Net primary production, growth and standing crop of *Macrocystis pyrifera* in Southern California

Research approach/methods:

Calculating net primary production

We investigate spatial and temporal variation in NPP of *M. pyrifera* by combining field measurements with a simple model of kelp dynamics. We calculate NPP by *M. pyrifera* as the total amount of biomass produced during the period between each sampling date (approximately 1 month) that explains the observed change in the foliar standing crop (FSC = total mass excluding the holdfast and sporophylls) given the loss rate of biomass during the period. Our model is based on the assumption that within a sampling period kelp grows at a constant mass-specific rate (g), such that new biomass is produced in proportion to existing FSC (S). The model also assumes that biomass is lost at a constant mass specific rate (l), which is equivalent to biomass having a constant probability of loss during the period. Thus, the instantaneous rate of change in FSC is equivalent to the FSC multiplied by the difference between the mass-specific growth rate and loss rate.

Equation 1: $$\frac{dS}{dt} = S(g - l)$$

We apply this model to each sampling interval of the study, combining it with field measurements of FSC and independent estimates of loss rates to calculate the growth rate and NPP of *M. pyrifera.* At each site, we sample *M. pyrifera* plants monthly in a permanent plot between 200 m^2 and 480 m^2 in area (see **Sample design/field methods**). We use allometric equations and conversion factors generated from extensive measurements of plants collected from our study sites to convert *in situ* length measurements of each plant into estimates of FSC

in terms of dry mass, carbon mass and nitrogen mass per unit area of ocean bottom (see **Sample design/field methods**). For each monthly sampling period we also independently measure the biomass loss rate (l) as the sum of the losses of: (1) whole plants, (2) whole fronds from surviving plants, (3) partial fronds from surviving plants due to boat propeller damage, (4) senescing blade material from surviving fronds, and (5) dissolved material released from blades and stipes on surviving plants.

Our field measurements of FSC and loss rates enable us to calculate the average mass specific growth rate of *M. pyrifera* on monthly time scales, but our estimates are much more reliable on seasonal and annual scales because a measurement error (for example an over-count of fronds in one month) tends to produce an overestimate of NPP in one month and an underestimate in the next, which offset when the measurements are aggregated on multi-month timescales. The model we use to describe kelp growth within the sampling period is based on explicit assumptions about how growth occurs. We tested alternative forms of the growth model (e.g., linear, exponential, logistic), and found that our calculations of NPP and growth rate are robust to the choice of growth model (see *Testing the robustness of assumptions of kelp growth).* All results presented here were calculated using the exponential model, because it makes the simplest assumptions about growth and loss (both occur as a constant proportion of FSC):

To determine NPP for the period between any two sampling dates, we use our measurements of FSC and loss rate to calculate the average mass specific growth rate of *M. pyrifera* during the sampling interval (T days) that explains the change in FSC:

Equation 2:
$$g = \frac{1}{T}\ln\left(\frac{S_t}{S_0}\right) + l$$

Returning to Eq.1, we see that the instantaneous rate of NPP at time (t) is the product of the growth rate (g) and the foliar standing crop (S_t), so we calculate the total production over a sampling interval from 0 to T, as the integral of this product:

Equation 3: $$\text{NPP} = \int_0^T g S_t dt$$

We assume that g is constant over the sampling interval and account for the fact that biomass is changing by expressing S_t at any time t as a function of FSC at the beginning of the sampling interval (S_0): $S_t = S_0 e^{(g-l)t}$. Mean daily NPP is obtained by integrating instantaneous NPP over each sampling interval and dividing by T:

Equation 4: $$NPP = \frac{\int_0^T g S_0 e^{(g-l)t} dt}{T}$$

Solving the integral gives:

Equation 5: $$NPP = \frac{g S_0}{g-l}\left(e^{(g-l)T} - 1\right)$$

We have used this approach to calculate NPP and specific growth rate seasonally at the three sites since spring 2002. Mean daily NPP and growth rate of *M. pyrifera* for each season are calculated as the average NPP and growth rate for all days in the season (seasons are: winter, spring, summer, and autumn as defined by the winter solstice, spring equinox, summer solstice, and autumnal equinox).

Testing the robustness of assumptions of kelp growth

Our calculations of NPP are based on the assumption that the rate of production of kelp biomass at each site is proportional to FSC (i.e. production at any time is the growth rate (g) multiplied by the standing stock (S). This assumption implies an exponential growth form, from which equations 1 through 5 are derived. To explore whether this assumption about kelp growth influenced our results, we performed all calculations using an alternative set of equations derived from the assumption that growth is not proportional to FSC (i.e. the rate of production is constant over the period, implying linear growth of biomass). NPP and mass specific growth rate are almost identical when calculated using the two growth forms (exponential versus linear; $r^2 > 0.99$, slope = 1.0 for both growth and NPP).

We also evaluated the robustness of our calculations using hypothetical datasets produced by an individual-based mathematical model of a kelp forest. We calculated NPP for each hypothetical dataset using the approach outline above (Eq. 1 through 5) and compared the model output to the true NPP of the simulated forest. This approach allowed us to determine if equations 1 through 5, which assume exponential growth, break down when kelp does not grow exponentially. In particular, we explored the accuracy of our calculations when kelp grows logistically, as has been assumed in other studies (reviewed in North 1994). Regardless of whether our simulated kelp forest grew linearly, exponentially, or logistically, our calculated values of NPP (using Eq. 1 through 5) matched the true NPP (i.e., the amount of production that occurred during the individual based simulation; $r^2 > 0.90$). Thus, our results are robust to the form of the growth model used.

Special cases – when there is no biomass

The three sites were chosen because they historically supported kelp forests. Indeed at least some giant kelp was present in over 93% of our 559 sampling events (between 2002 and

2017). However, occasionally giant kelp disappears entirely from our sampled plots. This presents an obstacle for a method of estimating growth and NPP that is based on an exponential growth model. For this reason, we apply special rules for the following categories of events: 1) If FSC is present at the beginning of a period but not at the end of the period we assign NPP a value of zero (n = 5 events). 2) Similarly, we assign NPP to zero if there is no FSC at either the beginning or the end of a period (n = 28 events). 3) If FSC is absent at the beginning of a period and present at the end of the period we calculate NPP based on a simple linear model. In these cases, we divide the amount of FSC present on the latter sampling date by the number of days elapsed since the previous sampling date to yield mass accumulation rate on a per day basis (n = 5 events). In all three cases the mass specific growth rate is undefined and is set to missing in the dataset. If loss rates are known, for example if tagged plants are still being monitored adjacent to, but outside of our sampling plots, then those loss rates are reported for these time periods. Note that these special cases represent a small number of events (38 out of 522) and a vanishingly small amount of potential NPP given the small amount of giant kelp present.

Sampling design/field methods:

Measuring standing crop

On each sampling date (approximately once a month) we measure *M. pyrifera* FSC in permanent plots at the three sites using SCUBA. Plots are either 200 m^2 (Arroyo Quemado and Mohawk; made up of an array of ten 20 m x 1 m transects) or 480 m^2 (Arroyo Burro; made up of three transects: 60 m x 2 m, 40 m x 2 m and 20 m x 2 m, respectively). We calculate FSC based on measurements of all *M. pyrifera* plants in the plot with at least 1 frond > 1 m in length. We characterize each plant using three distinct plant sections (Figure 1). The “sub-surface” section

consists of fronds that do not reach the surface, typically recently initiated fronds with small blades (Figure 1a, fronds shaded in light blue; Figure 1b). Fronds that do reach the surface are treated as having two sections: the "water column" section is the portion of these fronds that is underwater, stretching from the holdfast to the sea surface (Figure 1a, frond parts shaded in orange). This section usually has mature and senescent blades sparsely distributed along the stipe. The "canopy" section is the portion of these fronds that floats at the sea surface, typically consisting of mature blades spaced closely along the stipe (Figure 1a, frond parts shaded in dark blue).

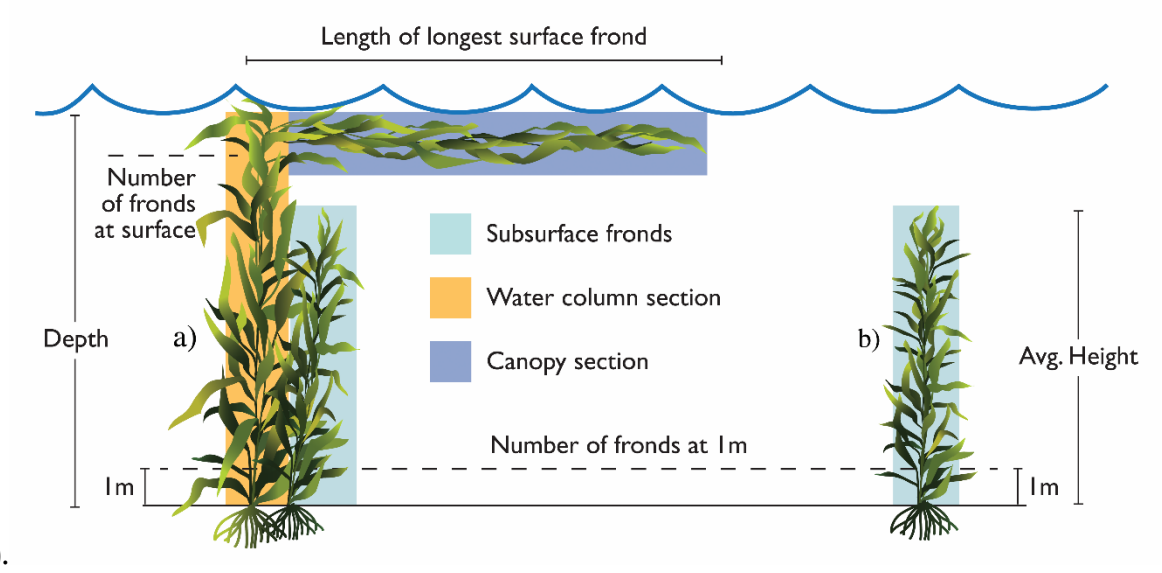

Figure 1: Diagram illustrating the measurements taken on each kelp plant. The different colored shading indicates which fronds (and frond portions) are included in each plant "section".

For each plant within the sampling area we count the number of fronds 1 m above the holdfast (N_{1m}), the number of fronds at the surface ($N_{surface}$), measure the water depth in meters at the top of the holdfast (D, equivalent to the length of the water column section of the fronds reaching the surface) and measure the length of the canopy portion of the longest frond in meters (MAX). We use these data to calculate the length of each plant section, according to the following equations:

Equation 6a: Length of subsurface section = $(N_{1m} - N_{surface})$ $(1+½ [D - 1])$

Equation 6b: Length of water column section = $(N_{surface})(D)$

Equation 6c: Length of canopy section = $(N_{surface})(½ MAX)$

The accuracy of equations 6a, b and c in estimating the length of each plant section in the field was tested by comparing estimates of length obtained using equations 6a, b and c to actual lengths. This was done by collecting a subset of plants measured in the field using the methods described above and transporting them to the laboratory where we measured the maximum frond length of each plant and the total length of the three frond sections relative to the depth where the plant was collected. Total frond length estimated using equations 6a, b and c explained 99% of the variation in the cumulative length of all fronds above the holdfast, when all fronds were measured individually (N = 55 plants, $r^2 = 0.99$, slope = 1.02). Similarly, we estimated total frond length of 147 plants in the field using equations 6a, b and c and found that those estimates agreed closely with more detailed field measurements of those plants, in which the length of each frond was measured to the nearest meter *in situ* (N = 147, $r^2 = 0.99$, slope = 0.99).

While plants reaching the surface account for more than 92% of kelp biomass in our data, young plants may have one or more fronds longer than 1 m, but no fronds reaching the surface (Figure 1b). For these plants, we measure N_{1m} (which is usually < 4 m) and estimate the average length of fronds on the plant in meters (*AVG*). The cumulative length of these fronds is calculated as $N_{1m} * AVG$, and these fronds are treated the same as water column fronds when their mass and elemental composition are calculated (see *Conversion from length to weight of dry mass, carbon, and nitrogen*).

Treatment of missing measurements

In approximately 1% of plants, the fronds become tangled with those of neighboring plants and prevent divers from obtaining reliable measurements of $N_{surface}$ and *MAX*. In these cases, the length of each section of the plant is estimated using only the number of fronds 1 m above the holdfast. The estimate is based on the relationship between fronds at 1 m and the length of each section for all plants successfully sampled at the given site within a three month window centered on the month in which missing data occurred (a moving average is used to smooth out month-to-month variation in the estimates). Using relationships matched by month accounts for systematic seasonal variation in length per frond at 1 m above the holdfast, while using relationships matched by site accounts for variation from site to site including variation in depth. These relationships were estimated using linear regression with a Y intercept fixed at zero (although a simple calculation of average length per frond at 1 meter yields identical relationships). The regressions excluded cut and partial plants (see *Plants at the edge of the sampling plots* and *Loss of partial fronds due to propeller damage*). In rare cases where depth was not recorded (0.3% of observations) depth was estimated using the average depth of all other plants sampled at that site.

Plants at the edge of the sampling plots

A small proportion of plants (6.3%) occurred on the edge of the transect such that only a portion of them was present in the sampled area. Before 2005, a plant was sampled if more than 50% of the plant was found within the transect. This approach was unbiased with respect to average plant density and biomass, but created high variance in biomass from month to month,

especially when a large plant was located near the edge of the transect and was sampled in some months and not in others depending on small deviations in how the transect tape was laid out. We changed the sampling protocol in 2005 so that when a plant was located partially within the transect, only the fronds occurring within that transect are sampled (and those fronds are noted as representing a "partial plant"). Counting fronds at the surface and estimating frond lengths of these "partial plants" is often not possible, and the length of each section of these plants is estimated from fronds at 1 m as described above in *Treatment of missing measurements*. In cases where divers are able to obtain all measurements without disturbing the plants, the normal allometric relationships are applied.

Conversion from length to weight of dry mass, carbon, and nitrogen

Standing crop is estimated by converting the total length (in meters) of each plant into the total wet mass (in kilograms). The length to wet mass conversion is based on 55 plants collected from the three sites during monthly surveys in 2003. These plants were transported to the laboratory where we first separated the fronds from each plant into the three sections (canopy, water column, and subsurface) and measured their length and weight. We then used linear regression to determine the relationship between weight and length of the fronds from each section for each plant. We apply the mean slope of the regression lines obtained for the 55 plants to the field data to convert the total length of *M. pyrifera* to FSC. The ratio of frond wet mass (kg) to frond length (m) was 0.117 for the subsurface section, 0.105 for the water column section, and 0.259 for the canopy section.

Ratios used to convert wet mass to dry mass, dry mass to carbon mass, and dry mass to nitrogen mass are derived from *M. pyrifera* tissue samples obtained from mature blades collected

at each site on each sampling date. Blades are collected from 15 different plants, approximately 2 m from the growing tip of a frond reaching the surface, or from the longest fronds available at the site (in cases when no canopy is present). Blades are transported to the laboratory in opaque insulated containers where they are cleaned of epiphytes, rinsed in a dilute acid solution and patted dry with a paper towel. A 5 cm^2 disk is excised from the central portion of each blade and weighed (using a Mettler AE 200 Analytical balance), dried in an oven for 2 to 5 days at 60^oC, and reweighed. The samples are ground to a powder using a mortar and pestle and the powdered samples from all 15 blades are combined to form a composite sample for each site on each sampling date. Because conversion from wet to dry mass was relatively consistent both across space and time, a single average ratio (0.094) calculated across all samples collected through 2016 (n = 1055) is used to convert wet mass to dry mass. The same ratio was used to convert wet stipe mass to dry mass, as dry:wet weight ratios were statistically indistinguishable for portions of blades (N=112) and stipes (N=114) sampled over the first 12 months of the project.

The carbon and nitrogen content of each composite sample is measured using an elemental analyzer (Carlo-Erba Flash EA 1112 series, Thermo-Finnigan Italia, Milano, Italy). The percent carbon and nitrogen of the composite sample from each sampling event (site*year*month) is used to convert dry mass of FSC on that sampling date to mass of carbon and nitrogen. In the event that kelp is present but kelp tissue data are not available (2 observations), we use an average value specific for that site and month calculated from our time series through 2016. Following the same logic by which missing plant measurements are estimated, we use the mean percent nitrogen and carbon for the given site in the given month averaged over all years. This approach accounts for systematic seasonal variation and inherent site differences that may contribute to variability in tissue carbon and nitrogen content.

Because we sample blades from the canopy only, we developed a conversion factor for each element that allows us to calculate the carbon and nitrogen composition of FSC as a whole. The conversion factors are based on tissue samples taken from each section of the 55 plants referenced above. The carbon and nitrogen content of subsurface, water column and canopy blades of these 55 plants were similar (differences are less than 5% of the mean), so we apply the canopy blade values to all blade mass. However, carbon mass was 12% lower and nitrogen mass was 44% lower in stipes than in blades. FSC is converted to units of carbon (C_{mass}) adjusting for the ratio of blades to stipes as follows:

Equation 7: $$C_{mass} = SC_{composite}\frac{C_{blades}m_{blades} + C_{stipe}m_{stipe}}{C_{blades}}$$

where S is FSC, $C_{composite}$ is the percent carbon in the composite sample, C_{blades} and C_{stipe} are average percent carbon in the blades and stipes of the 55 plants, and m_{blades} and m_{stipe} are the fraction of the mass of the 55 plants consisting of blades and stipes, respectively. Substituting nitrogen for carbon in Equation 7 yields an estimate of FSC in units of nitrogen.

We found that length to weight relationships and wet weight to dry weight conversion factors were consistent across space and time and so we apply the same factors to all three of our sites. However, considering the wide range of morphological variation found in this species around the globe, we caution that these relationships should be validated before applying our model to populations in other regions. We found carbon and nitrogen content to be relatively similar on blades from different sections of an individual plant, but this may not hold in other geographic or environmental contexts. Moreover, because carbon and nitrogen content varied substantially within our sites and across time, they are likely to vary across larger geographic and temporal scales.

Measuring loss rates

Our calculations of NPP incorporate five sources of biomass lost during the interval between sampling periods: (1) the loss of entire plants, (2) the loss of fronds from surviving plants, (3) the loss of partial fronds from surviving plants due to boat propeller damage, (4) the loss of blades or parts of blades from surviving fronds due to senescence, and (5) the loss of dissolved material released from blades and stipes on surviving plants due to exudation and senescence. So total loss rate (l), is the sum of the component loss rates (p, f, c, b and d). Methods for estimating each rate are described below.

Frond loss, blade deterioration, and dissolved losses occur throughout the year; with plants continuously losing biomass through these processes. Losses of whole plants are usually caused by water motion associated with large waves that rip plants off the bottom and are concentrated in winter months, while losses of partial fronds from propellers are similarly sporadic and mainly occur during the first few months of lobster season (chiefly October and November) when fishing boats are concentrated in the kelp forest. Our approach focuses on the average probability of loss, treating loss as a process that is distributed across the month in which it occurs.

Loss of whole fronds and whole plants

We use the change in the density of tagged fronds and tagged plants to calculate instantaneous per capita mortality rates (sensu Gurney and Nisbet 1998). Assuming that lost fronds and plants are of average size, these mortality rates are equivalent to mass-specific loss rates of FSC. We measure the loss of fronds on approximately 15 focal plants per site during each sampling interval. We count all fronds on each focal plant at the beginning of each

sampling interval, and marked all counted fronds with zipties. Prior to 2006, each frond was individually marked. Since then, the counted fronds have been collectively surrounded with a loose zip tie collar (as a bundle) to minimize contact between zip ties and the fronds. We rarely observed any frond mortality or damage associated with the zipties.

At the end of the sampling interval, we count the number of tagged fronds that remain from the previous sample. We also count the number of new fronds that grew to 1 m in size during the sampling interval and tag these fronds to prepare for the next sampling event. The loss rate of fronds from a single plant (f_k) is estimated based on the number of fronds at the beginning (F_0) and end (F_T) of the sampling interval:

Equation 8:
$$f_k = -\frac{1}{T}\ln\left(1-\frac{F_T}{F_0}\right)$$

We average f_k among the 10 to15 surviving focal plants to calculate a frond loss rate (f) for each site during each period. Note that our decision to calculate a loss rate for each plant and then average across plants leads loss rates on small plants to have a higher weighting on a per-frond basis. But the alternative of summing all fronds and then calculating loss rate of the aggregated population of fronds could lead to loss rates on the largest plant to dominate the calculation. As we observed no consistent relationship between plant size and plant loss rate, we opted for the former.

The loss rate of plants (p) is estimated similarly, using the same 15 plants that were tagged to estimate frond loss. Each plant is tagged with a unique ID fastened to its holdfast. We also map the location of each tagged plant so it can be easily re-identified if the tag is lost. In months where plants are lost, new plants are tagged to maintain a sample size of approximately

15 plants. We estimate the loss rate of plants (p) from the number of tagged plants at the beginning (P_0) and end (P_T) of each monthly sampling interval:

Equation 9: $$p = -\frac{1}{T}\ln\left(1 - \frac{P_T}{P_0}\right)$$

Equations 8 and 9 are not defined for cases in which all tagged fronds or all tagged plants are lost. In these cases we perform the calculations as though ½ of a frond or ½ of a plant remained at the end of the sampling. If no tagged plants or fronds were present at the beginning of the sampling period, loss rates from these processes are not estimated for that period, and NPP is set to undefined unless there is no biomass present at the end of the sampling period in which case it is set to zero as described in *Special cases – when there is no biomass* section above.

Loss of partial fronds due to propeller damage

The estimates of frond loss rate described above are based on counts of fronds at 1 m above the holdfast, and do not account for cases where part of the frond breaks off above that height while the bottom of the frond remains. Although this happens occasionally, it accounts for a small proportion of fronds under most conditions; fronds that break are typically undergoing senescence and the whole frond is lost quite rapidly. Across the 2,123 fronds counted on the 55 plants (see *Conversion from length to weight of dry mass, carbon, and nitrogen*), fewer than 7 percent were observed to be senescent and longer than 1 m, representing 2.9 percent of the biomass. A notable exception to this pattern occurs when the propellers of boats driving through the kelp forest cut fronds near the surface. Plants cut by propellers are readily recognized by divers when sampling because they appear as healthy plants with a large fraction of fronds that have been cleanly severed near the surface. Although cut plants make up

a small proportion in the dataset as a whole, they are relatively common in October and November at the beginning of lobster season when commercial fishing boats actively set and retrieve lobster traps in kelp forests. The occurrence of cut plants (defined as plants for which more than 50% of the fronds have been sliced off near the surface) in October and November can be as high as 47.2%, and averaged 7.2% during these months across all sites and years. Thus there is a potential to substantially understate NPP in these months if losses of biomass arising from fronds being cut by boat propellers are not accounted for.

To account for this form of loss, divers record plants with > 50% of fronds abruptly severed within 1 meter of the surface as being "cut". By comparing the average size of cut plants to that of uncut plants with a similar number of fronds at 1 m from that site on the same date we estimate that on average a cut plant has 81% of the mass of a similar-sized uncut plant. Comparisons were made by grouping plants into 10-frond size classes based on the number of fronds at 1 m above the holdfast and comparing cut to uncut plants within each group. From this observation we assume that for each plant marked as cut, missing biomass equivalent to 19% of the observed biomass had been lost. When cut plants are observed, we sum cut biomass across the whole site and calculate a per day loss rate (c), based on biomass at the beginning (S_0) and end (S_T) of the period, total biomass lost through propeller cuts (S_c), and the number of days elapsed between sampling dates:

Equation 10:
$$c = -\frac{1}{T}\ln\left(\frac{S_T}{S_0}\right) - \frac{1}{T}\ln\left(\frac{S_T + S_C}{S_0}\right)$$

Loss of mass due to blade senescence

Blades often undergo senescence and breakage before the frond to which they are attached is lost. We estimated the rate of biomass lost to blade senescence using data from a collaborative study in which we measured blade area in a cohort of tagged blades on a weekly basis that yielded size trajectories of 120 blades (Rodriguez *et al*. 2016). Using these data we developed a model simulating a population of blades of mixed ages, assuming blades grew and deteriorated according to those observed trajectories (Rassweiler *et al*. 2017). This model yielded daily deterioration rates (d^{-1}) for subsurface blades (b_{sub}), water column blades (b_{wc}), and canopy blades (b_{can}). Constant losses due to deterioration can account for a substantial fraction of NPP, but our estimates are somewhat conservatively low (and thus potentially lead to underestimates of NPP) given that our analyses assume a loss rate of zero during blade growing phases when growth rates exceed losses. We estimate the daily loss rate (b) of blades due to deterioration as the summation of the daily deterioration rate for subsurface (b_{sub}), water column (b_{wc}), and canopy blades (b_{can}) multiplied by the average fraction of biomass (*fracBld*) comprised of that tissue over the period:

Equation 11: $$b = b_{sub} fracBld_{sub} + b_{wc} fracBld_{wc} + b_{can} fracBld_{can}$$

Loss of dissolved mass

Our initial calculations of NPP (Rassweiler *et al*. 2008) did not include losses of dissolved organic matter (DOM) resulting from exudation and senescence. Recently, we quantified the release of DOM by giant kelp at our Mohawk study site and found that it was substantial and varied as a function of irradiance and tissue type (Reed *et al.* 2015a). Specifically, our results showed that blade mass released DOM at 2.5 times the rate of stipe mass, and both released DOM faster under high light conditions than in low light. To account for

these losses, we combined our estimates of blade and stipe biomass with ongoing measurements of average daily surface and bottom irradiance collected since 2008 (Reed 2017). Based on Reed *et al*. (2015a), the mass specific dissolved loss rate of blade biomass (d_{blade}) is:

Equation 12: $d_{blade} = 4.90 \times 10^{-4} + 1.66 \times 10^{-5} \times PAR$

Where *PAR* is the mean daily irradiance (μmol m^{-2} s^{-1}) averaged over a 24 hour cycle. Mass specific dissolved loss rates of stipe biomass were calculated based on the same equation, but discounted to 39% of the rates used for blades.

The daily irradiance used to calculate dissolved loss rates (*PAR*) differed for mass in the canopy section (exposed to relatively direct sunlight) and in the water column and subsurface sections (for which irradiance is reduced both by shading from the canopy and attenuation in the water column). For biomass in the canopy section we based *PAR* on the mean daily irradiance, measured at the surface over the sampling period. For blade biomass in the subsurface and water column sections, we based *PAR* on the depth-integrated irradiance calculated from measured mean daily irradiance at the surface and mean daily irradiance measured at 7 m depth, and assuming exponential attenuation of light with depth. This calculation assumes that attenuation was consistent with depth below the canopy section. Of course, the details of light attenuation likely vary from site to site and moment to moment due to environmental conditions such as water quality, current and canopy density. Daily irradiance prior to 2008 was not measured directly, so was estimated it using the average site-specific attenuation value for each day of the year based on surface and bottom irradiance data collected from 2008 – 2016. Mean daily mass specific dissolved loss rate (d^{-1}) for FSC as a whole is calculated as a weighted average of the loss rates for blade and stipe mass from each plant section, where weighting factors are based on the fraction of the total FSC made up by each tissue type, averaged across the period.

Quantification of uncertainty/error estimation:

Our estimates of NPP, FSC, and loss rates are each based on a lengthy set of calculations described above, and rely on a suite of periodically measured variables, along with some fixed parameters (such as conversion factors), each of which is estimated from a focused, shorter term set of measurements. Each of these measurements and parameters are imperfectly known, and the uncertainty/error in the measurements and parameters results in uncertainty around our estimates of each variable. Because an error in a measurement or an estimated parameter can propagate through the calculations in complex ways, we use Monte Carlo methods to propagate the uncertainty in these measurements (Harmon *et al*. 2007).

The general approach of the Monte Carlo method is to repeat the process of calculating NPP 1000 times, in which each replicate iteration represents an alternative possible dataset and set of parameters. Because the data and parameters used in each iteration are slightly different, each iteration yields a different calculated NPP value. We use the standard deviation of these values, which are distributed normally, as the standard error in our estimate of NPP. This Monte Carlo approach also yields distribution in the estimates of FSC, growth rate, loss rates, and other variables, which are used to calculate the associated standard errors around our best estimates.

Each replicate iteration is based on the actual measurements and on our best parameter estimates, but within each iteration each data point is drawn from a distribution centered on the actual measurement. The shape and variability in that distribution is based on independent

measurements of observer errors in some cases, or is estimated based on variation within the dataset. The errors we include in our calculations are summarized in Table 1.

The "spatio-temporal scale" column in Table 1 indicates the spatial and temporal scale at which random values are chosen within each Monte Carlo iteration. For example, errors in the "Count of plants" are applied on the "transect*period" scale, which means in each iteration we draw a different error value to modify the plant count observed on each transect in each sampling period (typically a month). Within any given period one transect might be assigned a positive error while another might get a negative error. By contrast, the error in the "Ratio of blade mass to stipe mass" is assigned at the "iteration" scale, so a single error value is applied to each iteration of the Monte Carlo (the same error is applied to all sites in all periods for the run).

Table 1. A summary of the errors included in the uncertainty analysis

Variable to which error is applied	**Spatio-temporal scale**	**Source of error estimate**
Count of plants	transect * period	Repeated sampling of the same transect by different investigators
Count of fronds	transect * period	Repeated sampling of the same transect by different investigators (0.63 correlation with error in "count of plants")
estimate of total length of all fronds	transect * period	Repeated sampling of the same transect by different investigators (0.83 correlation with error in "count of fronds")
Parameters converting length to weight	transect * period * plant	Regression errors from measurements of plant sections sampled in the laboratory
Parameters converting wet mass to dry mass	replicate iteration	Regression error based on replicate samples of plant tissue that were weighed dried and reweighted.

Ratio of blade mass to stipe mass	replicate iteration	Regression errors from measurements of plant sections sampled in the laboratory
% Nitrogen	site * period	Replicate composite samples of blade tissue collected from the same site*period
% Carbon	site * period	Replicate composite samples of blade tissue collected from the same site*period
Loss rate of whole plants	site * period	Draw from binominal defined by observed plant loss rate and number of tagged plants
Loss rate of fronds from surviving plants	site * period * plant	Site-specific variation in frond loss rates from different plants during a sampling interval (uncertainty is larger for plants with fewer tagged fronds)
Loss rate of blade mass from surviving fronds	Site * period	Variation in simulated population of blades (see Rassweiler *et al* 2017)
Loss rate of dissolved material through exudation	site * period	Observed variation in exudation among replicate blades and stipes measured on the same day