

On the Potential Use of the Leslie Davis Depletion Model for Estimating Population Size for Illex Squid: 1997-2018

Working Paper #xx from Illex Squid Working Group

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Introduction

All models rely on assumptions that ultimately circumscribe their utility for understanding the real world. With varying degrees of success some of the world's squid fisheries are managed using so-called depletion models (ref xx). The concept behind depletion models is simple; the rate of decline of some measure of abundance as harvesting occurs provides some insights into the initial population size. In the Leslie-Davis model (Leslie and Davis, 1939), catch per unit effort is plotted against cumulative catch. The intersection of the regression line with the x-axis is an estimate of the initial population size and the slope of the line is a measure of the efficiency of each unit of effort to reduce the population. In controlled experiments, using say a single type of gear, the slope can be interpreted as a measure of gear efficiency (Gould and Pollock, 1997, Rago et al. 2006). In many applications the focus of depletion models is on abundance estimation rather than gear efficiency, which is sometimes termed a "nuisance parameter." The analyses herein focus on potential applicability of the simple Leslie-Davis model to estimate abundance for Illex squid in the Northeast US.

The key assumptions of a depletion model are:

1. All individuals have the same probability of being caught in a sample
2. The expected catch in a sample is proportional to sampling effort
3. The catch depends on the cumulative catch of preceding samples
4. All removals from the population are known
5. All additions to the population are known

Assumption 1 implies that the probability of capture does not vary with size or other variables. One such variable for squid might be time of day such that squid closer to the bottom are more likely to be caught than those higher in the water column. Although fishing occurs primarily during the day, squid rising from the bottom at dusk or returning to the bottom at dawn may not be as vulnerable. Illex grow rapidly during the period of the fishery and gear selectivity is known to vary with squid size. Selectivity adjustments might be necessary for any serious application of this method.

Assumption 2 is the usual assumption that catch per unit effort decreases linearly with population size. Fishing activity is generally deployed to areas where squid are most concentrated so movement to other areas could violate this assumption. Depending on the gradient of the concentration profile, hyperdepletion could occur wherein CPUE declines faster than the overall population abundance.

Assumption 3 expresses the effect that cumulative removals in a closed population will reduce CPUE if the population is totally mixed and randomly distributed within the total habitat.

Assumptions 4 and 5 build on this premise of population closure. Natural mortality estimates in

the literature typically range from 0.1 to 0.14 per week (Hendrickson and Hart 2006) with a sizable increase in natural mortality at full maturation. But actual predation losses from piscivores are difficult to quantify and cannibalism is even more difficult. Immigration is thought to be associated with eddies of the Gulf Stream and warm core rings although the precise effects are unknown. Finally, it is important to remember that the fishery takes place over a period of time (6 months) nearly equal to the lifespan of *Illex*. Hence recruitment of juvenile squid is expected to occur during the period of the fishery.

At face value, it would appear that all of the assumptions for a valid depletion-based estimate are violated to some extent. Seber (1973, p. 304) noted “In conclusion we make the obvious remark that the above methods will only work if sufficient individuals are removed from the population, so that there is a significant decline in the catch per unit effort.” Given the potential influences of immigration and emigration, recruitment, variable growth and natural mortality rates, it is also possible that good statistical fits could arise due to factors other than removals. In context of much less complicated natural conditions, Seber (1973, p. 298) cautioned,

“A plot of Y_i vs x_i will provide a rough visual check on the adequacy of the regression model, including the assumption of constant variance. However, such graphical evidence should not be taken as final, for a straight-line fit is still possible in some situations, even when the assumptions do not hold. For example, a linear model is still possible even with natural mortality or migration taking place.”

In this Working Paper, the focus is on the potential applicability of a simple depletion model to the weekly catch per unit effort rates of *Illex* derived from Vessel Trip Reports (VTR). A simple two bin population model with seasonal migration rates is used to examine the potential behaviors of a CPUE vs cumulative catch.

Data and Methods

Vessel Trip Report data for 1997 to 2018 were graciously provided by Lisa Hendrickson. Through a joint effort of industry and the NEFSC (Hendrickson, Holmes and others), biological samples from freezer boats (SeaFreeze Ltd, Lapp per comm) were used to derive average weights by week for the same period of years, excluding 2006 and 2007. Catches are reported in catch per trip by vessel and date landed. Estimates of fishing effort include total days absent, and days fished. Days absent is computable to a resolution of one day, whereas finer scale information on days fished is supplied by fisherman reports. Crude measures of CPUE were estimated as the total catch divided by the number of trips, the total days absent over all trips, or the total days fished summed over all trips within a given standardized week (i.e., week 1 = Jan 1 to 7, week 2 = Jan 8-14, etc). The primary fishing season for these analyses was restricted to standard weeks 22 to 44. Historically this window constitutes 95% of the annual landings by weight.

Catches in weight were converted to catches in number by dividing the total catch by the estimated average weight. When weekly average weight samples were not available, average weights were borrowed from the next available week. Capture probabilities are applicable to individuals rather than biomass, all quantities in the Leslie Davis model were expressed in terms of numbers of individuals. The Leslie-Davis model is written as

$$CPUE_t = qN_0 - q \sum_{i=1}^{t-1} C_i$$

Which is a simple linear regression $CPUE_t = a + b K_{t-1}$ where K_{t-1} is equal the sum of catches up to $t-1$. In theory, the estimated total number of individuals in the population occurs when all of the individuals are captured. This corresponds to $CPUE=0$, so that the estimate of N_0 is simply equal to $-a/b$.

The preferred method for estimating the parameters of the Leslie Davis model is to use maximum likelihood estimation because the variance of CPUE changes with each observation (Gould and Pollock, 1997). In practice, a simple linear regression of CPUE vs cumulative catch is sufficient to get estimates fairly close to the ML estimates. For the purposes of this working paper, the simple linear regression was judged sufficient.

Leslie Davis Model Results

Results of the Leslie Davis model are summarized in Figures 1 to 19 for 1997 to 2018. Average weights were not available for 2007 and 2008 so no analyses were done. A fourth-order polynomial was used to illustrate the seasonal variation in CPUE vs time in the top and center panels for CPUE in numbers and weight, respectively. In a closed population subject to depletion only from harvesting one would expect CPUE to decrease continuously. This occurred in only 4 of the 19 years, notably in 1998, 2010, 2017 and 2018. Three of these years were judged by fishermen as excellent harvest years (1998, 2017, 2018). The Leslie Davis model appeared to fit reasonably well in these years with average R^2 exceeding 0.7 for all models. The proportion of the variance explained by total removals was about 50% in 2011 and 2016. In all other years, the R^2 values were below 0.22 and in many cases near zero. From a broad overview, the model would be judged acceptable statistically in 4 of the 19 years, marginal in 2 years, and unacceptable in the remaining 13 years. In seven years the Leslie Davis model had positive slopes for at least one of the CPUE measures, resulting in negative population estimates.

These results suggest that the violations of assumptions of the Leslie Davis model overwhelm any simple application of the model. Variations in temporal timing of migrations and interannual variations in growth may be primary factors underlying lack of model fit. To gain some insights into the potential effects of migration a simple population model consisting of an inshore and offshore population was constructed, $N_{in}(t)$ and $N_{off}(t)$, respectively. In the model the unfished offshore population moves inshore with a seasonal rate $T_{in}(t)$. The inshore population is both fished and moves offshore with a seasonal rate $T_{off}(t)$. Both populations have the same seasonal average weight $W(t)$ and have the same natural mortality $M(t)$. The structural equations can be written as:

$$N_{off}(t+1) = N_{off}(t)e^{-M(t)} - T_{in}(t)N_{off}(t) + T_{off}(t)N_{in}(t)$$

$$N_{in}(t+1) = N_{in}(t)e^{-M(t)} - N_{in}(t)T_{off}(t) + T_{in}(t)N_{off}(t) - qE(t)N_{in}(t)$$

Migration rates were defined as quadratic functions of time of the form $T(t)=r(t-\delta)+r(t-\delta)^2/\Delta$ where d defines the initial time of the migration process and Δ defines the duration. The r parameter controls the magnitude of the migration rate and $T(t)=0$ when $r(t-\delta)+r(t-\delta)^2/\Delta < 0$.

The total catch is $C(t) = q E(t) N_{in}(t)$ where q is the catchability parameter and $E(t)$ is effort. To mimic the apparent behavior of the fishery wherein success in previous time steps, effort was modeled as a time series model

$$E(t + 1) = E(t) \left(\beta \frac{CPUE(t - 1)}{CPUE(t - 2)} + (1 - \beta) \frac{CPUE(t - 3)}{CPUE(t - 4)} \right)$$

Where $CPUE(t)=C(t)/E(t)$ and β effectively damps the response between newer and older information on previous catch rates. The above function is somewhat arbitrary but it does seem to follow responses of fishermen who indicated that participation in the fishery increases as catch rates increase. Total catch and population biomass were estimated by multiplying $N(t)$ by $W(t)$ and $Y(t)=C(t)*W(t)$ where average weights are similar to those observed in the industry supplied data.

The simple spatial model is designed to improve understanding of actual data and illustrate the interplay of complex relationships that underlie the observations. Figure 20 demonstrates that the Leslie Davis depletion model can have a straight line portion (lower left plot). Slight changes in the timing of migration and major changes in M result in a nearly flat Leslie Davis function (Fig. 21). A comparison of two scenarios for the derived Leslie Davis function is shown in Fig. 22.

It is hypothesized that model parameters can be varied to derive catch curves that look much like the empirical curves. Alone, this proves nothing. However, when combined with other factors, including fishing behavior and environmental drivers, it can give some insights into seasonal dynamics and what might be driving catch patterns. Hence the model could be a useful starting point for more detailed discussions of critical factors and potential use of oceanographic models that may have predictive value for inshore-offshore migrations.

References

- Gould, W. R. and K. H. Pollock. 1997. Catch-effort maximum likelihood estimation of important population parameters. *Can. J. Fish. Aquat. Sci.* 54:898-906.
- Leslie, P. H. and D. H. S. Davis. 1939. An attempt to determine the absolute number of rats on a given area. *J. Anim. Ecol.* 8:94-113.
- Rago, P. J., J. R. Weinberg, and C. Weidman. 2006. A spatial model to estimate gear efficiency and animal density from depletion experiments. *Can. J. Fish. Aquat. Sci.* 63:2377-2388.

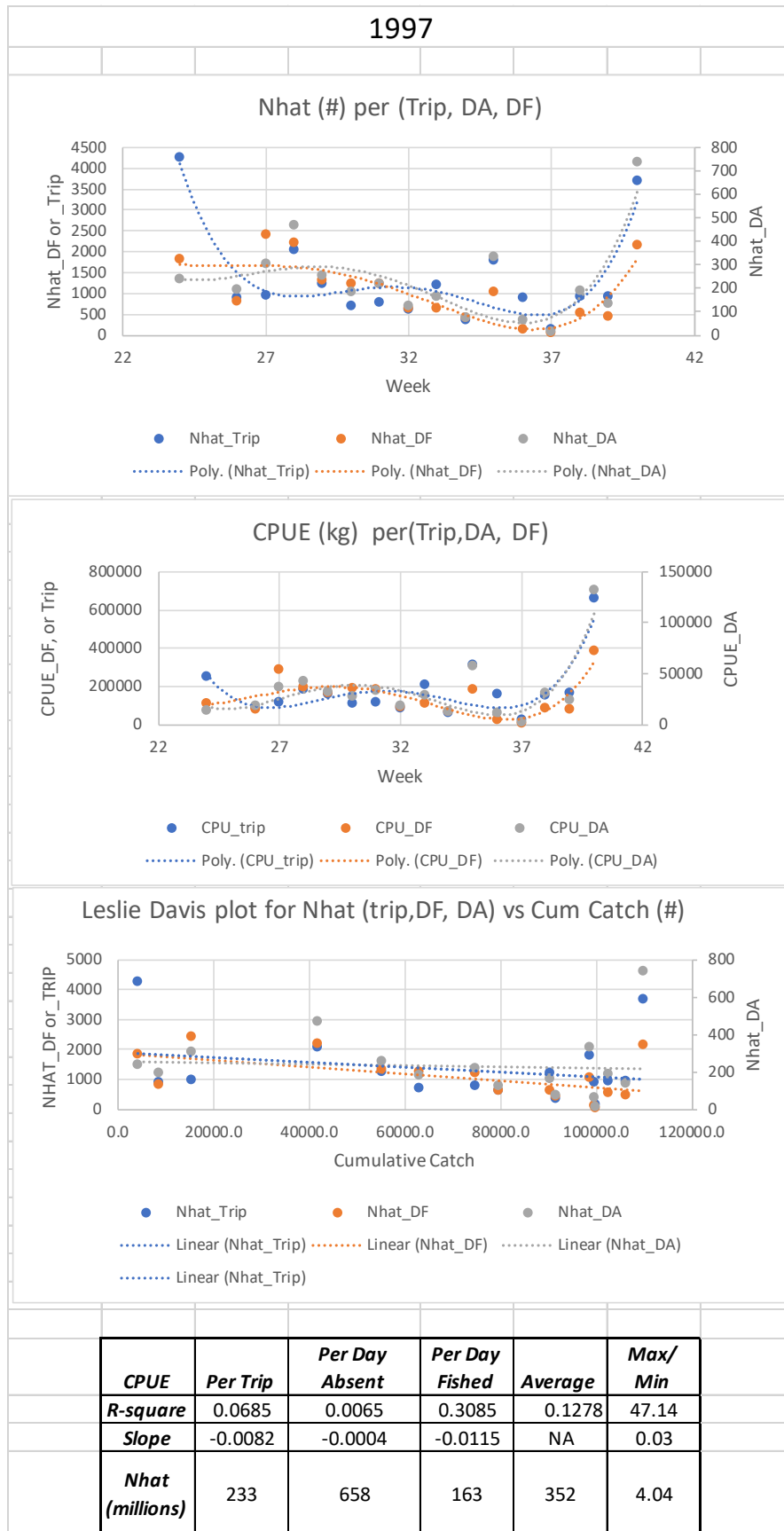


Figure 1. Summary of Leslie Davis Model results for 1997. [top]CPUE expressed as numbers per trip (blue), numbers per days absent(gray) or number per day fished(orange) vs standard week, [middle] CPUE by weight for same effort measures, [bottom] CPUE by numbers vs cumulative catch (in numbers). Statistics for degree of fit and population size are based on simple linear regression.

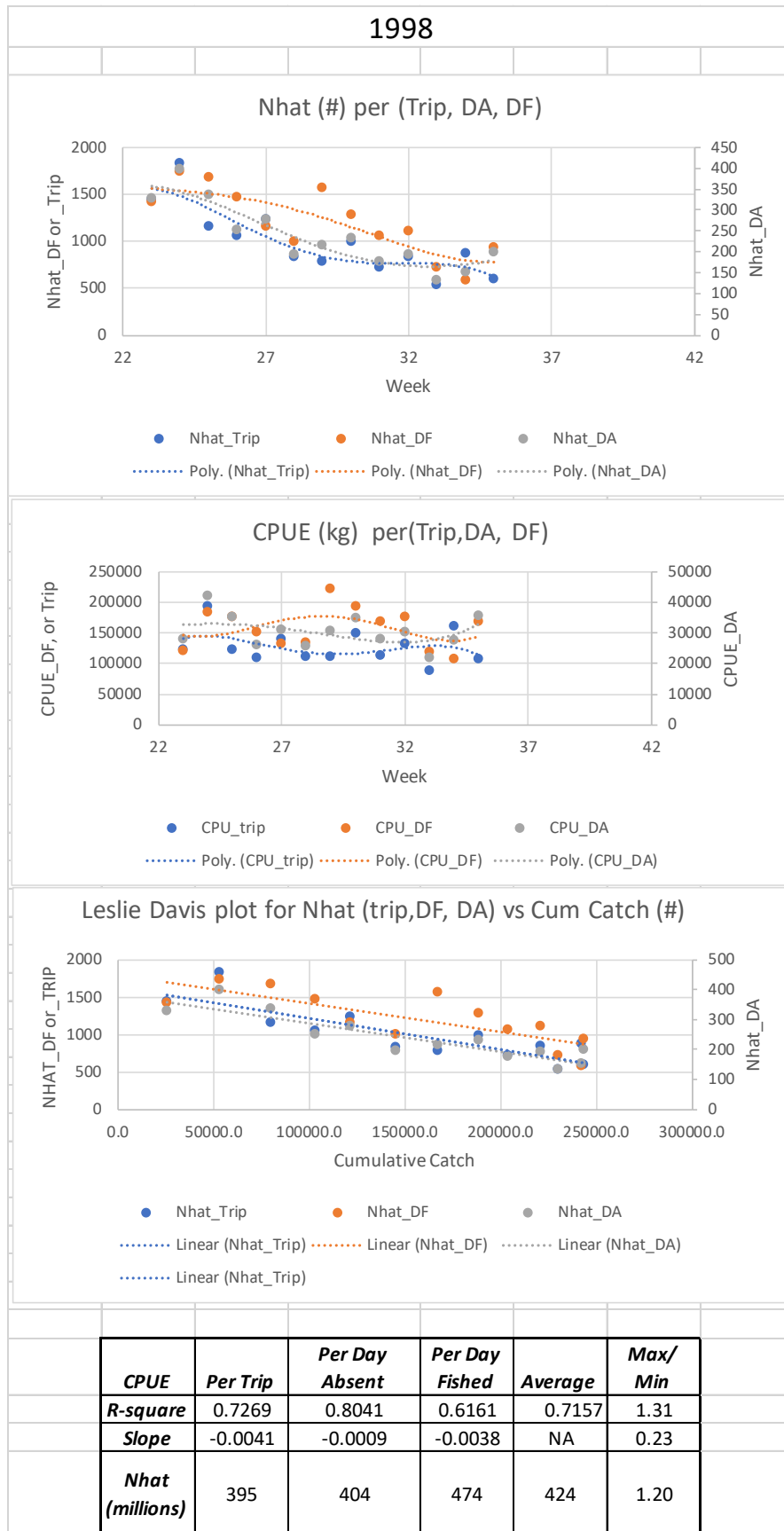


Figure 2. Summary of Leslie Davis Model results for 1998. [top]CPUE expressed as numbers per trip (blue), numbers per days absent(gray) or number per day fished(orange) vs standard week, [middle] CPUE by weight for same effort measures, [bottom] CPUE by numbers vs cumulative catch (in numbers). Statistics for degree of fit and population size are based on simple linear regression.

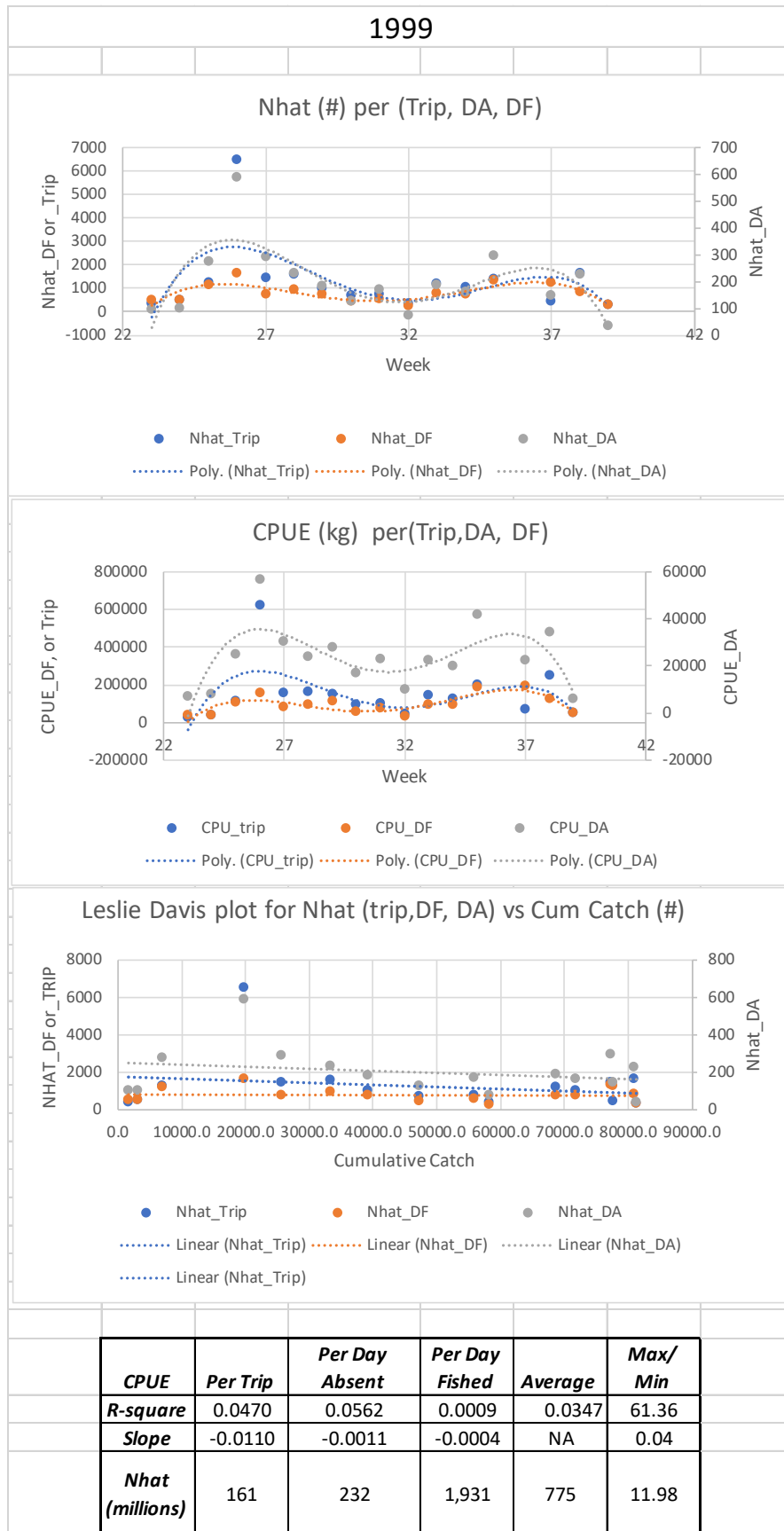


Figure 3. Summary of Leslie Davis Model results for 1999. [top]CPUE expressed as numbers per trip (blue), numbers per days absent(gray) or number per day fished(orange) vs standard week, [middle] CPUE by weight for same effort measures, [bottom] CPUE by numbers vs cumulative catch (in numbers). Statistics for degree of fit and population size are based on simple linear regression.

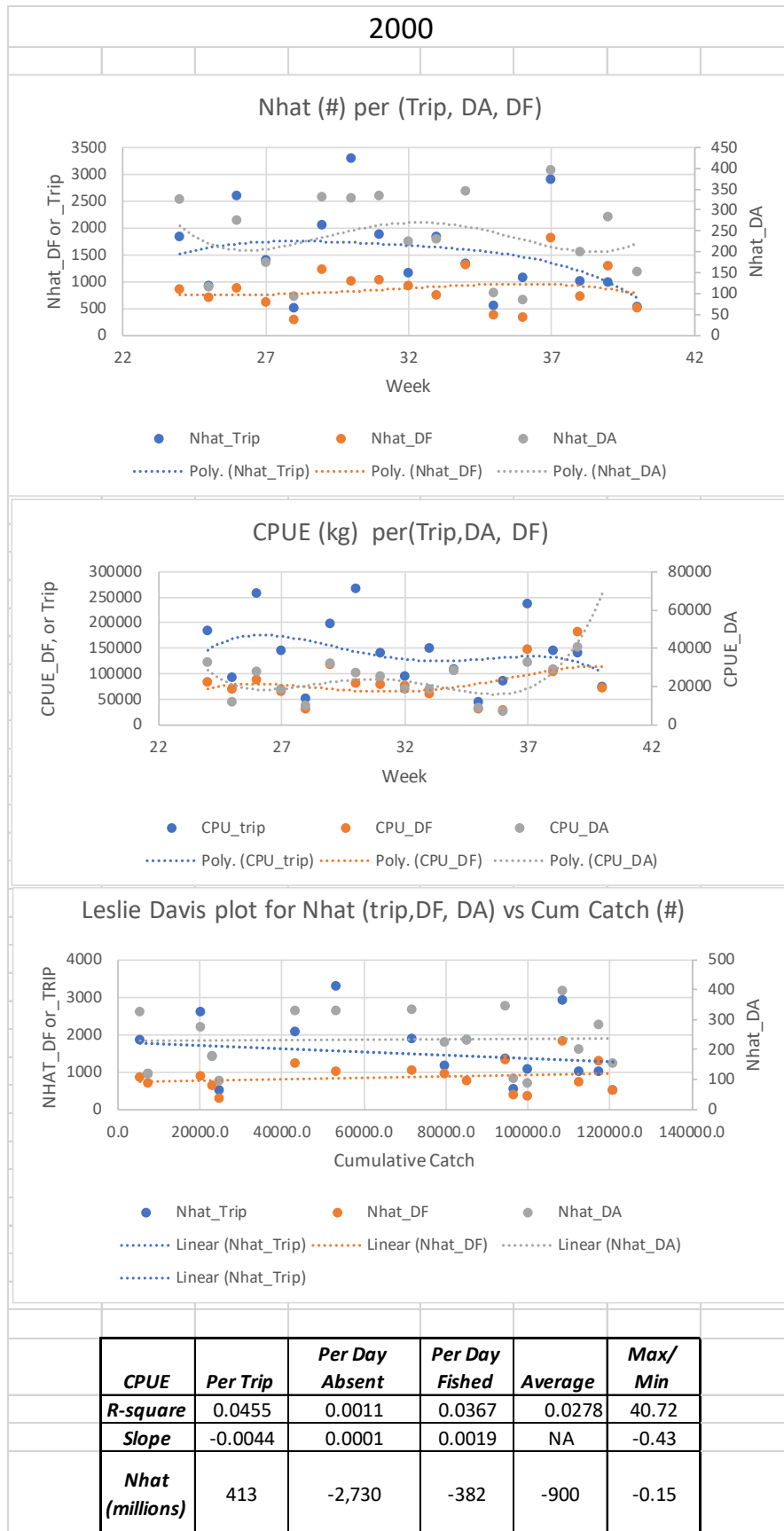


Figure 4. Summary of Leslie Davis Model results for 2000. [top]CPUE expressed as numbers per trip (blue), numbers per days absent(gray) or number per day fished(orange) vs standard week, [middle] CPUE by weight for same effort measures, [bottom] CPUE by numbers vs cumulative catch (in numbers). Statistics for degree of fit and population size are based on simple linear regression.

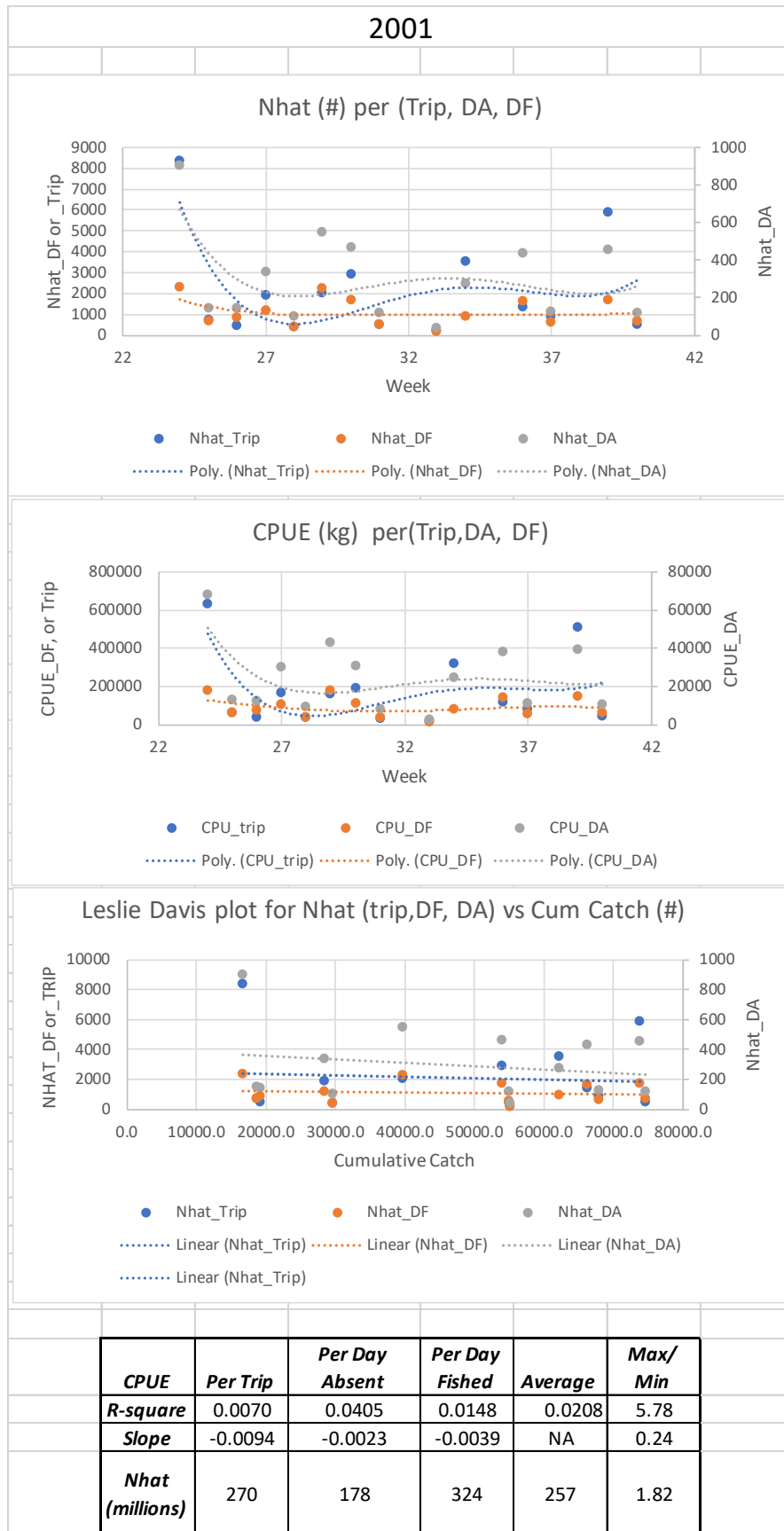


Figure 5. Summary of Leslie Davis Model results for 2001. [top]CPUE expressed as numbers per trip (blue), numbers per days absent(gray) or number per day fished(orange) vs standard week, [middle] CPUE by weight for same effort measures, [bottom] CPUE by numbers vs cumulative catch (in numbers). Statistics for degree of fit and population size are based on simple linear regression.

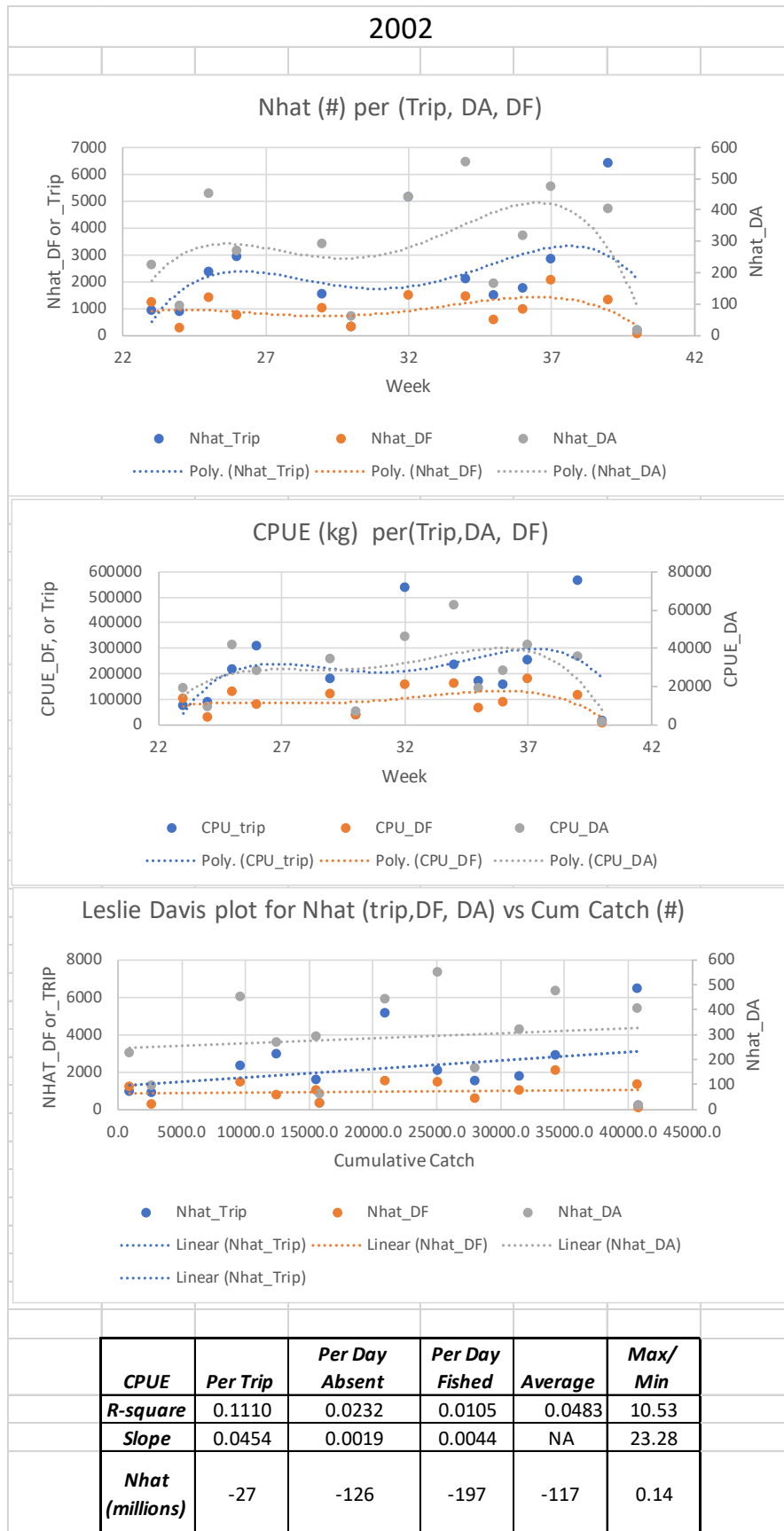


Figure 6. Summary of Leslie Davis Model results for 2002. [top]CPUE expressed as numbers per trip (blue), numbers per days absent(gray) or number per day fished(orange) vs standard week, [middle] CPUE by weight for same effort measures, [bottom] CPUE by numbers vs cumulative catch (in numbers). Statistics for degree of fit and population size are based on simple linear regression.

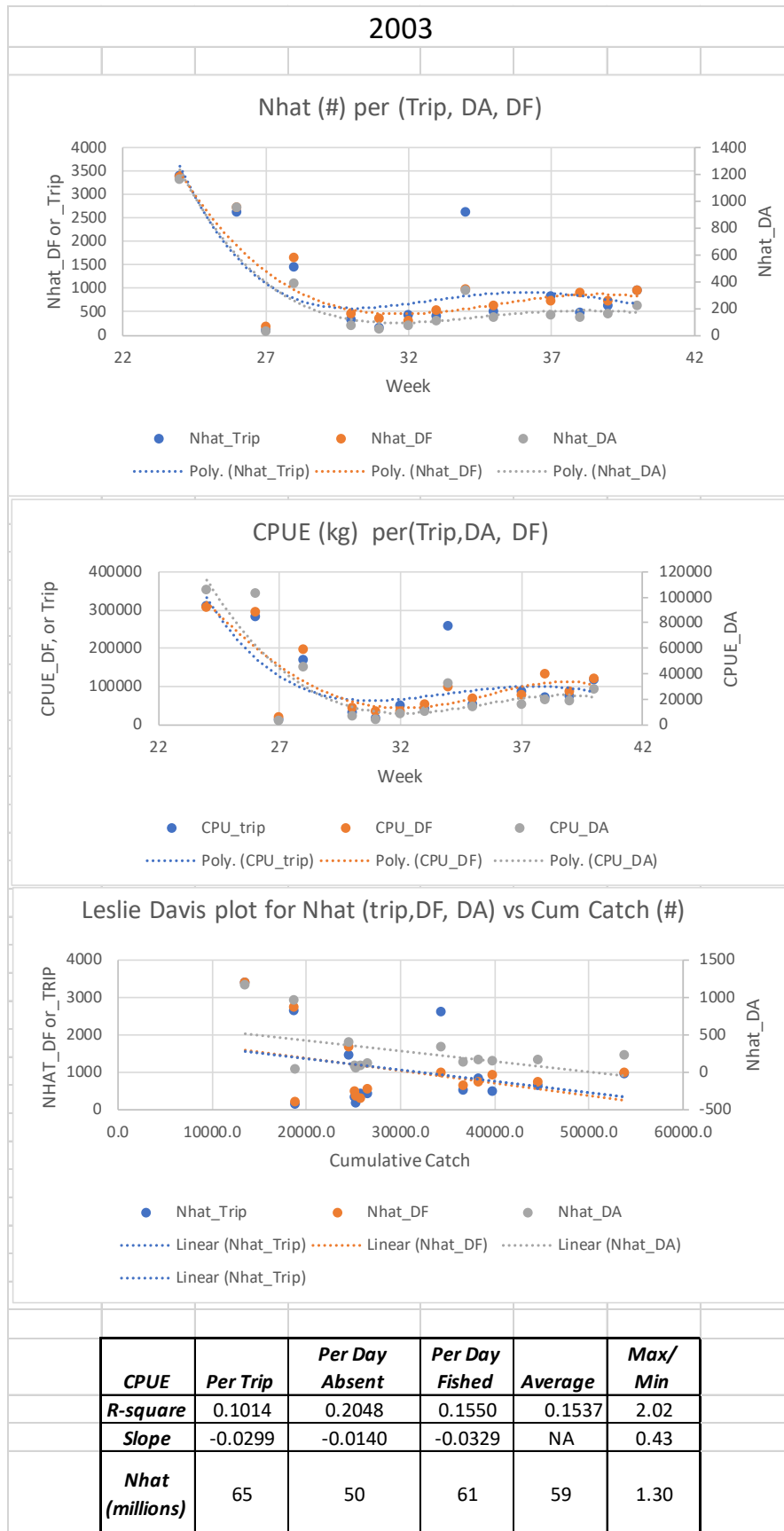


Figure 7. Summary of Leslie Davis Model results for 2003. [top]CPUE expressed as numbers per trip (blue), numbers per days absent(gray) or number per day fished(orange) vs standard week, [middle] CPUE by weight for same effort measures, [bottom] CPUE by numbers vs cumulative catch (in numbers). Statistics for degree of fit and population size are based on simple linear regression.

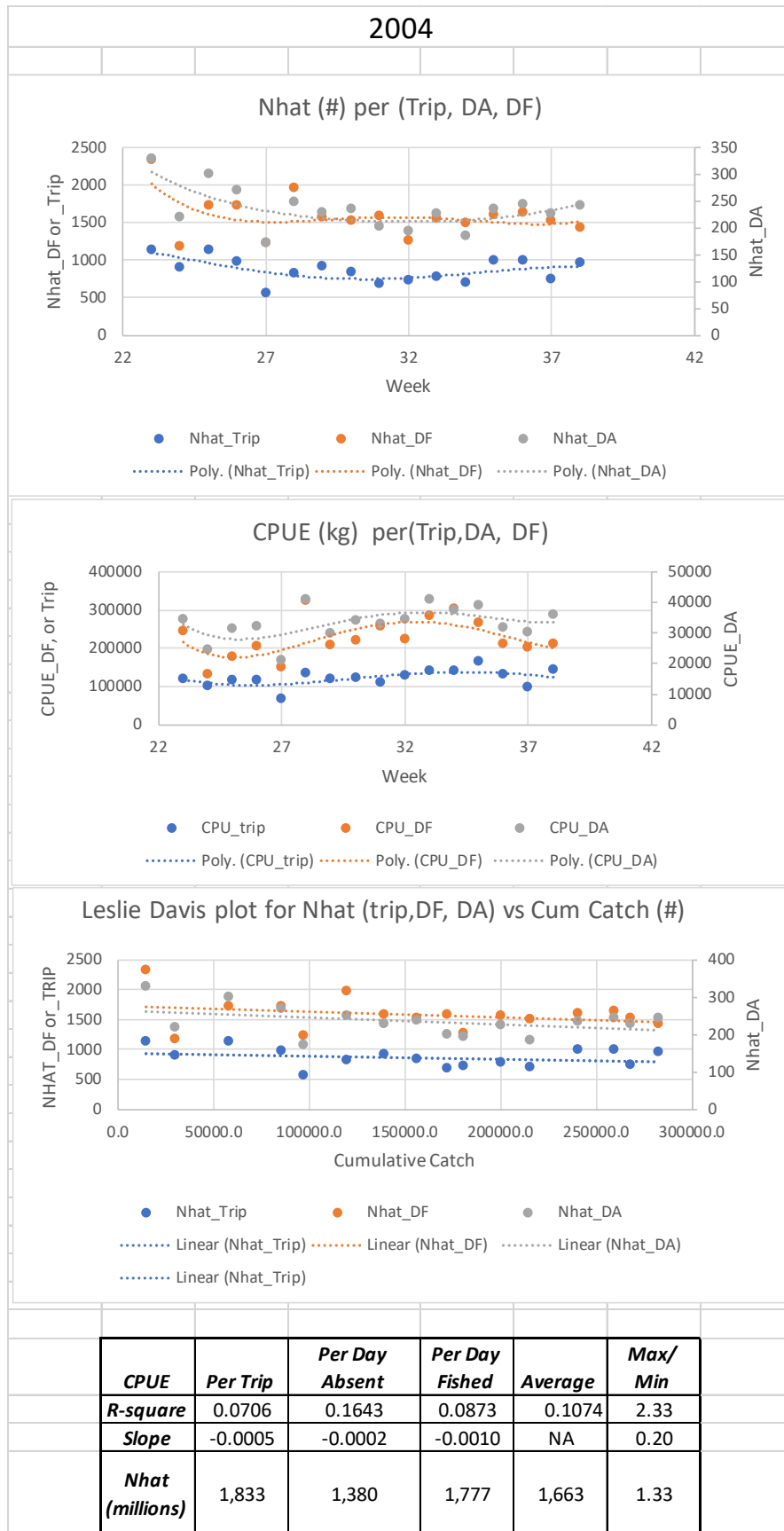


Figure 8. Summary of Leslie Davis Model results for 2004. [top]CPUE expressed as numbers per trip (blue), numbers per days absent(gray) or number per day fished(orange) vs standard week, [middle] CPUE by weight for same effort measures, [bottom] CPUE by numbers vs cumulative catch (in numbers). Statistics for degree of fit and population size are based on simple linear regression.

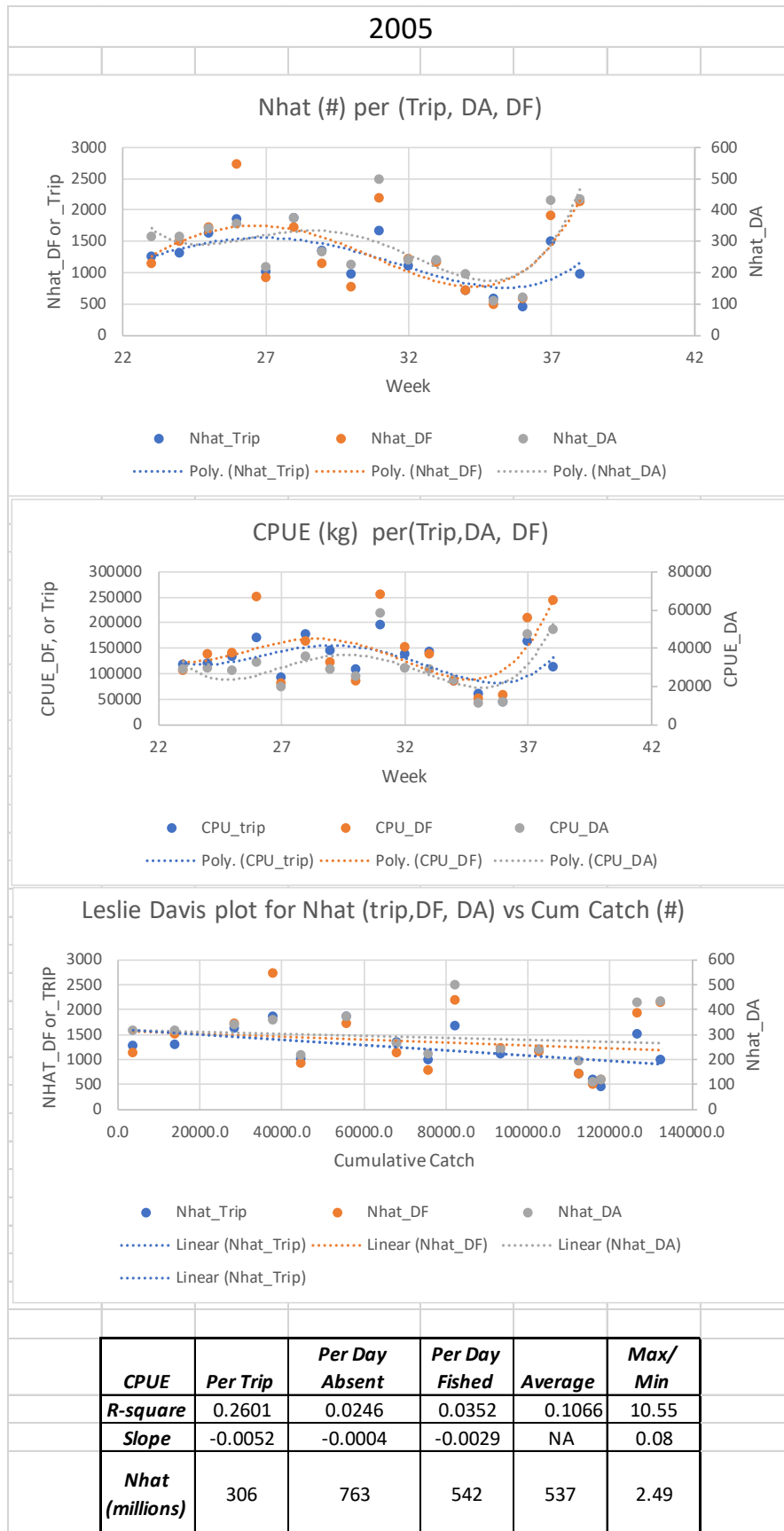


Figure 9. Summary of Leslie Davis Model results for 2005. [top]CPUE expressed as numbers per trip (blue), numbers per days absent(gray) or number per day fished(orange) vs standard week, [middle] CPUE by weight for same effort measures, [bottom] CPUE by numbers vs cumulative catch (in numbers). Statistics for degree of fit and population size are based on simple linear regression.

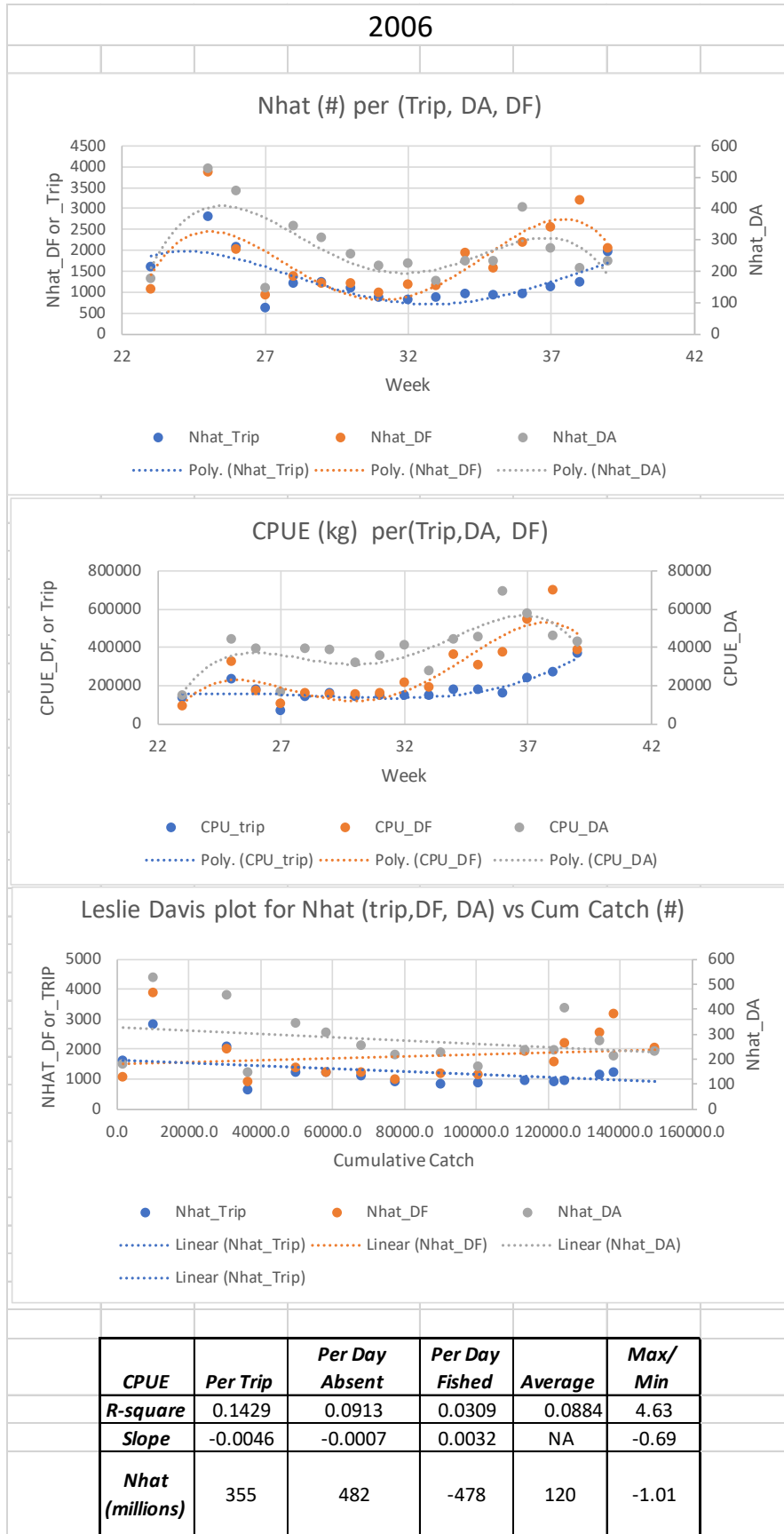


Figure 10. Summary of Leslie Davis Model results for 2006. [top]CPUE expressed as numbers per trip (blue), numbers per days absent(gray) or number per day fished(orange) vs standard week, [middle] CPUE by weight for same effort measures, [bottom] CPUE by numbers vs cumulative catch (in numbers). Statistics for degree of fit and population size are based on simple linear regression.

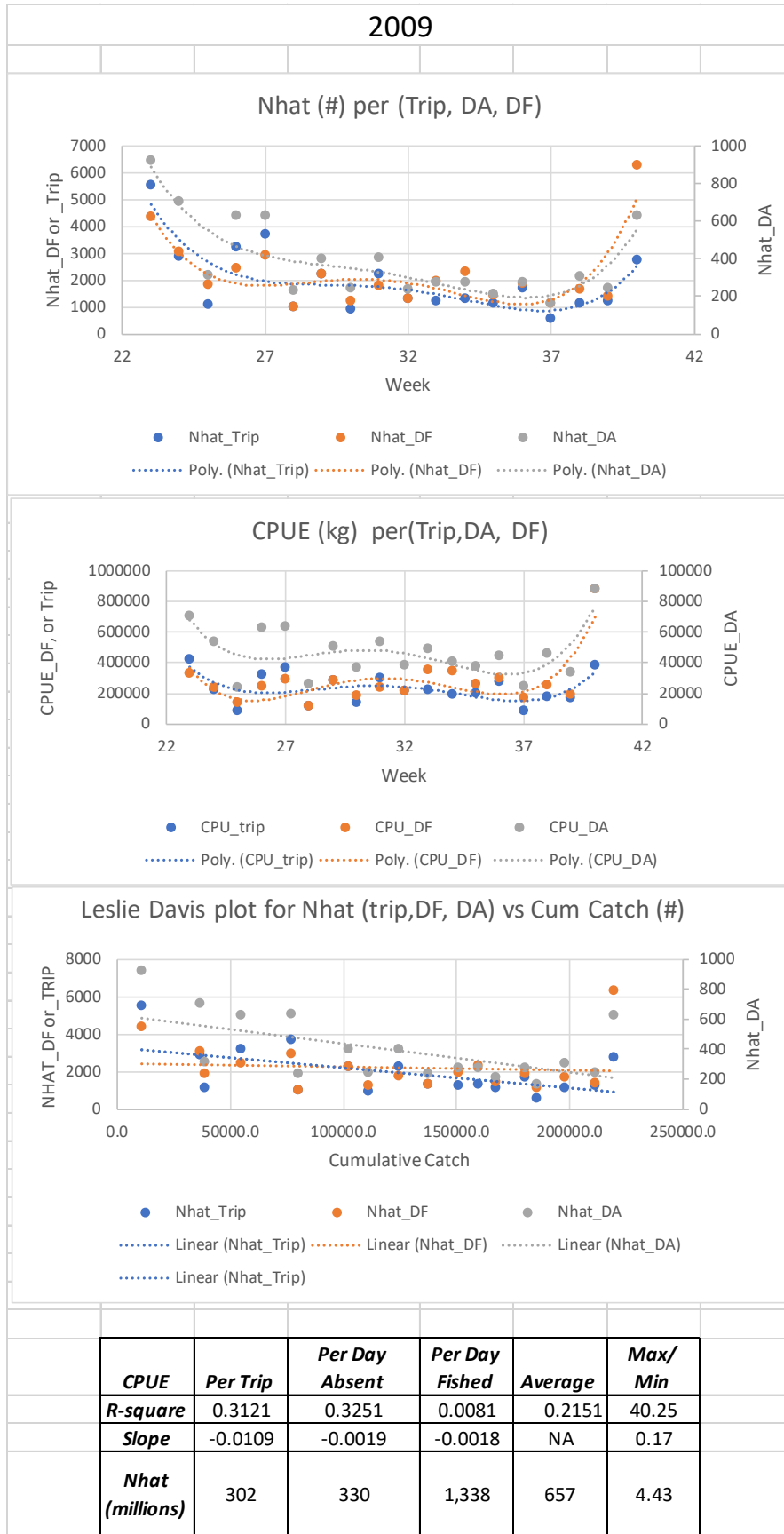


Figure 11. Summary of Leslie Davis Model results for 2009. [top]CPUE expressed as numbers per trip (blue), numbers per days absent(gray) or number per day fished(orange) vs standard week, [middle] CPUE by weight for same effort measures, [bottom] CPUE by numbers vs cumulative catch (in numbers). Statistics for degree of fit and population size are based on simple linear regression.

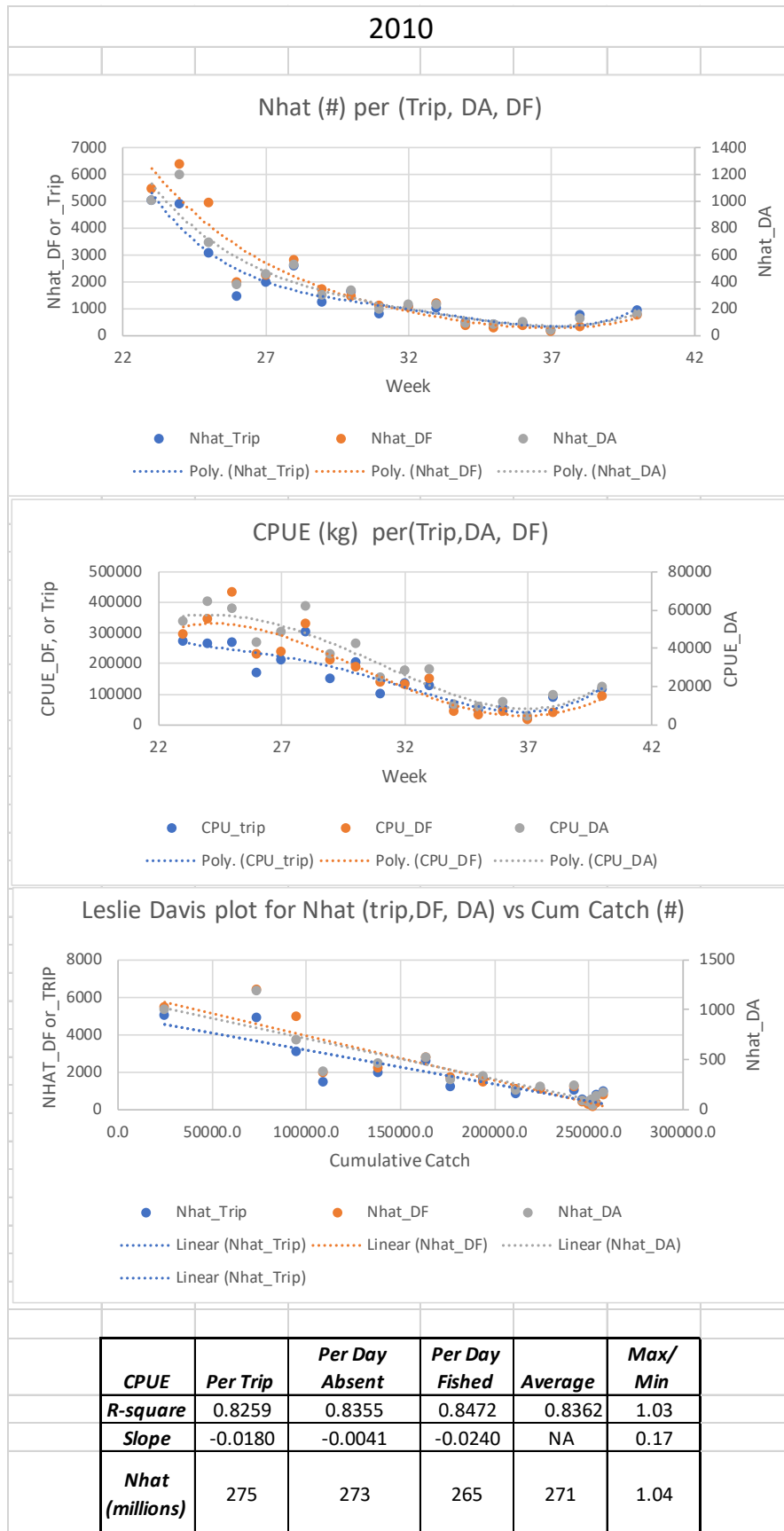


Figure 11. Summary of Leslie Davis Model results for 2010. [top]CPUE expressed as numbers per trip (blue), numbers per days absent(gray) or number per day fished(orange) vs standard week, [middle] CPUE by weight for same effort measures, [bottom] CPUE by numbers vs cumulative catch (in numbers). Statistics for degree of fit and population size are based on simple linear regression.

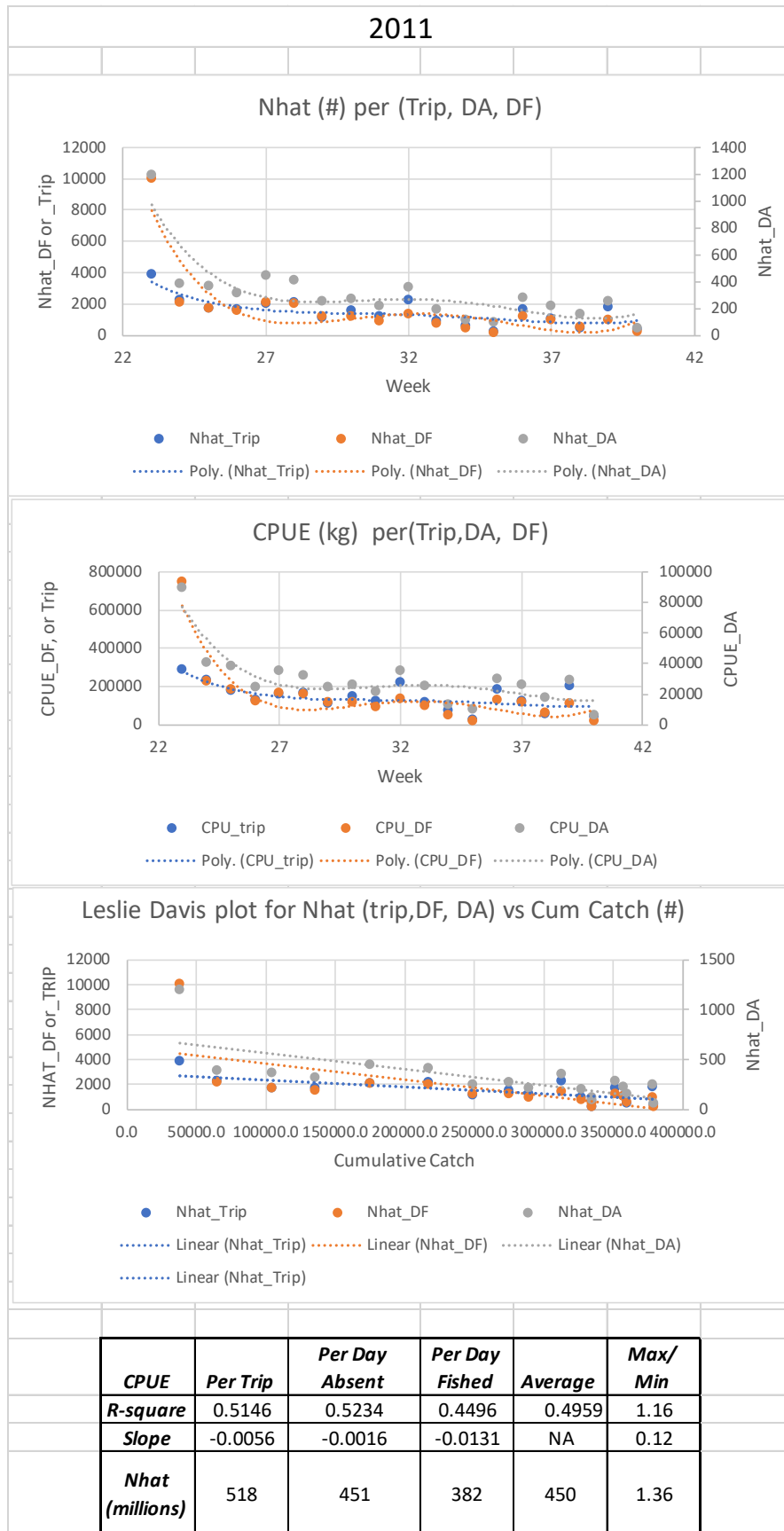


Figure 12. Summary of Leslie Davis Model results for 2011. [top]CPUE expressed as numbers per trip (blue), numbers per days absent(gray) or number per day fished(orange) vs standard week, [middle] CPUE by weight for same effort measures, [bottom] CPUE by numbers vs cumulative catch (in numbers). Statistics for degree of fit and population size are based on simple linear regression.

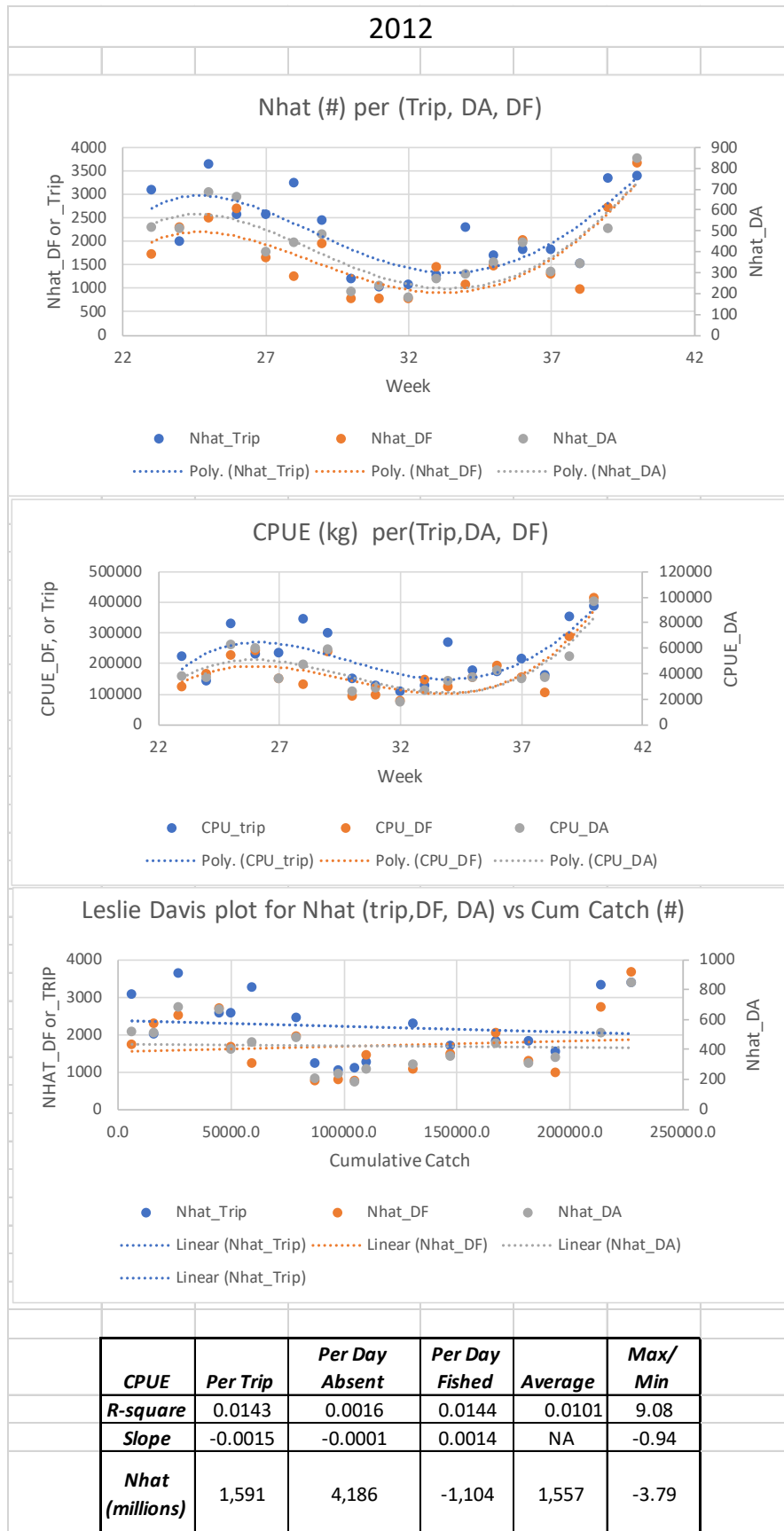


Figure 13. Summary of Leslie Davis Model results for 2012. [top]CPUE expressed as numbers per trip (blue), numbers per days absent(gray) or number per day fished(orange) vs standard week, [middle] CPUE by weight for same effort measures, [bottom] CPUE by numbers vs cumulative catch (in numbers). Statistics for degree of fit and population size are based on simple linear regression.

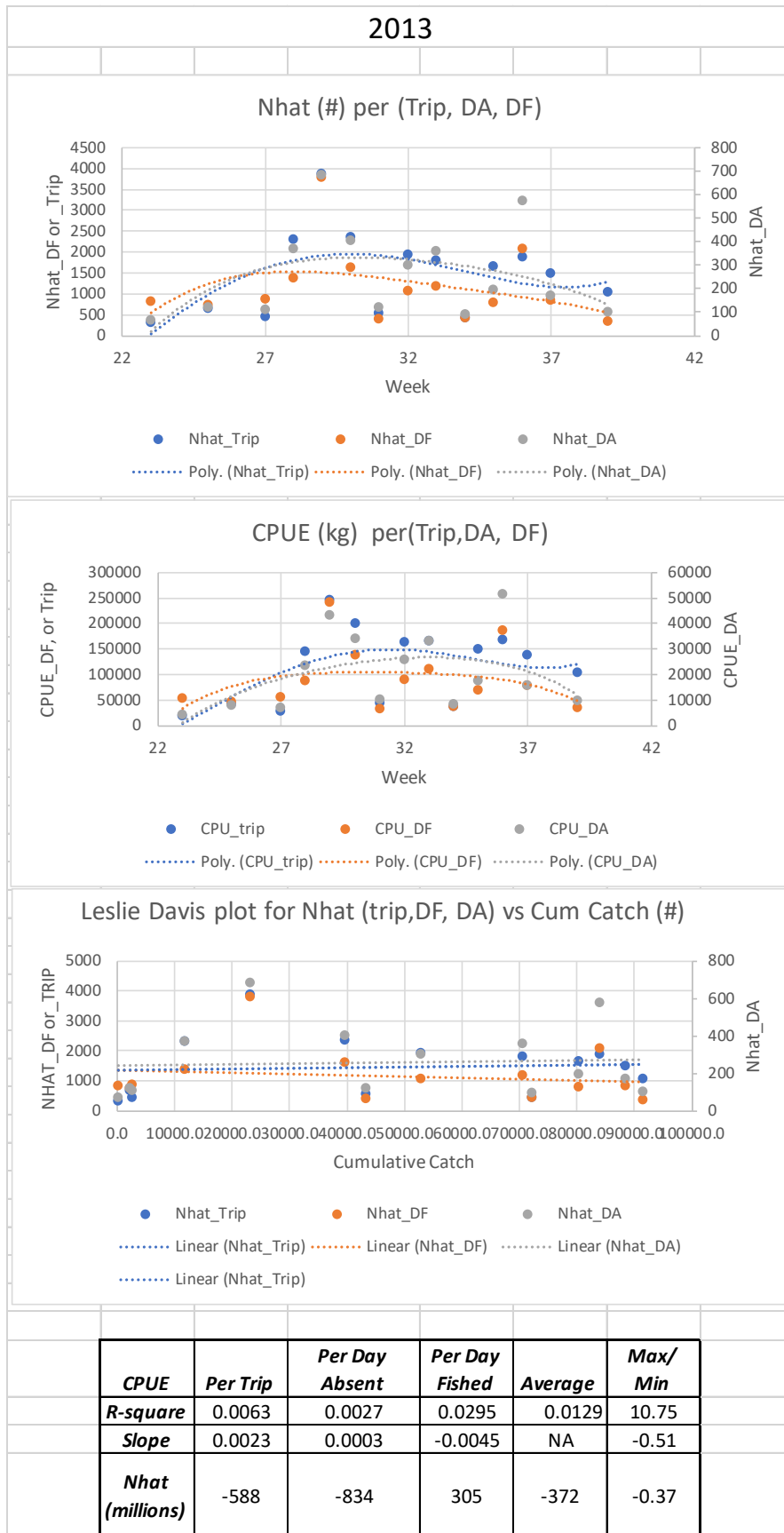


Figure 14. Summary of Leslie Davis Model results for 2013. [top]CPUE expressed as numbers per trip (blue), numbers per days absent(gray) or number per day fished(orange) vs standard week, [middle] CPUE by weight for same effort measures, [bottom] CPUE by numbers vs cumulative catch (in numbers). Statistics for degree of fit and population size are based on simple linear regression.

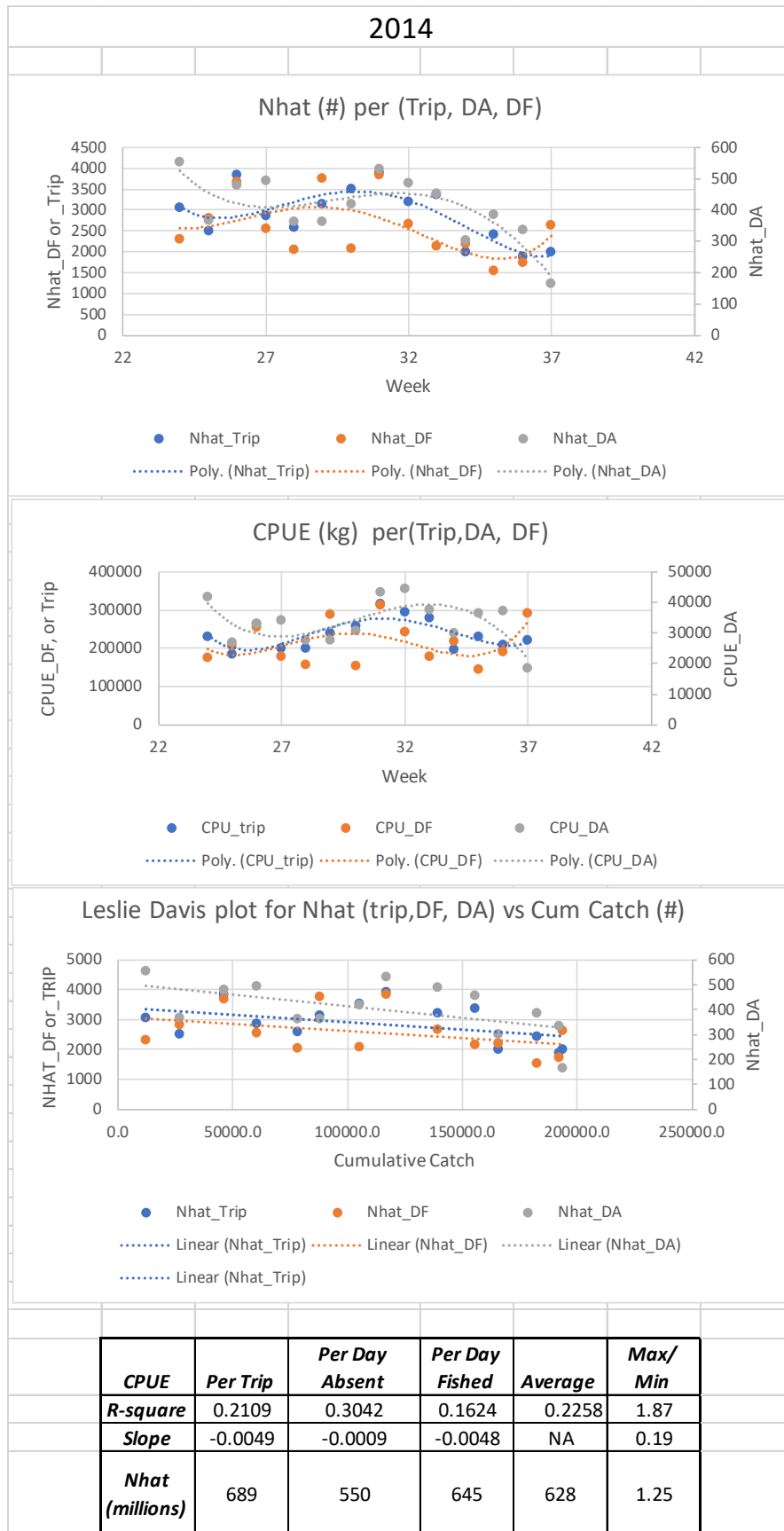


Figure 15. Summary of Leslie Davis Model results for 2014. [top]CPUE expressed as numbers per trip (blue), numbers per days absent(gray) or number per day fished(orange) vs standard week, [middle] CPUE by weight for same effort measures, [bottom] CPUE by numbers vs cumulative catch (in numbers). Statistics for degree of fit and population size are based on simple linear regression.

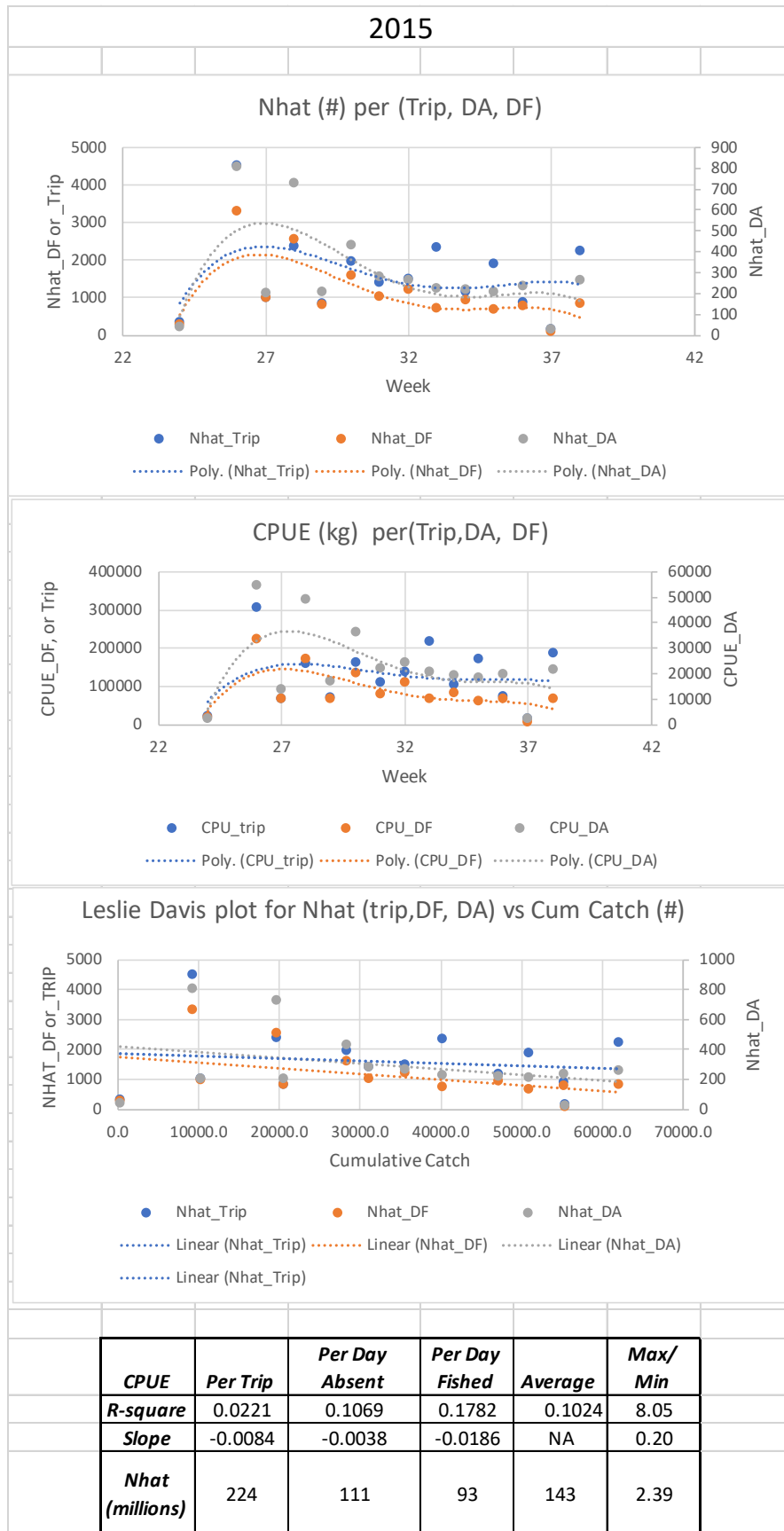


Figure 16. Summary of Leslie Davis Model results for 2000. [top]CPUE expressed as numbers per trip (blue), numbers per days absent(gray) or number per day fished(orange) vs standard week, [middle] CPUE by weight for same effort measures, [bottom] CPUE by numbers vs cumulative catch (in numbers). Statistics for degree of fit and population size are based on simple linear regression.

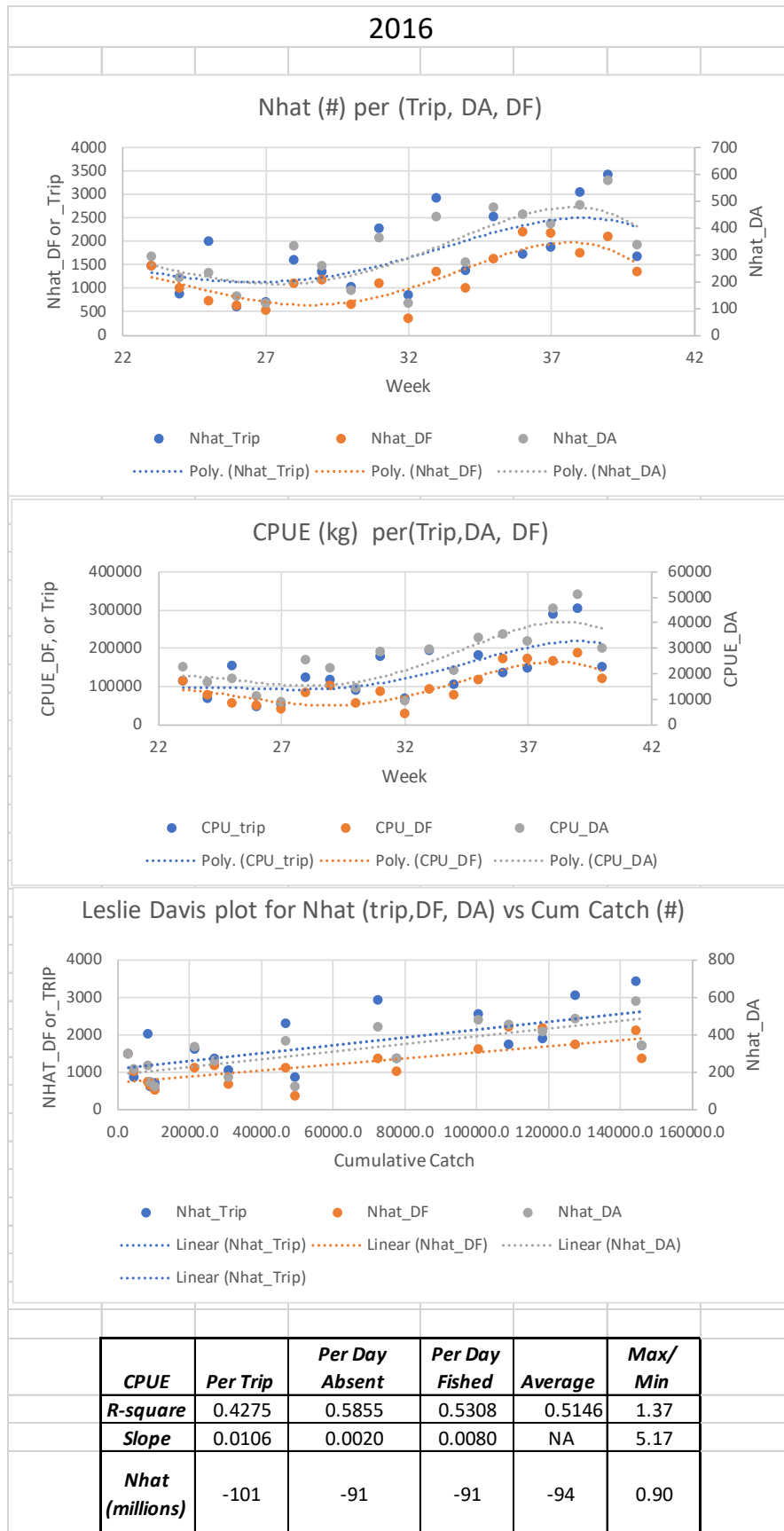


Figure 17. Summary of Leslie Davis Model results for 2016. [top]CPUE expressed as numbers per trip (blue), numbers per days absent(gray) or number per day fished(orange) vs standard week, [middle] CPUE by weight for same effort measures, [bottom] CPUE by numbers vs cumulative catch (in numbers). Statistics for degree of fit and population size are based on simple linear regression.

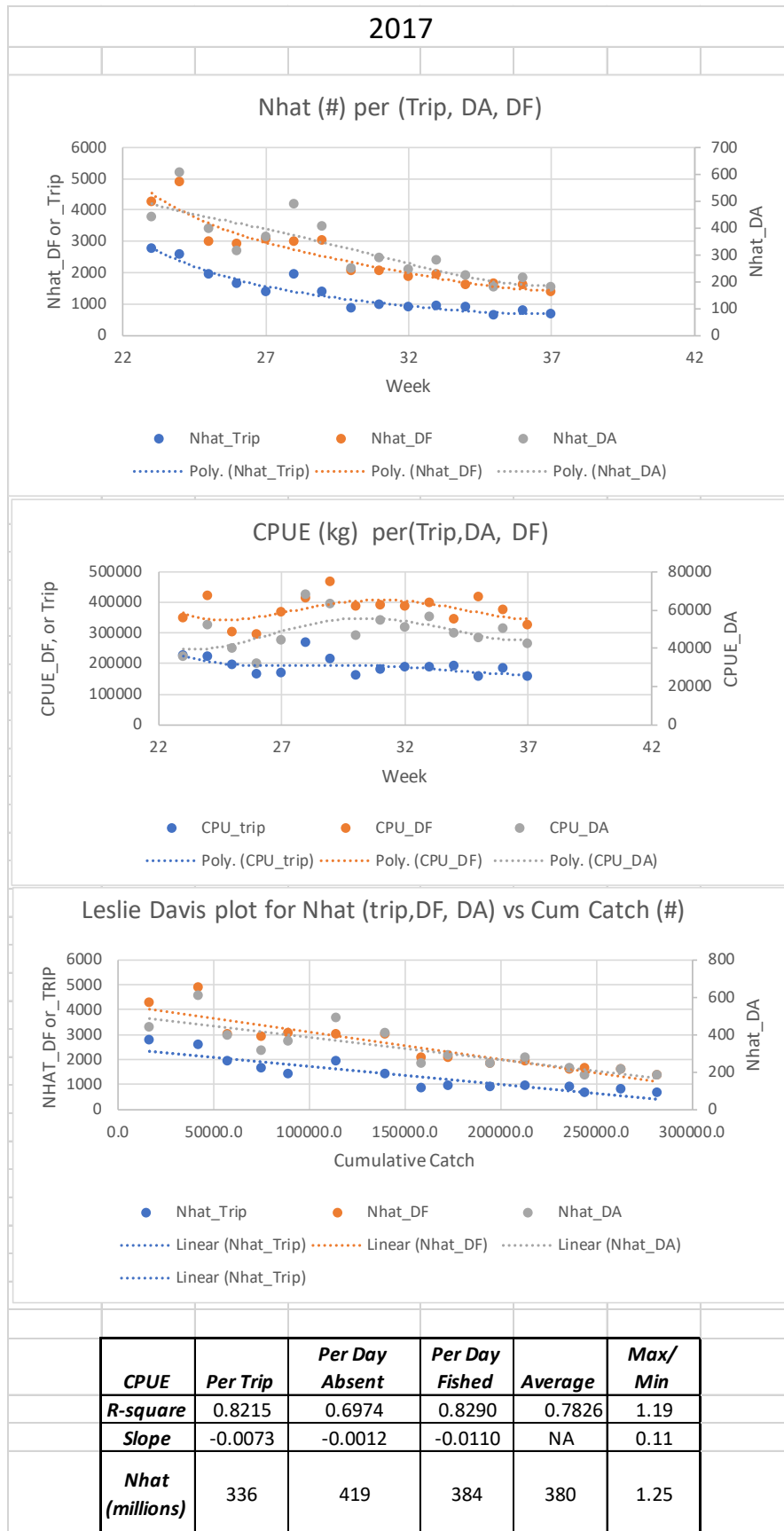


Figure 18. Summary of Leslie Davis Model results for 2017. [top]CPUE expressed as numbers per trip (blue), numbers per days absent(gray) or number per day fished(orange) vs standard week, [middle] CPUE by weight for same effort measures, [bottom] CPUE by numbers vs cumulative catch (in numbers). Statistics for degree of fit and population size are based on simple linear regression.

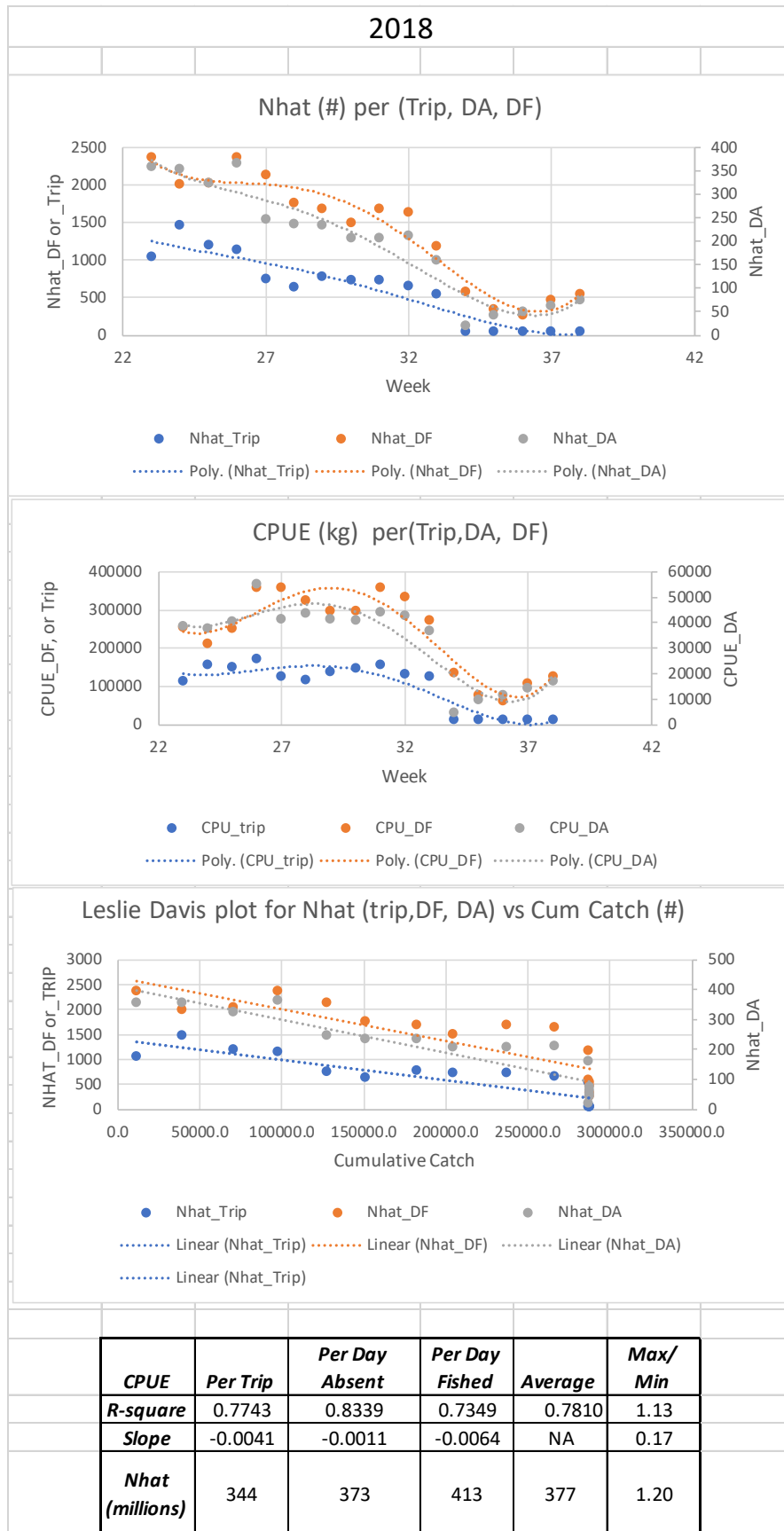


Figure 19. Summary of Leslie Davis Model results for 2018. [top]CPUE expressed as numbers per trip (blue), numbers per days absent(gray) or number per day fished(orange) vs standard week, [middle] CPUE by weight for same effort measures, [bottom] CPUE by numbers vs cumulative catch (in numbers). Statistics for degree of fit and population size are based on simple linear regression.

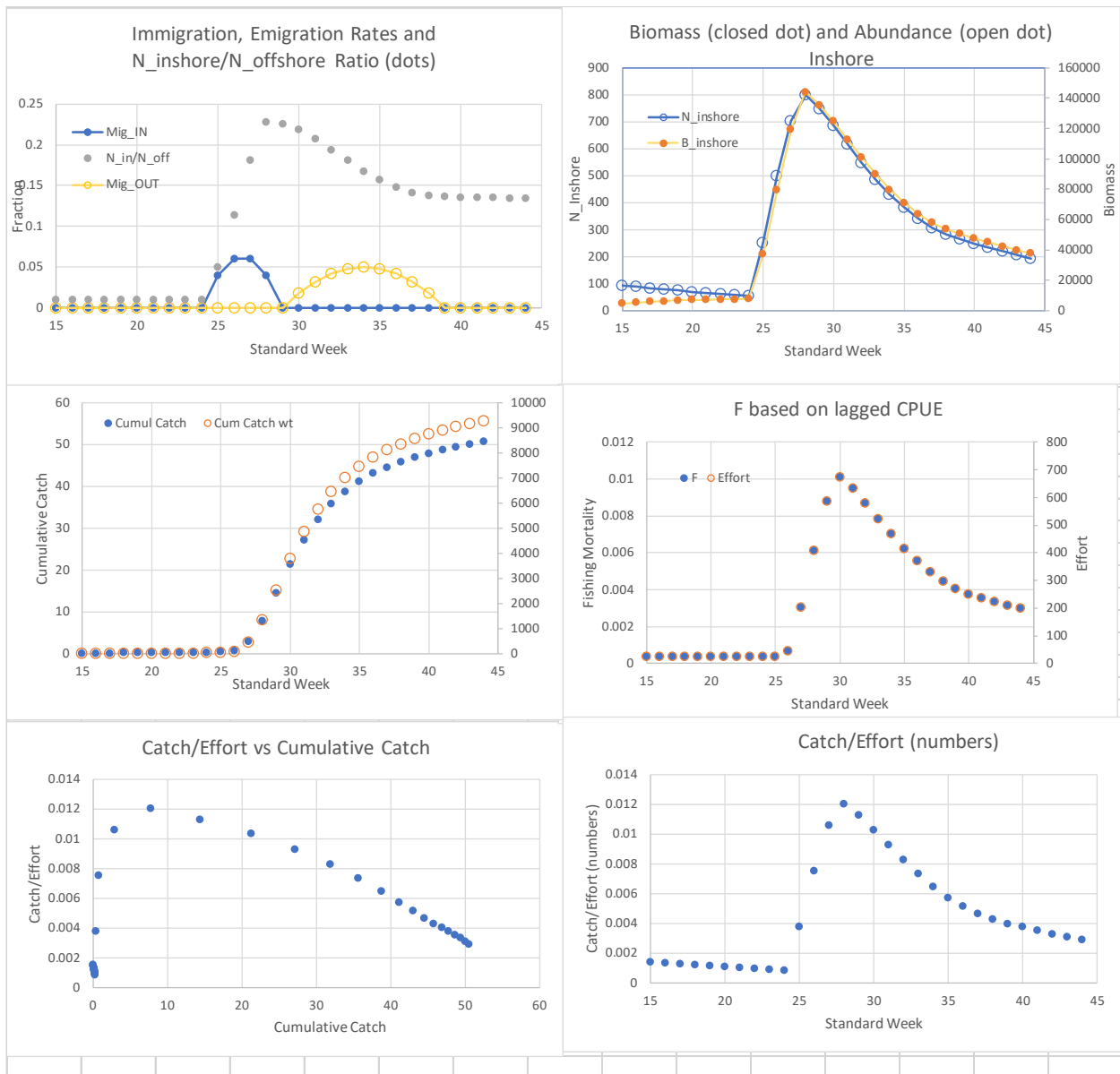


Figure 20. Example run #1 of two bin population model using model structure and parameters defined in the working paper. $M=0.06/wk$. In this run most of the population remains offshore.

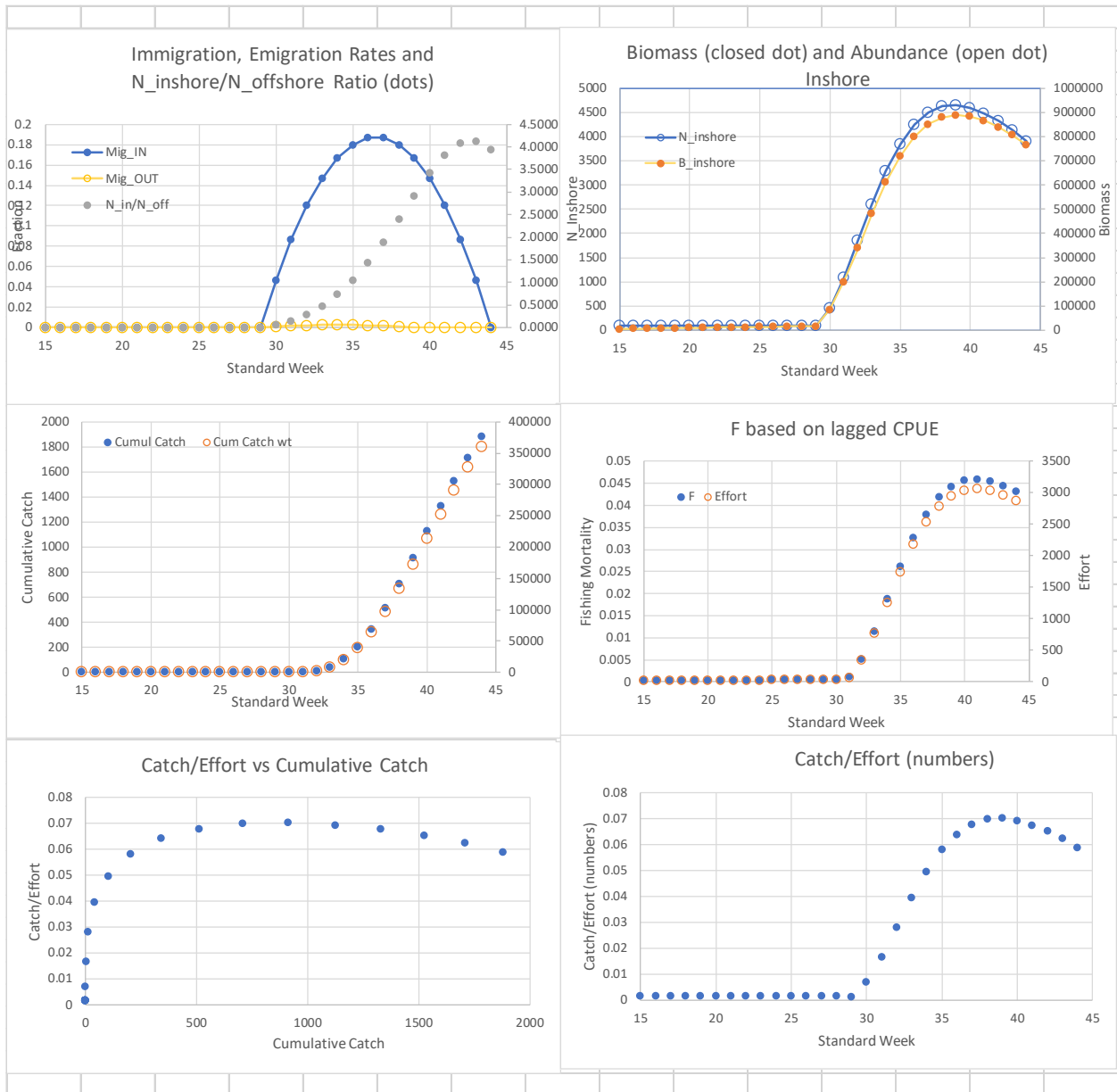


Figure 21. Example run #2 of two bin population model using model structure and parameters defined in the working paper. $M=0.01/\text{wk}$. In this run most of the offshore population migrates inshore (top left Panel) and offshore migration is delayed.

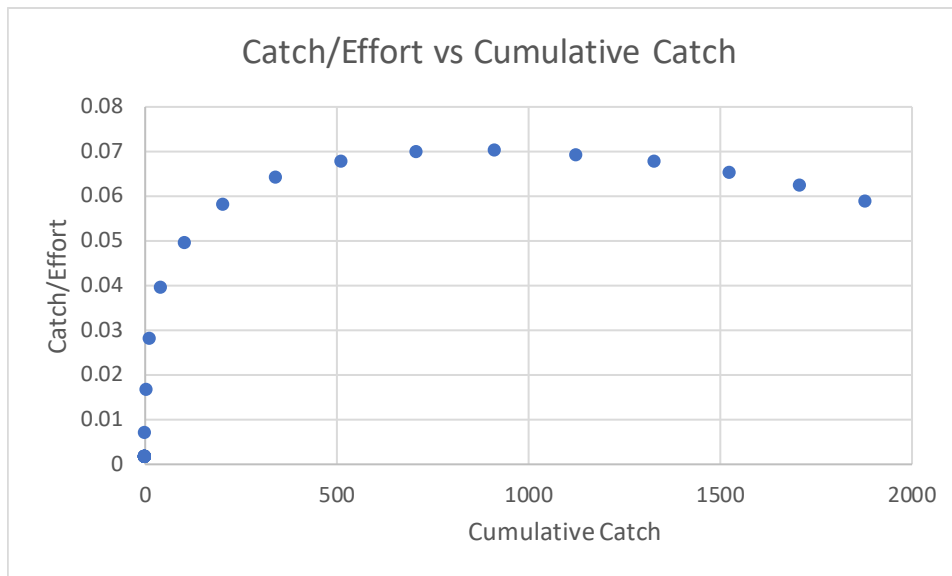
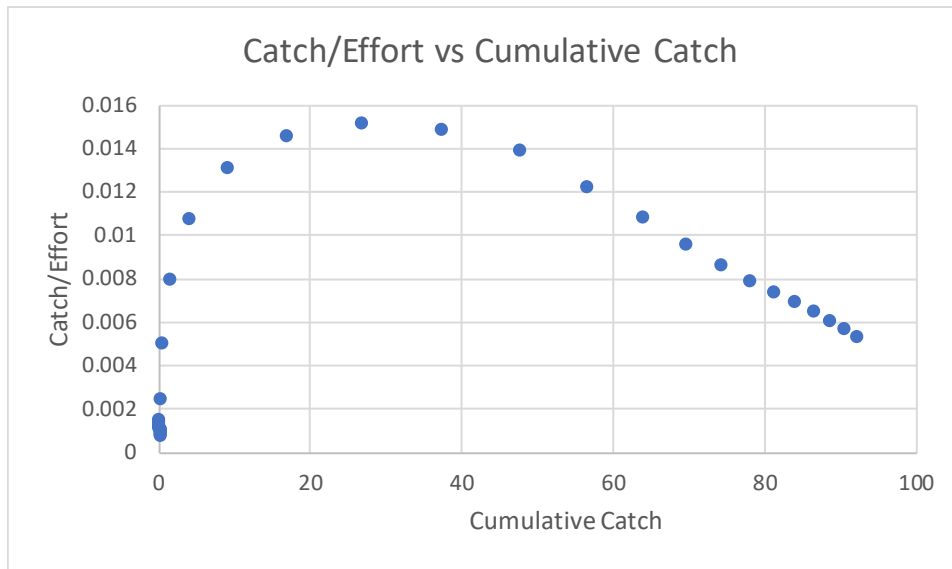


Figure 22. Comparison of hypothetical depletion curves for Scenarios 1 [top](from Fig. 20) and 2 [bottom] (from Fig. 21) for two bin model. Note the much higher CPUEs and cumulative catch in scenario 2 where a greater fraction of the resource migrates inshore and natural mortality is lower (0.01/wk vs 0.06/wk).

