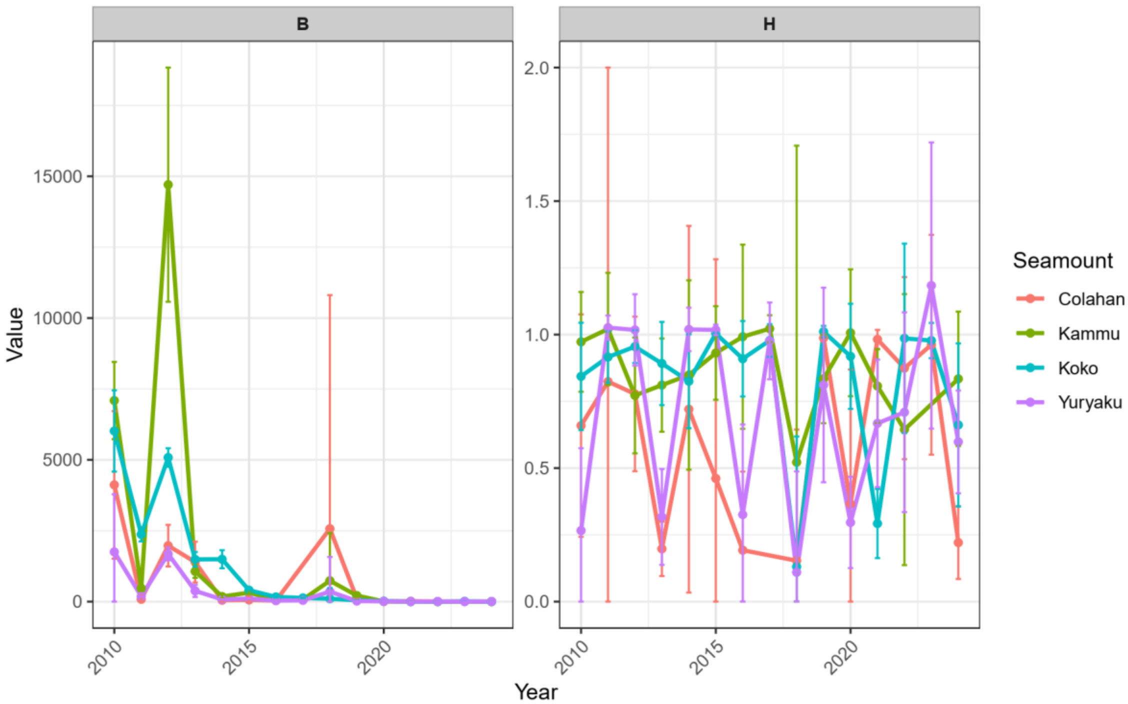

Figure 6. Estimated biomass at the beginning of the fishing season (B) and harvest rate (H) derived from depletion model fits with the mixed effects linear regressions for NPA at the four seamounts considered (Colahan, Kammu, Koko, and Yuryaku) between 2010 and 2024. Each vertical line represents annual estimates with 95% confidence intervals for each seamount.

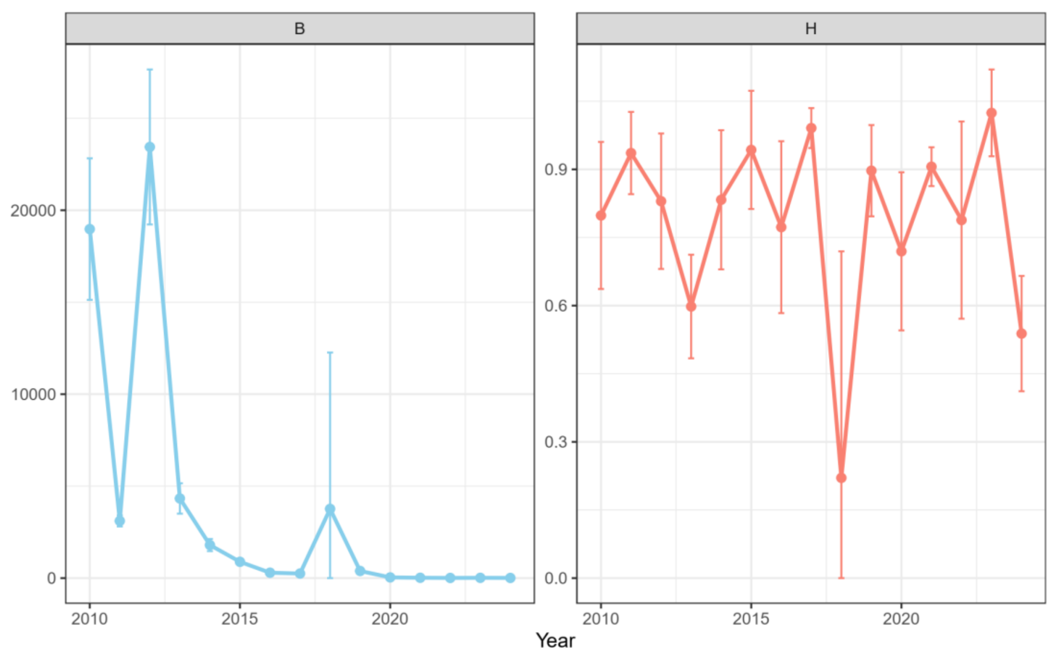

Figure 7. Estimated biomass at the beginning of the fishing season (B) and harvest rate (H) derived from depletion model fits with mixed effects linear regressions for NPA between 2010 and 2024 for all seamounts combined. Each vertical line represents annual estimates with 95% confidence intervals for each year.

4. Conclusions

Both the simple and mixed-effects regression models consistently indicated a clear depletion signal within fishing seasons across seamounts. In most cases, average CPUE declined with increasing cumulative catch, reflecting localized depletion of NPA aggregations as fishing progressed.

Estimates of biomass at the beginning of the fishing season showed a marked decline over time, particularly after the early 2010s, suggesting that the initial abundance of NPA available to the fishery has substantially decreased. In contrast, harvest rates have remained consistently high, generally between 0.5 and 1.0, across years and seamounts, indicating that most of the available biomass continues to be removed each season.

Results from the mixed-effects models were broadly consistent with those from the simple regressions, confirming the robustness of the observed temporal patterns.

The low biomass estimated in recent years aligns with the low catches observed over the past decade, suggesting that the stock may be in poor condition or that a regime shift leading to low recruitment has occurred. The overall pattern observed is consistent with a reduction in the size of the NPA aggregations, potentially signaling local depletion and limited recovery between fishing seasons.

5. Limitation of current analysis and data

Simple and mixed-effects linear depletion regressions assume a constant (linear) relationship between CPUE and cumulative catch and simple catchability. If catchability is non-linear or time-varying the estimates of B and H can be biased.

Changing targeting could be another limitation for the analysis. Based on the Japanese data which has information of intended target species, NPA has not being target of the fishery since 2020. If catchability changed through time, CPUE may no longer be a proportional index of local abundance and estimates will be biased.

When a population becomes highly depleted within or between seasons, the shape of CPUE–catch relationships can change (hyperstability, hyperdepletion) and simple linear fits are not appropriate.

In terms of data-limitations, the reduced sample sizes for the last decade can bias temporal trends. Also, ignoring process error, spatial spillover, or connectivity between seamounts jeopardies mis-estimating trends and uncertainty.

Some seamount–year combinations produced harvest-rate estimates greater than one. This does not imply exploitation beyond the total biomass, but reflects statistical limitations of the simple depletion model. The calculation of $H = C/B$ is highly sensitive to the intercept–slope ratio, and small estimation errors, especially when slopes are steep or data are noisy, inflate B downward, producing $H > 1$. A key source of bias is the potential misidentification of the CPUE peak, which in practice may not correspond to the true unfished biomass. If the identified peak occurs after some fishing has already reduced abundance, the model underestimates B, mechanically elevating H. Additionally, departures from strict linearity or imperfect CPUE–abundance proportionality can increase uncertainty in the fitted parameters and propagate into the derived harvest rates. Thus, values slightly above one should be interpreted as indicators of high exploitation combined with estimation uncertainty, rather than literal overharvest beyond total biomass.

6. Acknowledgements

We thank the SWG participants for their valuable contributions and constructive discussions throughout the development of this work.

7. References

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