The Cable-CDFW Model and Calculation of Spawning Potential Ratio

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INTRODUCTION

The California spiny lobster (*Panulirus interruptus*) Fishery Management Plan (FMP) utilizes the Cable-CDFW Model to calculate spawning potential ratio (SPR), one of the three reference points used within the Harvest Control Rule (HCR) (CDFW 2016). SPR serves as an indicator of the reproductive potential of the stock by comparing the number of eggs produced under current conditions relative to a theoretical unfished state. The model calculates the SPR of the lobster stock by simulating the life history of a single 1000-individual cohort. In addition to SPR, the model estimates the yield in weight per recruit (YPR) and instantaneous fishing mortality (F), also incorporating the effects of Marine Protected Areas (MPAs), which prohibit the take of lobster within their boundaries. This model allows CDFW to estimate and evaluate the effects that varying degrees of fishing pressure and MPA protection might have on the SPR and YPR of the lobster stock.

The model was originally developed by Dr. Richard Parrish under contract with the South Bay Cable Liaison Committee (Parrish 2013), and it subsequently underwent revision through collaboration with California Department of Fish and Wildlife (CDFW) staff as a part of FMP development. Dr. Parrish aided CDFW with some refinements of the model, in particular regarding lobster growth (Parrish 2014), and CDFW staff later continued to explore alternative growth models. Further refinements were made following an independent, external, scientific review of the FMP (Ocean Science Trust, 2015).

This report describes the structure, parameters, and the principal mathematical relationships in the model in its final form as approved by independent reviewers. Focus is given to the primary results produced by the model in this form. However, sensitivity of the model results to alternative structures and parameter values are also presented. Implications for the use of SPR as a biological reference point within the FMP are discussed as well as other management implications and directions for future research.

BASIC STRUCTURE

The Cable Model is an EXCEL spreadsheet model that calculates the yield of 1000 age-1 recruits over a 25 year lifespan. The model relies on the estimates of the average weight of commercially caught lobster derived from fisheries-dependent data (CDFW Daily Lobster Logs and Landing Receipts) to infer fishing pressure and generate outputs. It does not include a stock-recruitment relationship, so it cannot directly address reproductive overfishing. However, egg production per-recruit associated with a range of fishery conditions can be assessed. Growth, fecundity, and mortality rates are calculated using the best currently available data.

Attempts have been made to parameterize these relationships for the entire Southern California Bight (SCB) but some estimates are regionally specific where data is limited.

The model proceeds by 3-month time steps. An initial 500 male and 500 female recruits grow and die according to a series of size-specific rates to supply the number of males and females present at the next time step. Egg production occurs in the 2^{nd} quarter and fishing in the 4^{th} and 1^{st} quarters. This seasonality, the current minimum carapace size limit of 82.5 mm, and an estimate of the percentage of available lobster habitat in MPAs are the aspects of the current management regime included in the model. The fishing mortality rates (F) and harvest rates are estimated by calculating the average weights in the landings during the 2000-2001 to 2014-2015 lobster seasons. The user iteratively adjusts F as an input parameter until the correct average weight within the catch of simulated lobsters matches fisheries-dependent estimates.

The principle mathematical steps used to calculate the number of lobsters occurring in each time step, the commercial fishery catch, and egg production include:

- 1. Age-length (growth)
- 2. Weight
- 3. Vulnerability to traps
- 4. Instantaneous fishing mortality
- 5. Natural mortality
- 6. Fishing mortality not recorded due to ghost fishing and handling
- 7. Lobster habitat in MPAs and survival of lobsters inside and outside MPAs
- 8. Migration and movement rates of lobsters into and out of MPAs
- 9. Catch and landings
- 10. The length-maturity relationship of females
- 11. The length-fecundity relationship of females

The form of the relationships, their purposes, and the sources of their data inputs are outlined below in the Equations and Parameters section.

The three primary outputs of the model are instantaneous fishing mortality (F), yield in weight per recruit (YPR), and spawning potential ratio (SPR). While F is an output of the model, it functions like an input parameter. This is because F is iteratively found by adjusting its value until the known average weight of *P. interruptus* in the catch from fishery-dependent data matches the average weight in the catch of simulated *P. interruptus*. This simulated average weight is calculated by dividing the total weight caught in all model time steps by the total number. The yield per 1000 recruits is simply the total weight in the catch in all time steps.

Calculation of SPR requires two model runs because it represents a ratio of the number of eggs produced in two alternate scenarios. For the purposes of the FMP, we calculate a ratio relating the current conditions of the fishery to the number of eggs that would theoretically be produced with no fishing mortality and no habitat protected by MPAs. Other alternate scenarios could be compared in this way (*e.g.*, equal fishing mortality and different percent of habitat within MPAs).

RESULTS

Primary Output

The SCB-wide average weight of *P. interruptus* in the catch for the 2000-2014 fishing seasons was 1.626 lbs. As Figure 1 illustrates, average size increases as F decreases, and regulation of fishing effort can be used to balance against a different size limit to maintain a desired average size. There are apparent differences in the average weights of the catch in the northern and southern regions of the SCB. When dividing these regions at approximately Dana Point on the mainland with north including the northern Channel Islands and the south including Santa Catalina and San Clemente Islands, average weight for the same time period in the north and south was 1.711 and 1.537 lbs respectively.

Different rates of F also interact with size limit to result in variation in YPR and SPR. Yield increases rapidly as F increases from zero while the increase in yield with decreasing size limit is more gradual (Figure 2). At the current size limit, the statewide fishery as well as both the northern and southern regions, are achieving 80-90% of the maximum possible yield. Yields within 90-100 are achieved only under a narrow range of F and size limit. This is likely because some simulated lobsters within MPAs are never available to the fishery and can't contribute to yield. At lower size limits (i.e., less than 82.5 mm), SPR decreases rapidly as F increases from zero then declines gradually (Figure 3). At higher size limits (i.e. greater than 82.5 mm), SPR declines rapidly with increasing F but cannot pass below approximately 30% within the range of F values examined.

The impact of MPAs on the relationship between average weight in the catch and F is illustrated in Figure 4. As expected, the average weight of individuals in the catch at very low values of F is very similar between the current condition of 14.6% of *P. interruptus* habitat within MPAs and a no MPA scenario. As F increases, the difference in average weight between these scenarios is modest. Average weight in the catch with MPAs would not be expected to be much higher because this represents the average size of lobsters caught by the fishery (lobsters outside MPAs plus those that spill over MPA boundaries). A comparison of the average weight of lobsters inside versus outside MPAs, when MPAs are in place, produces a larger difference. Model factors that limit larger differences in the average weight in the catch include natural mortality limiting the number of lobsters achieving large ages inside MPAs and spill over rates.

The presence of MPAs has a demonstrable impact on model estimates of YPR and SPR. YPR is reduced under current MPA coverage conditions similarly across estimates for F at the northern, southern and SCB-wide levels (Figure 5). Current MPA coverage also provides a similar increase in SPR of approximately eight percentage points across all current estimates for average weight in the catch (Figure 6). Interestingly, increasing the percentage of habitat covered within MPAs up to 27% results in only modest increase in SPR of about 10 percentage points at typical F rates for this fishery (Figure 7).

Model Limitations

The model estimates of F and corresponding impacts on YPR and SPR are relatively insensitive to the average weight of individuals in the catch at smaller average weight values. Therefore, when the average weight is relatively high, incremental change in average weight leads to small change in F. When average weight is low, small change in average weight leads to large change in F. This effect can be seen in the shape of the curves in Figures 1 and 4. This is of

concern because as average weight is reduced because of increasing F, the accuracy of our fishery-dependent estimates of average weight becomes increasingly important. Our estimates of F would become less reliable at a time when detecting incremental changes F resulting from management action is of high importance. Changing the reporting requirements on landing receipts to include both the number and weight of lobsters sold would greatly improve the accuracy of our estimates of average weight of individuals in the catch and help to mitigate some of this lack of certainty in F estimates at low average weight.

The relationship between average weight and F under the current size limit and MPA coverage conditions asymptotes at approximately 1.4 lbs (Figure 4). Values of F below 1.4 lbs cannot be estimated by the model. However, based on CDFW creel survey data, the average weight of *P. interruptus* at legal size is 1.3 lbs. Therefore a catch level that would drive the average size of a landed individual down to this figure should be possible in the actual fishery. For the fishing seasons to date, the smallest average weight estimated has been 1.59 pounds, which is above the model's weight limitation (Table 1).

The Cable-CDFW model is an equilibrium model and, therefore, suffers from limitations common to many equilibrium models. It applies the same treatment to every member of a cohort, even though different individuals would encounter different experience in the real world resulting in plasticity of traits. An important example of this is the application of a growth equation to every individual in a cohort, resulting in the same length increase for every individual and a stepped rather than continuous growth pattern. This stepped growth pattern produces an issue with knife-edge selection in other model functions based on size. For example, unrealistic jumps in size create artificial patterns in fishing mortality when quarters allowing fishing do not align with legal sized lobsters because a time step "jumped over" a legal size category. For this reason we chose to allow growth in every model quarter rather than programming growth only during the summer quarter when molting and growth actually takes place for adults. This results in a more continuous growth pattern but does not fully alleviate this modeling artifact.

A common problem with equilibrium models is an inability to accurately represent recruitment dynamics. The Cable model assumes constant recruitment spread evenly across space, implicitly assuming that all levels of harvest are sustainable. In reality, strong lobster recruitment pulses are sporadic in time and space. Representation of realistic recruitment is particularly important for semelparous species that breeds only once in a lifetime because combining high harvest levels with a poor recruitment year can easily lead to local extinctions. Iteroparous species which breed multiple times over a relatively long lifespan can be better represented by an equilibrium model because the vagaries of multiple recruitment events over the life of a cohort may be represented by their average. However, an equilibrium model with constant recruitment cannot simulate recruitment overfishing which is defined as a fishing mortality that depletes the spawning stock to a level producing recruitment failure.

Caution should be used with regard to the model's geographic scale. There is no set geographic scale for the model; therefore, it can represent any region or amount of area if provided appropriate input parameters. CDFW recommends managing *P. interruptus* as a single stock until more information about regionally specific dynamics indicates a need for regional management. However, some of the available parameters describing lobster population dynamics have not been estimated on a SCB-wide basis. Rather, they represent information from a variety of local areas and time periods and may not be representative of average conditions through time or across the entire SCB. This is a limitation for SCB-wide results.

Although we present results based upon average weight of commercially caught lobsters from the northern and southern regions of the SCB, other input parameters specific to a north and south division are not available. Therefore caution should be used when interpreting these results. For example, higher average weights in the northern region indicate higher SPR. However, Yaeger (2015) estimated higher egg production in the southern region of the SCB by considering both the number and size of lobsters taken in the north and south through an at-sea sampling program. The model produces these results because lower F simulates more lobsters and larger size lobsters within the model. Both contribute to higher estimates of SPR when compared with lower average weights observed in the southern region of the SCB. However, factors other than fishing pressure may contribute to the differences in observed average weights between these regions. These could include differences in habitat, water temperature, and recruitment. Higher recruitment levels in the south could result in a greater number or density of lobsters in that region even while fishing pressure is high and lobsters are typically caught earlier and at smaller sizes. As long as the minimum legal size is placed such that lobsters have an opportunity to spawn before being vulnerable to fishing, the higher number in the south might more than compensate for smaller sizes at spawning to result in higher SPR. This dynamic is not captured when using equivalent recruitment for model runs intended to represent different regions.

Finally, validation of several model parameters is needed. Vulnerability parameters could be improved using data on trap density, size frequency data from transect surveys, and spatially co-located data on size frequency in commercial traps. Fecundity and size at sexual maturity are also key data needs.

MANAGEMENT IMPLICATIONS

According to the HCR, CDFW would have a duty to investigate the status of the fishery and potentially take management action whenever the SPR of the stock falls below a threshold level. That threshold is set at the average SPR during a reference period between the 2000-2001 and 2007-2008 fishing seasons, when the fishery was deemed stable and productive by the stock assessment (Neilson 2011). SPR for the 2014-2015 fishing season, under current model conditions, is calculated to be 32% and the threshold value based on an average of the reference years is 25% (Table 1). The current value is calculated using MPA habitat coverage of 14.6% while 4.5% is employed for the reference years. CDFW is aware that the effects of the recent increase in MPA area as of 2012 are unlikely to have come to equilibrium. However, current SPR would remain above the threshold by three percentage points if an MPA coverage value of 4.5% were used (Figure 8). Observation of the effects of MPAs on lobster density and size are of a high priority and CDFW will look to make the appropriate model adjustments.

SPR output is a direct result of the value for the average weight of commercially landed lobsters input to the model. CDFW's estimate for current average weight is the highest observed since commercial log data required for the analysis became available in 2000. The increasing trend began in 2011 coincident with a rise in price, effort and total landings. Caution should be applied when interpreting that this increasing average weight and SPR reflects increasing stock productivity and decreasing F as the model concludes. Data on increasing effort and catch suggests that fishing mortality has been increasing, not decreasing. Moreover, a shift in the proportion of landings from south to north has been observed since 2012 (Figure 9). A gradient of increasing lobster size from south to north has been long-observed and may be a result of a variety of factors other than fishing mortality. Therefore the increasing SCB-wide average weight may actually result from proportionally greater fishing pressure being applied in the north as take in the south achieves maximum capacity. While the Catch, CPUE and SPR reference

points were chosen in the California Spiny Lobster FMP to identify specific fishery issues that may signal trouble in the fishery, the HCR Matrix is designed to assess these measures collectively (CDFW 2015, Table 4-3). Investigations that are prompted by any of the three reference points being below threshold will include detailed analysis of these interactions. In addition, implementation of the proposed commercial trap limit may reduce overall fishery effort and potentially lead to a shift in regional dynamics. CDFW will take these changes into consideration when operating the HCR as the fishery equilibrates.

Many fishery managers calculate their respective SPR values differently. Therefore comparison between SPR values computed by different teams using different assumptions and methodology can be problematic. Some calculate baseline condition using model projections of a theoretical unfished state while others derive baseline conditions with real-life unfished populations in remote locations (Bohnsack et al. 1990). Among the managers who calculate baseline using model projections, some account for density-dependent population factors while others do not (Hall & Chubb 2001, Puga et al. 2005). Alternative options for describing lobster growth within the model were investigated (see "Model Variations and Sensitivity Analysis" below). The new growth curves developed by CDFW staff led to much higher SPR values than the threshold values calculated for other lobster fisheries (reviewed in CDFW 2015). The higher value can be attributed in part to the effects of MPAs, however, even if MPAs are discounted, the model still cannot produce an SPR value lower than 40% (Figure 17). While these high values may be atypical, it should be stressed that the relative position of annual SPR values to the SPR threshold based on reference years is robust to the growth model used as well as many other model changes investigated. CDFW will seek to acquire improved information on all aspects of *P. interruptus* ecology and life history, particularly in the areas of growth, reproductive dynamics and the effects of MPAs. Because the SPR threshold employed here is based on the stock in question and calculated using the same methods as annual SPR, adjustments to the Cable-CDFW model may be made to improve SPR output for both current and reference (threshold) conditions without changing their relative positions.

EQUATIONS AND PARAMETERS

1. Age-length (growth):

Lobster growth, or size at a given age, is calculated using the von Bertalanffy growth equation, which written as

$$l_t = L \infty \left(1 - e^{-K(t - t_0)} \right).$$

Where l_t is the size at time t, L^{∞} equals the average maximum achievable size, K is a growth constant that represents a rate, t is the time step, and t_0 is the size at age zero. Separate parameter values for males and females were derived by Vega (2003) for the Mexican P. *interruptus* stock and are used here. For males $L^{\infty} = 149$, K = 0.125, and $t_0 = 0.21$ and for females $L^{\infty} = 145.8$, K = 0.1, and $t_0 = 0.01$. The model is initialized in the third quarter, corresponding to August when peak settlement of pueruli is observed. Because of the long lobster pelagic larval duration, pueruli are approximately 1 year old at settlement; therefore, 1 is the age at this first time step.

2. Weight

Length is converted to weight using separate power functions (W = a * Lt^b) for males and

females where W = weight in grams and L = carapace length (CL) in millimeters. Male parameters are a = 0.0053, and b = 2.6247 and female parameters are a = 0.0129 and b = 2.4455. Equations were parameterized from CDFW Sport Creel Census data collected in 1992 and 2007.

3. Vulnerability to traps

Vulnerability describes gear selectivity with the current legal trap configuration. Young lobsters are invulnerable to traps because they are small enough to walk out of escape vents. They quickly reach 100% vulnerability to traps as they grow to a size that is large enough that they have difficulty entering traps. Vulnerability is then reduced for these larger lobsters as they continue to grow. These two phases of vulnerability are represented by separate equations for lobsters greater than and less than 110 mm CL. For smaller lobsters vulnerability = $1 / (1 + e^{(19 + (-0.304)(L))})$ and for larger lobsters vulnerability = $1 / (1 + e^{(19 + (-0.304)(L))}) - (1 + (110/L)^4)$. Parameters were informed by comparisons of size frequency distributions of *P. interruptus* caught in traps with and without escape ports (Kay 2011). Additionally, the simulated percent of sub-legal individuals in the cumulative cohort catch was fitted to the percentage of sublegals reported on CDFW commercial fishing logs by adjusting vulnerability equation parameters.

4. Instantaneous fishing mortality

The model uses two types of instantaneous fishing mortality (F): 1) population level F is iteratively adjusted by the user until the simulated average weight in the catch matches that seen in fisheries-dependent data and 2) an F value at each time step that is adjusted according to both season and lobster size.

Harvest rate represents the percent of available biomass that is harvested. Instantaneous fishing mortality (F) is related to harvest rate by the equation

Catch % = $1 - \exp(-(M+F)) * (F/(F+M))$ where M = natural mortality

Population level harvest rate, and thus F, is calculated by dividing the sum of all simulated landings by the sum of all available biomass across all time steps and lobster sizes.

Fishing effort varies across the season as the availability of legal-sized lobsters declines. To calculate an F value for each time step, the iteratively adjusted F input parameter is multiplied by the size-based vulnerability and adjusted by either the Foct or Fjan parameters where Foct = 64% and Fjan = 36%. Those parameters simulate differences in landings at the beginning and end of the fishing season based on fishery-dependent data. Fishing mortality is zero during the second and third quarters of the year when the fishery is closed.

5. Natural mortality

Kay (2011) found an average total mortality (Z) for *P. interruptus* among the interior of several

northern Channel Island reserves of 0.17. Assuming no fishing mortality applies in these areas this can be used as an estimate of instantaneous natural mortality (M). A constant instantaneous natural mortality rate of 0.17 was also used for the California spiny lobster stock assessment (Nielson 2011) based on the findings of Chavez and Gorostieta (2010). A natural mortality of 0.17 was used to convert harvest rate to F as noted above. Natural mortality is modified in each time step to be size-based, rather than constant. Natural mortality is initially very high for newly settled lobsters then quickly asymptotes for adult lobsters. This is reasonable because it is well understood that newly settled marine organisms experience high predation. The equation (M = (-0.17 - 12.5/weight)/4) takes what would be an annual M rate, adjusts by lobster weight, and applies a quarter of annual morality at each time step.

6. Fishing mortality not recorded due to ghost fishing and handling mortality

There are additional sources of mortality associated with commercial fishing apart from direct take of lobsters. *Panulirus interruptus* smaller than the legal size but large enough to be captured in traps are brought to the surface, handled, and thrown back into the water. These individuals suffer some rate of mortality due to injury during the process and increased susceptibility to predators while returning to appropriate habitat (handling mortality). Unrecorded mortality can also occur when lost traps continue to fish for a period of time until the destruction clips fully disintegrate (ghost fishing). Additionally, lobsters in traps are vulnerable to increased predation from octopus and this mortality is not represented in fishing mortality or estimates of natural mortality.

The model includes an equation for fishing mortality that is not recorded (FNR) that scales F with a parameter for handling mortality and two parameters for ghost fishing. This is then included as an additional source of mortality in the survival equations applied to lobsters. The two parameters that describe ghost fishing are the rate of trap loss and the fishing rate of those traps. Reliable data on these processes are not available; therefore, these parameters have been set to zero. The functionality for estimating their effects has been retained in the event these data become available. The model does not currently incorporate a function to account for poaching or predation within traps.

7. Application of MPA protection to survival

The model accounts for the effect of MPAs by modifying the survivorship of all the members of a model cohort based on their projected location. Survivorship of *P. interruptus* in the interior of MPAs is calculated as an exponential function of the natural mortality rate. No fishing mortality is applied because these individuals are assumed to be fully protected from fishing. Individuals in the MPA and within 0.75 miles of a boundary were given a fishing mortality equal to 20% of the value in the open area on top of natural mortality to account for nightly foraging movements that might bring them across the boundary and, thus, make them vulnerable to fishing. *Panulirus interruptus* outside of MPAs survive according to their combined natural and full fishing mortality rates.

8. Lobster habitat in MPAs, migration and movement rates

The Northern Channel Islands was one of the first regions to implement a network of MPAs in California. Since then, a statewide coastal MPA network was completed in 2012. The percentage of *P. interruptus* habitat inside MPAs in southern California is not clearly known as there are gaps in the benthic habitat data for rocky intertidal and shallow kelp forest habitats. The local impacts of MPAs on *P. interruptus* will depend on MPA size and the local mix of habitat types. In the absence of complete habitat data for the entire region, it was estimated that 14.6% of *P. interruptus* habitat across the region is within MPAs. This estimate utilized the most recent GIS analyses of the percentage of rocky substratum covered by MPAs.

The model treats every MPA in the SCB as the same size and they are distributed evenly along the coast. Assuming regular spacing of MPAs along the coastline, and an average MPA width alongshore of 3 miles, an average of 17.55 miles of coastline open to lobster fishing is calculated to exist between each MPA. In order to pursue a more realistic spatial representation of existing MPAs, CDFW would need to develop an individual-based model capable of simulating more complex movement patterns and other spatial dynamics.

Movement rates of *P. interruptus* across MPA boundaries are estimated based on tag-recapture data collected by Lindberg (1955) who found an average movement of 0.75 miles in 3 months with 2% of the population moving each 3 months. In addition, Lindberg (1955) suggested that the nightly foraging distance of *P. interruptus* was about 0.25 miles. Each 3-mile MPA was divided into two regions: 1) the edge of the MPA within 0.75 miles of a border with open fishing grounds (IN) and 2) the interior of the MPA greater than 0.75 miles from the border (IN-IN) (Figure 10). Therefore, it was assumed that 2% of the *P. interruptus* within a 0.75 mile section of MPA will move into or out of that section at each 3-month time step, resulting in a 1% migration rate in each of two directions alongshore (Mig_{out} parameter). Similarly, 1% of *P. interruptus* in the IN-IN region will migrate to the IN region in either direction. Migration rates into MPAs from open fishing grounds were calculated by estimating the proportion of *P. interruptus* that would occur in the 0.75-mile wide strip of fished area that is adjacent to MPAs, then assuming 1% of those will migrate in the direction of the MPA (to the IN region) on both sides of the MPA at each time step. This results in a migration rate into MPAs from fished regions of 0.09 (mig_{in} parameter).

The number of *P. interruptus* occurring in each region (IN-IN, IN, and Open) at each time step is a function of the number in the previous time step and their survival and immigration and emigration rates. On the first time step the number of the 500 individuals of each sex is distributed to each region according to the percent of available habitat each region represents.

9. Catch and Landings

Catch is calculated for both the IN and Open regions separately using the numbers of individuals present in those regions. The catch equation is applied above the legal size limit:

Catch = $(F/Z)(N_t)(1-e^{-Z})$

Where N_t = the number of *P. interruptus* in that time step and Z = Total mortality (F+M+FNR). A separate catch equation is applied to lobsters below the size limit:

Catch = $N_t(-F(1+M/2))$.

This equation accounts for replacement of sublegals after they are caught.

Because there is a size limit and catch below the size limit isn't retained, catch and landings are not equal. An additional calculation in the model equates landings with the catch in IN and Open regions when above the legal size and zero when below.

10. Length-Maturity of Females

The proportion of sexually mature females at each time step is described by the equation:

Maturity = $1 / (1 + e(^{23.49 - 0.304*L)})$

Where L = mm CL. This equation was parameterized by data collected at the Northern Channel Islands (Kay 2011).

11. Length-Fecundity of Females

Improving estimates of fecundity at size is a key research priority. Currently data are available from four female *P. interruptus* collected by Allen (1916) and 12 by Lindberg (1955). The following equation was derived from those data sets:

Fecundity = $(0.9197*L^2.7)*Maturity$.

MODEL VARIATIONS AND SENSITIVITY ANALYSIS

Through development of the Cable-CDFW model several iterations containing different mathematical relationships have been created. Changes have been in response to new information as well as recommendations from peer reviewers. The largest changes have related to efforts to identify the most appropriate growth, or size at age model for *P. interruptus*. This investigatory process and the model variations are described below. Sensitivity analyses are used to compare differences in model output resulting from different aspects of model construction and the sensitivity of the model to changes in lobster growth rate is presented below. Some mathematical relationships or parameters are uncertain for *P. interruptus* due to a lack of empirical information. Sensitivity analyses are also useful for examining the impact of these uncertainties on model results.

Growth Model Variations

Estimation of crustacean growth rates is difficult because an individual's shell, the only hard structure which might be used for aging, is shed periodically. Indirect estimation of growth can be performed through tag-recapture data. Lobster growth has commonly been described using

a von Bertalanffy model (Hall & Chubb 2001, Hobday & Punt 2007, Chavez & Gorostieta 2010, Nielson 2011). Earlier versions of the Cable model included von Bertalanffy growth using parameters derived for the Mexican *P. interruptus* stock, but examination of raw growth data from California showed that von Bertalanffy produced a poor fit (Parrish 2013, 2014). CDFW staff acquired additional growth data and again observed a poor fit for the combined dataset (Figure 11) prompting efforts to identify an improved growth model.

Three tag-recapture studies of *P. interruptus* were available for growth estimation at the time of this work. Newly settled and larger juvenile spiny lobsters from Santa Catalina Island were surveyed on SCUBA, tagged, and studied in the laboratory by Engle (1979). Tag-recapture studies of adult *P. interruptus* using commercial traps have been performed in the San Diego region by Hovel et al. (2015) and at sites around the northern Channel Islands by Kay (2011). A summary of the raw data for each these three studies is provided in Table 2.

The raw growth increment data was filtered in several ways to eliminate data inappropriate for extrapolation to annual growth. First, for individuals that were recaptured and measured multiple times, only the sizes and time at liberty for the initial capture and last recapture event were used. Second, only measurements from individuals that experienced a sufficient time at liberty and were at large through summer-fall between captures were included to ensure that a molt occurred between the first and second size measurements.

Engle (1979) showed that juvenile *P. interruptus* molt an average of nine times per year. Frequency of molting and the amount of growth per molt varies with temperature. To ensure that several juvenile molts representing a range of growth per molt values were used in extrapolation of growth to one year, only growth increments over 150 days at liberty and greater were included. Time at liberty for juveniles was not restricted to a particular time of year. Adult lobsters are thought to molt once per year following sexual maturity and the molting season spans July through November with most lobsters molting in September (Mitchell et al. 1969). Reliable estimates of size at sexual maturity are not available. Therefore, it was assumed any lobster greater than 50 mm CL could be sexually mature and restricted the Hovel and Kay datasets to measurements occurring over 200 or more days at liberty that must span this molting period. The treated data and their associated annual growth are presented in Figure2.

Raw and untransformed data from all three studies was combined and the differences in male and female growth over all sizes were examined. Annual growth for males and females were not significantly different for sizes below 82.5 mm CL. Because of this similarity, growth was modeled for the sexes combined from the size at the first January post-settlement (17.2 mm CL) up to legal size at 82.5 mm. For this 17.2-82.5 mm CL size range, SigmaPlot was used to test the fit of several equations described by Rogers-Bennett et al. (2003) as well as other equations suitable for modeling growth. Von Bertalanffy, Ricker, logistic dose-response, and Gaussian 3parameter and 4-parameter models were examined. A Gaussian 4-parameter model with the equation $f = y0 + a * e^{(-0.5((x-x0)/b)^2)}$ where f = annual CL increase and x = initial CL, resulted in the most appropriate fit (Figure 13, Table 3).

For individuals greater than 82.5 mm CL, male *P. interruptus* grew significantly faster on an annual basis (Kruskal-Wallis, p < 0.001, df = 1, H = 164.42, n(females) = 389, n(males) = 182) (Figure 14) and variability in their growth was higher. Males show a "hump" shaped distribution, whereas females show a gradual decline in growth. For individuals >60 mm CL, a separate Gaussian 4-parameter model was fit to males (Figure 15, Table 3) and an exponential decay equation was fit to females (Figure 16, Table 3). Although these curves were constructed using individuals 60mm CL and up, they were used in the model for individuals greater than 82.5 mm CL.

Peak settlement of *P. interruptus* is thought to be in August and the average size of field collected young of the year in January was 17.2 mm CL (Engle 1979). Therefore an initial age of 1.42 years and initial size of 17.2 mm for males and females was used. Because the model proceeds in 3-month time steps, one quarter of the calculated annual growth was added to the previous size in each step.

Peer reviewers recommended returning to the von Bertalanffy growth model for reasons described below. Parameters for that equation had previously been taken from Vega (2003) who developed them for the Mexican *P. interruptus* stock. A von Bertalaffy equation was fit to the tag-recapture data described above, deriving new parameters. However, that equation produced clearly unrealistic results including a maximum female size far below the size of actual adult females. Therefore, Vega parameters were used. Adjustments were also made to lobster age and season at the first time step to suit von Bertalanffy model requirements. The first time step begins with lobsters at age 1 and quarter 3 because pueruli first settle at approximately 1 year of age with settlement peaking in August. Size at that first time step is based on the von Bertalanffy equation rather than field observations of the actual size of newly settled lobsters in January.

Growth Sensitivity

Model runs using von Bertalanffy growth and the growth models developed by CDFW staff differ in several important outputs (Table 4). The age of legal sized individuals using von Bertalanffy growth is approximately half of what it is calculated to be using CDFW growth. This shorter length of time to reach legal size for entry into the fishery produced by von Bertalanffy growth results in fewer spawning seasons before F is applied. SPR is smaller across the full range of F values because fishing mortality has a greater potential to reduce spawner biomass relative to an unfished state (Figure 17). Conversely, SPR using CDFW growth is high because natural mortality acts upon lobsters for a greater length of time before they reach legal size. Therefore, fishing mortality has less potential to reduce spawner biomass relative to an unfished state. Survival to the fishery using von Bertalanffy growth, and therefore yield, is also higher because individuals have not been subject to natural mortality for as many years (Figure 18).

It is important to note that while SPR values calculated using von Bertalanffy growth are substantially lower than those using CDFW growth, the relative difference in SPR between the reference years and most recent fishing season are very similar, suggesting that the results are robust when interpreted this way. The fishing seasons between 2001-2002 and 2007-2008 were defined as a reference period due to relatively high, stable catch. The SPR calculated based on average weight in the catch over that time period and using MPA coverage of only 4.5%, reflective of the channel island MPAs present at that time, serves as a threshold reference point in the California Spiny Lobster FMP. Model runs using von Bertalanffy and CDFW growth both show that SPR is currently above the threshold by seven percentage points under quarterly growth and current MPA coverage.

Growth Schedule Variations

Earlier versions of the Cable model applied quarterly growth until an estimated size at sexual maturity is reached and annual growth is applied thereafter because adult *P. interruptus* are thought to molt once per year. This results in a stepped growth pattern that doesn't represent the continuous increase in mean size among individuals within a cohort that occurs in reality due to variability among individuals. Therefore, the current model applies quarterly growth across all lobster sizes. Sensitivity of key model outputs to application of annual growth versus

quarterly growth across all time steps is presented in Table 4. Differences are relatively minor and relate to when simulated lobsters reach a size that subjects them to fishing. Delay in growth until the molting quarter can cause lobsters to "jump over" a fishing season because they are not yet 82.5 mm CL. Importantly, the number of percentage points between current SPR estimates and the SPR threshold is equal within the same growth model. Thus, results relevant to management through the HCR are again robust to this modeling choice.

MPA Parameters

The Cable-CDFW model simulates some impacts to lobster population dynamics from MPAs by allowing lobsters within MPA boundaries to experience less fishing pressure. Parameter estimates related to this feature are informed by empirical data as described above. Application of an MPA benefit when assessing the status of the resource with the use of this model is an important feature of the HCR and therefore it is also important to describe the effects of uncertainty in these parameters. Parameters were the percentage of lobster habitat protected by MPAs (MPA), the rate of migration out of MPAs to fished habitat (Migout), the percent of F applied to MPA edge habitat simulating risk to fishing due to nightly foraging movements (Fin), and the average width of MPAs (MPAmi). Each of these parameters was left at current or default values, doubled and reduced by half.

The parameter with the largest effect on yield and SPR was MPA (Figure 19 and 20). Higher MPA leads to lower yield and higher SPR, as expected. Higher Migout leads to higher yield but has a negligible effect on SPR. A larger Fin also increases yield and decreases SPR by a small amount. Recent studies of *P. interruptus* movement have noted homing behavior (Withy-Allen and Hovel, 2013) as well as only 0 - 4.7% of lobsters crossing MPA boundaries, depending on the MPA, over a period of two years (Hovel et al. 2015). This new information, combined with the model results showing little impact of movement parameters, may indicate a small role for movement's effects on MPA effectiveness for *P. interruptus*. MPAmi also has a negligible impact on yield and SPR.

Interestingly, MPA has little impact on the average weight of lobsters in the landings (Figure 21). A larger MPA coverage leads to very slightly larger lobsters in the catch. The direction of this impact matches expectations because MPAs allow for survival of lobsters to a larger size and some of these are landed due to spill-over. All other parameters have a negligible impact on average weight.

Natural Mortality

Natural mortality is critically important to population dynamics but is also very difficult to measure. Knowledge of *P. interruptus* natural mortality is relatively good because estimates have been based on empirical data from the interior of MPAs within the SCB and not on proxy species or regions. However, our understanding could be improved by expanding studies to a greater range of *P. interruptus* life stages and sub-regions within the SCB. Kay et al. (2011) estimated a constant natural mortality of 0.17. The original Cable-CDFW model implements a size-based natural morality with a base value of 0.17 with higher values for young lobster and lower for older lobster. Impacts of variation in natural mortality on Cable-CDFW model outputs were investigated by comparing this scenario with constant natural mortality of 0.17 as well as double and half of 0.17.

Higher values of constant natural mortality result in reduced yield, lower average weight, and higher SPR (Figure 22). SPR is higher with high natural mortality for reasons that are similar to

those described above for the growth models. Greater natural mortality prior to fishing mortality results in less opportunity for fishing mortality to impact spawner biomass relative to an unfished state. Therefore, SPR cannot achieve low levels regardless of the degree of fishing pressure. Size-based natural mortality results in greater survival to the minimum legal size than a constant value of 0.17 and therefore greater yield, lower SPR and higher average weights.

Vulnerability

The vulnerability of lobsters to traps clearly varies with size, but the form of that relationship is unknown. The equation originally used in the Cable-CDFW model produces low vulnerability for small lobsters, a quick rise in vulnerability as legal size is approached, and a decrease in vulnerability for large lobsters. Model outputs resulting from this equation and an asymptotic equation, i.e. without increased vulnerability for large lobsters, were compared. This variation in the form of vulnerability had little impact on model output. There is a slight difference in the yield and average weight outputs at intermediate fishing mortality but no difference at low and high fishing mortality (Figure 23). This is reasonable because at low fishing mortality, gear selectivity is unimportant and natural mortality dominates. At high fishing mortality, few to no lobsters reach the large sizes that would be impacted by this change in the vulnerability curve. These differences in output are small enough that they don't translate to SPR which appears equal under these two scenarios.

Ghost Fishing and Handling Mortality

Ghost fishing is additional mortality which results from lost traps continuing to fish and goes unrecorded by fisheries-dependent data streams. Model parameters related to this dynamic include a rate of trap loss and mortality per trap. The model also contains a parameter for handling mortality which can result from injury to undersized lobsters caught in traps among other factors. These are currently set to zero due to a lack of data. Outputs under scenarios with no ghost fishing or handling mortality, the parameter levels used by Dr. Parrish in his Cable 6.0 model version, and double and half those levels were compared. Some impacts to yield are apparent but do not translate to SPR or average weight (Figure 24).

Future Investigations

Other sensitivity analyses that CDFW recognizes as valuable but have not yet been completed include fecundity and age at maturity. Females with eggs have recently been observed at sizes substantially smaller than the age at maturity used in the model, particularly in the southern region of the SCB. Other processes likely to impact SPR and yield include long distance migratory movements, recruitment dynamics, and more detailed spatial aspects of MPAs and habitat quality. Other modeling techniques would be required to investigate these dynamics. The average weight of lobsters in the commercial catch reflects the effects of both commercial and recreational fishing, and therefore recreational fishing is indirectly included in model results. However, inclusion of the average weights of lobsters landed specifically in the recreational fishery would improve the model's ability to reflect the status of the stock and the effects of both fisheries. Implementation of a creel survey would be required to collect this data.

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Table 1: SPR of the SCB *Panulirus interruptus* stock over time based on the average weight of a landed lobster.

14.0% for the 2012-13 fishing season					
Fishing Season	Average Weight (lbs)	SPR			
2000-01	1.643	26%			
2001-02	1.648	27%			
2002-03	1.615	25%			
2003-04	1.628	26%			
2004-05	1.629	26%			
2005-06	1.594	24%			
2006-07	1.615	25%			
2007-08	1.616	25%			
2008-09	1.624	25%			
2009-10	1.624	25%			
2010-11	1.607	25%			
2011-12	1.616	25%			
2012-13	1.622	30%*			
2013-14	1.642	31%			
2014-15	1.669	32%			

*% of habitat protected by MPAs is increased from 4.5% to 14.6% for the 2012-13 fishing season

Table 2: Summary of *Panulirus interruptus* mark and recapture data for Engle (1979), Hovel (unpublished data), and Kay (2011) data sets used in growth estimates.

Source	Sex	n	Initial CL size range (mm)
Engle	F	125	9.55-43.05
	М	115	10.05-40.85
Hovel	F	171	55.00-86.00
	М	266	51.00-101.00
Kay	F	520	64.00-143.00
	М	254	69.00-146.00

Table 3: Selected equations and parameter values and R-squared values for *Panulirus interruptus* growth.

Sex and Size Class	Equation	Parameters	R-squared
Male + Female, Initial	F=y ₀ +a*e ^{(-0.5*((x-x0)/b)^2)}	a=31.96, b=12.22,	0.808
size 0-82.5 mm		x ₀ =21.63, y ₀ =3.22	
Female 60-150 mm	F=a*e ^(-b*x)	a=8.37, b=0.01	0.073
Male 60-150mm	F=y ₀ +a*e ^{(-0.5*((x-x0)/b)^2)}	a=4.78, b=18.57,	0.272
		x ₀ =112.37, y ₀ =2.59	

Table 4: Results of sensitivity analyses comparing quarterly with annual growth using the CDFW growth curve, and a von Bertalanffy growth curves using annual growth.

Growth Model	CDFW		von Bertalanffy	
Growth Schedule	Quarterly	Annual	Quarterly	Annual
SPR Threshold	43%	38%	25%	26%
SPR Current	50%	45%	32%	33%
Age to legal male	12.7	11.17	6.25	6.25
Age to legal female	12.7	11.17	8.5	9.25
Max size for male	150.4	154.4	142.6	142.0
Max size for female	114.9	117.6	133.8	132.9
% survival to legal	6.6%	6.3	12.9%	9.59%



Figure 1: Response in average weight of lobsters in the catch to fishing mortality and legal size. Stars represent weights observed for the entire Southern California Bight (SCB) and the northern and southern regions. MPA coverage is 14.6% and size limit is 82.5 mm carapace length.



Figure 2: Response in percent of maximum yield to fishing mortality and legal size. Stars represent weights observed for the entire Southern California Bight (SCB) and the northern and southern regions. MPA coverage is 14.6% and size limit is 82.5 mm carapace length.



Figure 3: Response in spawning potential ratio (SPR) to fishing mortality and legal size. Stars represent weights observed for the entire Southern California Bight (SCB) and the northern and southern regions. MPA coverage is 14.6% and size limit is 82.5 mm carapace length.



Figure 4: Relationship of average weight in the catch with instantaneous fishing mortality (F) with 14.6% MPA coverage (blue) and no MPAs (red).



Figure 5: Relationship of percent of the maximum yield with instantaneous fishing mortality (F) with 14.6% MPA coverage (blue) and no MPAs (red).



Figure 6: Relationship of spawning potential ratio (SPR) with instantaneous fishing mortality (F) with 14.6% MPA coverage (blue) and no MPAs (red).



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Figure 7: Response in spawning potential ratio (SPR) to instantaneous fishing mortality and proportion of *Panulirus interruptus* habitat within marine protected areas (MPAs).



Figure 8: Number of percentage points above the spawning potential ratio (SPR) threshold in years following the reference period. Levels using 4.5% MPA coverage are shown in black and additional points resulting from 14.6% MPA coverage in grey. No bars indicate no difference between annual SPR and the threshold.



Figure 9: Percent of total commercial landings coming from the Santa Barbara, Los Angeles and San Diego regions since the 2000-01 fishing season.



Figure 10: Division of coastal lobster habitat into areas unprotected by MPAs (OPEN) and within MPA interior (IN-IN) and MPA edge (IN) habitat (Figure taken from Parrish, 2014).



a)

Figure 11: Von Bertalanffy growth model (f = J^{∞} (1-e^{-K})- Jt (1-e^{-K}) fit to annual growth with initial size over the entire size range for a) females and b) males.



Figure 12: Treated data used in growth curve analysis comparing Initial size (mm carapace length) with annual increase in size (mm) for females (F) and males (M).



Figure 13: Male and female combined Gaussian 4-parameter curve fit to annual growth for initial sizes from 0-82.5 mm CL.



Figure 14: Comparison of male and female mean annual growth within 5 mm initial size bins.



Figure 15: Male Gaussian 4-parameter curve fit to annual growth for initial sizes greater than 60 mm CL.



Figure 16: Female exponential decay curve fit to annual growth for initial sizes greater than 60 mm CL.



Figure 17: Relationship between instantaneous fishing mortality (F) and spawning potential ratio (SPR) using the von Bertalanffy growth model (red) and growth curves developed by CDFW (black).



Figure 18: Relationship between instantaneous fishing mortality (F) and percent of maximum yield using the von Bertalanffy growth model (red) and growth curves developed by CDFW (black).



Figure 19: Sensitivity of the relationship between the percent of maximum yield and instantaneous fishing mortality (F) to parameters related to MPA dynamics. Parameters are the percentage of lobster habitat protected by MPAs (MPA), the rate of migration out of MPAs (Migout), the percent of F applied to MPA edge habitat simulating risk to fishing due to nightly foraging movements (Fin), and the average width of MPAs (MPAmi). Parameter levels are the current levels (black) and double (red) and half (blue dashed) of current.



Figure 20: Sensitivity of the relationship between spawning potential ratio (SPR) and instantaneous fishing mortality (F) to parameters related to MPA dynamics. Parameters are the percentage of lobster habitat protected by MPAs (MPA), the rate of migration out of MPAs (Migout), the percent of F applied to MPA edge habitat simulating risk to fishing due to nightly foraging movements (Fin), and the average width of MPAs (MPAmi). Parameter levels are the current levels (black) and double (red) and half (blue dashed) of current.



Figure 21: Sensitivity of the relationship between average weight and instantaneous fishing mortality (F) to parameters related to MPA dynamics. Parameters are the percentage of lobster habitat protected by MPAs (MPA), the rate of migration out of MPAs (Migout), the percent of F applied to MPA edge habitat simulating risk to fishing due to nightly foraging movements (Fin), and the average width of MPAs (MPAmi). Parameter levels are the current levels (black) and double (red) and half (blue dashed) of current.



Figure 22: Impacts of natural mortality on the relationship between yield, spawning potential ratio (SPR), and average weight (lbs) to instantaneous fishing mortality (F). Natural mortality is time varying with base 0.17 (black) and constant 0.085 (red), 0.17 (red dashed), 0.34 (blue dashed).



Figure 23: Impacts of vulnerability to traps on the relationship between yield, spawning potential ratio (SPR), and average weight (lbs) to instantaneous fishing mortality (F). Vulnerability increases for large lobsters simulating difficulty entering traps (black) and asymptotic simulating full vulnerability for large lobsters (red).



Figure 24: Impacts of unrecorded fishing mortality on the relationship between yield, spawning potential ratio (SPR), and average weight (lbs) to instantaneous fishing mortality (F). Parameter levels are current settings with trap loss (Tloss), ghost fishing (Ghost) and handling mortality (HandM) set to zero (black solid), levels used by Dr. Parrish (red solid), and double (red dash) and half (blue dash) those levels.