



Research article

Anchoring permits kelp to acquire an ecological niche in coastal oceans: A model analysis

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ABSTRACT

Kelps (brown algae of the order Laminariales) are foundation species in coastal temperate oceans. As ecosystem engineers, they moderate local environments, provide habitats and food, and shape community structure. Despite their high rates of primary production, kelps overall growth rates are lower than co-occurring phytoplankton, and their competitive strength remains elusive. Here we developed a coastal ecological model including physical and biological processes to examine the most important factors for kelp survival. By comparing the distribution of kelp and phytoplankton, we found that kelp can accumulate larger biomass than phytoplankton because anchoring prevents them from being swept offshore away from high coastal nutrients. Slower water speed can eliminate kelp's advantage, which may explain the effect of El Niño and La Niña on kelp forests. Our simulation highlights the competitive ability of kelp and informs future in situ measurements and coastal ecosystem models.

1. Introduction

Kelps (brown algae, Laminariales) are important organisms in the coastal ocean [1], which dominate subtidal rocky reef ecosystems in cold-water marine habitats and may contribute to global change mitigation [2]. They can fix CO₂ through photosynthesis [3], and transform the fixed carbon into refractory ones, which substantially facilitates carbon sequestration [4]. As primary producers, kelps are the foundation of kelp forest ecosystems and provide three-dimensional habitat structures for an array of organisms [5]. However, they are not the only primary producers in this ecosystem. For instance, kelp can compete with phytoplankton for resources such as light and nutrients [6], a phenomenon that has been well-reported by a previous experiment [7] and a modeling study [8].

Phytoplankton are competitive within their ecological niche. An ecological niche can be defined as a species' match with a specific set of abiotic and biotic factors [9]. Phytoplankton can survive across a multitude of different environments [10] with high ecological resilience [11] and contribute more than 45 % of the earth's photosynthetic primary production [12]. They have an efficient nutrient uptake system [13] resulting in high maximum growth rates. Compared with phytoplankton, the nutrient (N) uptake of kelp is lower [14], which constrains the availability of nutrients and growth, and may make kelp less competitive [15]. Since kelp and phytoplankton co-occur in the same coastal environment, kelp must have evolved strategies to reduce direct competition with phytoplankton for nutrients. In other words, kelp must have evolved into an ecological niche to co-exist with phytoplankton. The ecological niche of kelps can be related to their distribution [16]. Most kelp forests are distributed in temperate coastal areas with abundant

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nutrients, intermediate light and temperature [17]. They are also well-reported in upwelling zones such as the California coast [18], the west coast of southern Africa [19], central Chile [20], and the equatorial upwelling around the Galápagos Islands [21]. Thus, it is reasonable to assume kelps are highly competitive in near-shore high-nutrient regions. However, the explanation for how they remain competitive in these areas remains elusive.

Determining the niche of kelp and their competitive strength is meaningful for the future study of kelp distribution and cultivation, as well as their response to and effect on climate change [22]. Simulating kelp distribution could find potential areas suitable for protection and restoration. Building coastal models has become increasingly important for predicting shifts in kelp communities in response to global ocean change. Since kelp forests provide habitats and food-web foundations for sea urchins and some other fish [23], understanding kelp's niche and shift in global ocean change (e.g., warming, acidification, etc.) could guide the fishery strategies, e.g., how to increase production sustainably. Additionally, investigating the niche of kelps could help us understand where kelp can sequester carbon, a key process in understanding the ocean carbon cycle and mitigating the effects of climate change.

One of the key uncertainties about kelp's ecological niche is how they survive under competition with phytoplankton and what the surrounding evolutionary mechanisms are. So, we asked this question, "Given the low nutrient affinity of kelp, how do they acquire their ecological niche while in competition with phytoplankton in the coastal ocean?" Our question and study are important as we are facing ocean change, including ocean acidification, warming, and altered upwelling patterns. By answering this question, we can also predict how the distribution and productivity of kelp forests may shift in response to global change, thereby informing more effective sustainable aquaculture strategies. Our research contributes to a modeling framework (Fig. 1) for future coastal dynamics and offers insights into how to manage and cultivate kelp effectively in a changing ocean.

2. Methods

Here we describe our coastal ecological model (Fig. 1). The model aims to simulate the spatial distribution (from boundary to open water, along the x direction) of phytoplankton, kelp, and nutrient (nitrate) concentration, as well as their temporal dynamics. In the simulation, we considered both physical and biological factors. Our model is based on regions with upwelling and offshore water movement (e.g., the California Current), and we used the advection equation to represent these processes. As for biological factors, we considered two different organisms: phytoplankton and kelp. We considered their growth and death, as well as remineralization. All definitions and units for the parameters are included in the supplementary (Table S1).

Fig. 2 is a general flow chart of our modeling processes. Firstly, we set the initial boundary conditions, including the initial nutrient concentration, biomass, and wind speed. Then, we calculated water movement, nutrient uptake rates, and remineralization. Based on these values, we calculated the nutrient concentration. Using nutrient concentrations and uptake rates, we can calculate

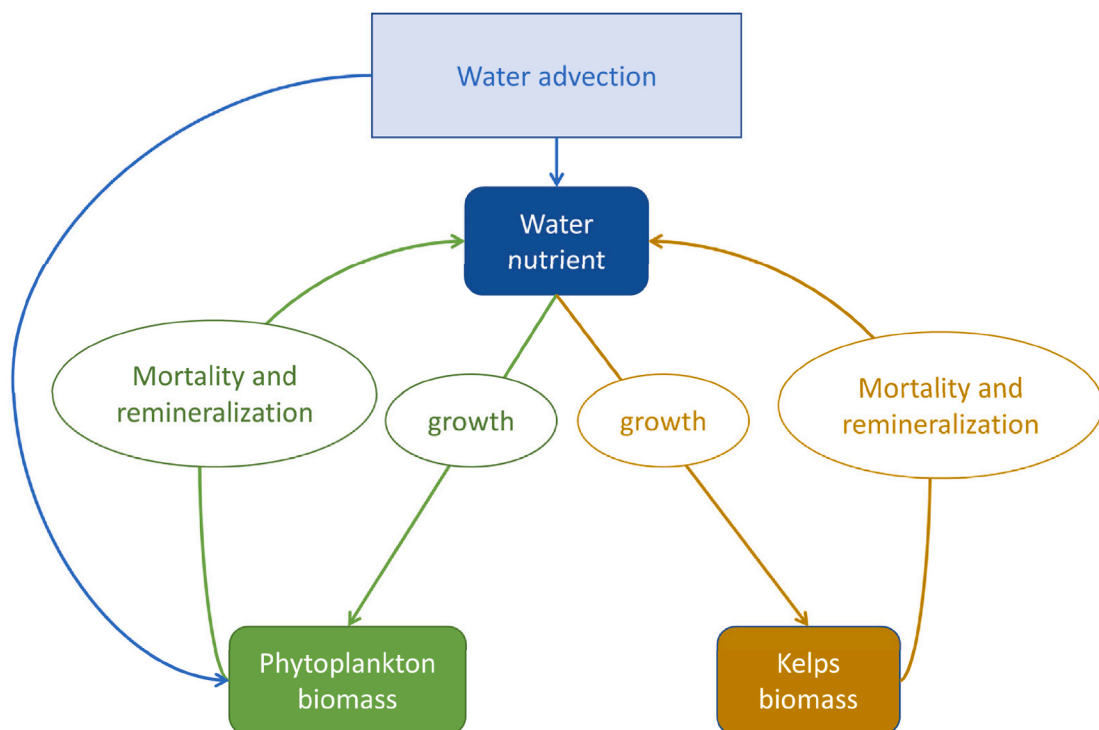


Fig. 1. Model frame. Round corner rectangles are pools: green represents phytoplankton biomass, brown represents kelp biomass, and blue represents dissolved nutrients. Arrows and ovals are pathways: green represents processes caused by phytoplankton, brown represents processes caused by kelp, and blue represents processes driven by physical factors. The blue rectangle is the physical factor (water advection).

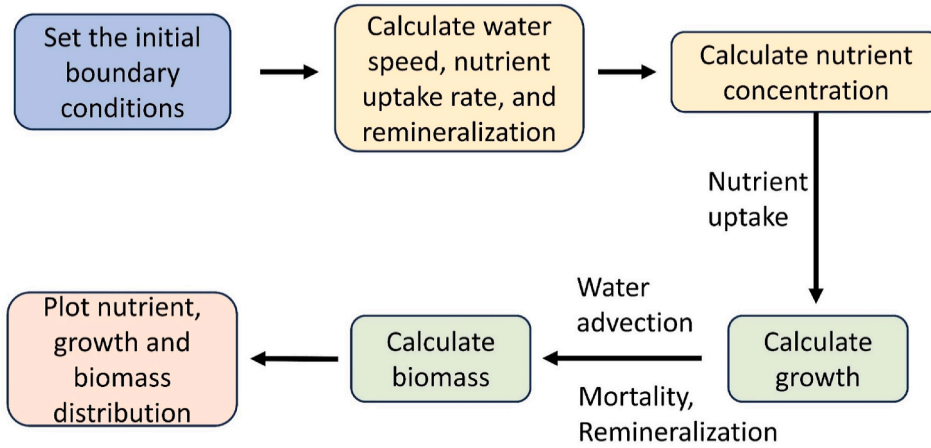


Fig. 2. Flow chart of simulation. The blue frame sets the initial value. The yellow frames mean the calculation of background values, including nutrients, water speed, and remineralization. The green frames mean the calculation of kelp and phytoplankton (including growth and biomass). The pink frame is the plotting step to get the figures.

phytoplankton and kelp growth. For phytoplankton and advected kelps (i.e., kelp that flows with the water), we used water advections, mortality, and remineralization to calculate their biomass. To simulate biomass in anchored kelp, we considered mortality and remineralization. Finally, we simulated this model from the boundary to 500 km in the open ocean after 1 year of dynamics and then plotted the patterns.

2.1. Advection

We calculated the offshore water advection speed by using Equation (1). Here, we consider the water speed (U , unit: m/s) as a function of time (t , unit: s). U_0 (m/s) is the initial speed, and the sine term ($A\sin(wt)$) means the speed is a periodical function. Here, A (dimensionless unit) is the amplitude of oscillation, and w (unit: s^{-1}) is the frequency of oscillation.

$$U = U_0 + U_0 \times A\sin(wt) \quad \text{Equation 1}$$

We used a simplified equation (Equation (2)) to include advection in the x direction (red arrow in Fig. 1) in our model. Here we assume that the concentration changing rate with water movement in the x direction ($\frac{\partial C}{\partial x} \times U$) equals the concentration changing rate in a fixed point ($\frac{dC}{dt}$, unit: $\mu\text{M}/\text{s}$) (detailed explanation in supplementary Equation S(1)). In this equation, C represents concentration, including nitrogen (N) concentration in phytoplankton (N_{phyto} , unit: μM) and kelp (N_k , unit: μM) (hereafter, we summarize these two as N_i , i means different organisms, phytoplankton or kelp), and environmental nitrogen (N, e.g. nitrate) concentration: N_{nut} (unit: μM). We calculated $\frac{dC}{dt}$ by biological processes (Equation (3), Equation (6)) and used this equation to calculate spatial and temporal dynamics (Equation (8)).

$$\frac{dC}{dt} = \frac{\partial C}{\partial x} \times U \quad \text{Equation 2}$$

2.2. Biological processes calculation

To calculate $\frac{dC}{dt}$, we specified it in two forms: $\frac{dN_i}{dt}$ (Equation (3)), $\frac{dN_{\text{nut}}}{dt}$ (Equation (6)). We used Equation (3) to calculate the N changing rate in organisms ($R_{\text{bio}}^{N_i}$, unit: $\mu\text{M}/\text{s}$, i means phytoplankton or kelp), which is the difference between N increase in organisms' growth ($R_{\text{grow}}^{N_i}$, unit: $\mu\text{M}/\text{s}$) and N decrease in mortality ($R_{\text{mort}}^{N_i}$, unit: $\mu\text{M}/\text{s}$). Here we used the Monod type equation (Equation (4)) to calculate growth. We assumed that the growth increases with N nutrient in water (N_{nut} , unit: μM) and can reach maximum growth (μ_i , unit: s^{-1}). K_{N_i} (unit: μM) means half-saturation concentration of water N nutrient for organism i . Equation (5) was used to calculate $R_{\text{mort}}^{N_i}$ in Equation (3), and m_i (unit: $s^{-1} \mu\text{M}^{-1}$) means quadratic mortality rate. Both growth and mortality increase with N in organisms (N_i).

$$\frac{dN_i}{dt} = R_{\text{bio}}^{N_i} = R_{\text{grow}}^{N_i} - R_{\text{mort}}^{N_i} \quad \text{Equation 3}$$

$$R_{\text{grow}}^{N_i} = \mu_i \times N_i \times \frac{N_{\text{nut}}}{(N_{\text{nut}} + K_{N_i})} \quad \text{Equation 4}$$

$$R_{\text{mort}}^{N_i} = m_i \times N_i^2 \quad \text{Equation 5}$$

Then we calculated the N nutrient changing rate ($\frac{dN_{nut}}{dt} = R_{nut}^N$, unit: $\mu\text{M/s}$, Equation (6)) by using the difference between the remineralization rate (Re_{N_i} , unit: $\mu\text{M/s}$) and uptake rate in organisms ($\sum R_{bio}^{N_i}$, unit: $\mu\text{M/s}$; we summed the changing rates in different organisms up). We calculated the remineralization rate (Re_{N_i} , Equation (7)) by using local remineralization fraction (φ) times uptake rate by organisms ($\sum R_{bio}^{N_i}$).

$$\frac{dN_{nut}}{dt} = R_{nut}^N = Re_{N_i} - \sum R_{bio}^{N_i} \tag{Equation 6}$$

$$Re_{N_i} = \varphi \times \sum R_{bio}^{N_i} \tag{Equation 7}$$

2.3. Dynamics simulation

This model uses the initial concentration near the boundary to predict the concentration distribution along the x direction for the present and future. Transformed from Equation (2) (supplementary Equations S1-S7), Equation (8) represents how we calculate each concentration in the present time and space step from the concentration in the previous time step and space step. C_{j+1}^t means concentration (including N_i and N_{nut} , unit: μM) in the present time (t) and space ($j+1$). C_j^t means concentration in the present time and the last space. C_{j+1}^{t-1} means concentration in the last time and the present space. $\left(\frac{dc}{dt}\right)_{j+1}^{t-1}$ means the changing rate in the last time and the present space. dt and dx means the length of the time step and space step, and U means the water speed. We set the initial values for initial time (including the initial time values for all space steps) and initial space (initial space values for all time steps). Using this equation, we calculated the concentration values for all time and space steps. The simulation results in the following result sections are the values for 1 year after the initial time.

We have two simulations in this study, including the kelp anchoring situation and the kelp advection situation. For the kelp anchoring situation (more like a real situation), we set the initial water speed U_0 to 0 m/s to calculate N_{kelp} . To compare faster and slower water movement conditions, we set U_0 to 0.1 m/s and 0.01 m/s to calculate N_{phyto} and N_{nut} . For the kelp advection situation, we do all the calculations by setting U_0 to 0.1 m/s.

$$C_{j+1}^t = \frac{\left(\left(\frac{dt}{dx}\right) \times U \times C_j^t + C_{j+1}^{t-1} + \left(\frac{dc}{dt}\right)_{j+1}^{t-1} \times dt\right)}{\left(1 + \left(\frac{dt}{dx}\right) \times U\right)} \tag{Equation 8}$$

2.4. Parameters and values

Here we describe the values we used to simulate the model. For the physical parameters, we used 0.1 m/s as the initial water speed value (U_0), which is similar to the previous reported values [24]. The parameter $A = 0.5$ was used to define the amplitude of oscillation, which has been tested as a non-sensitive parameter for nutrients, phytoplankton biomass, and kelp biomass (Fig. 6). Similarly, w was set to $2\pi/T$. T equals 31,536,000 s, which means 1 year in seconds. w implies frequency of oscillation, representing a 1-year seasonal cycle. For the biological parameters, we used 2.25 d^{-1} as the maximum growth rate for phytoplankton (μ_{phyto}) (calculated from previous experimental study [25] and 0.18 d^{-1} for kelp (μ_{kelp}) [26]. We used $1.025 \mu\text{M}$ as the half nitrogen saturation

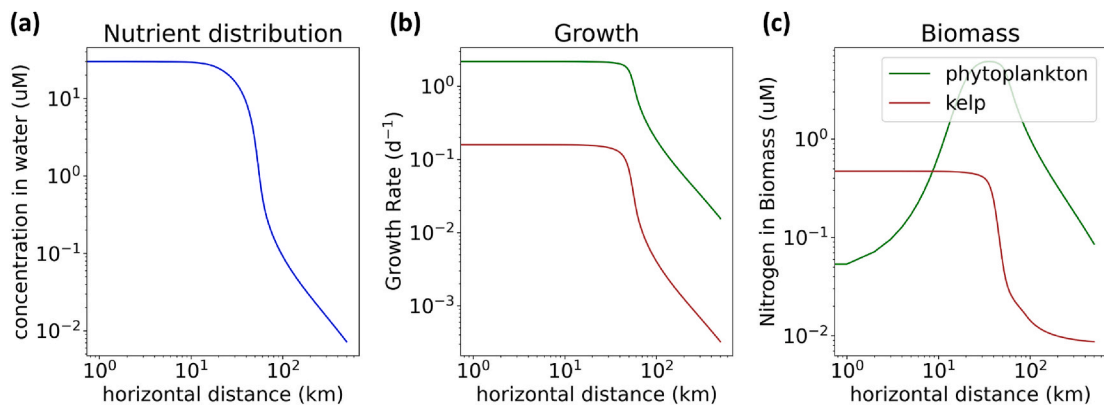


Fig. 3. Simulation results with kelp anchored to the seafloor (no advection, real condition simulation): nutrient distribution (a, the blue line), growth rate comparison (b) between phytoplankton (the green line) and kelp (the brown line), and biomass nitrogen comparison (c).

concentration for phytoplankton ($K_{N_{\text{phyto}}}$) and $4 \mu\text{M}$ for kelp ($K_{N_{\text{kelp}}}$) [26]. The values set for phytoplankton and kelp assumed that phytoplankton could grow faster and have a higher nutrient affinity than kelp. According to previous studies, the values for kelp parameters are in a reasonable range [27]. The value of remineralization fraction ($\varphi = 0.5$) is based on DOM-POM (dissolved organic molecule-particulate organic molecule) partitioning rate of detritus originated from eukaryotic phytoplankton in a previous modeling study [28]. The application of this value assumes that DOM is remineralized within a short time period and POM sinks, thus exiting the surface ocean. As for the initial values, we set nutrient concentrations (nitrate) in water N_{nut} as $30 \mu\text{M}$, which is in the range of the observed data from a previous study [29]. And to compare kelp and phytoplankton, we used the same initial biological N values (N_i , $0.3 \mu\text{M}$) for them. All definitions and units of parameters are included in Table S1 in the supplementary.

3. Results and discussion

3.1. Distribution of nutrients, kelp, and phytoplankton

Our simulation results show nutrient (Fig. 3a), kelp, and phytoplankton (Fig. 3b and c) distribution from the coastal boundary to the open ocean. We assume that recently upwelled water from the deep has low phytoplankton biomass. In our results, as the distance from the boundary increases, the water column nutrient concentration decreases (Fig. 3a), and the growth rate (Fig. 3b) and biomass (Fig. 3c) of kelp decrease, which suggests that kelp should be abundant in higher-nutrient areas. As for phytoplankton, the growth rate (Fig. 3b) decreases with distance, and biomass (Fig. 3c) increases at first, then decreases, and the peak in biomass occurs between 10 to 100 km. This trend for phytoplankton biomass is due to the combination of nutrient distribution (Fig. 3a) and advection in the offshore direction. Near the coastal area, upwelling carries deep nutrient-rich water [30]. However, in these areas, the upwelling water has low phytoplankton biomass, and the offshore advection moves phytoplankton out of the direct competition with kelp. As the distance from the coast increases, phytoplankton can accumulate, forming a peak in biomass. After the peak, phytoplankton biomass and growth rate decrease because of the decrease in nutrient concentration.

3.2. Possible ecological niche of kelp

Compared to the phytoplankton, kelp's biomass (Fig. 3c) is higher near coastal areas. The result suggests that kelps are more abundant in these areas than phytoplankton. According to a previous data analysis study [31], the abundance of an organism at a site should be related to the position of the site in ecological niche space, and the highest abundance should correlate to the center of the niche (niche-distance abundance relationship, NDA) [32]. Based on our model results, coastal upwelling and offshore advection provide the niche space for kelp.

3.2.1. Anchoring is the main factor for kelp to acquire their niche

To examine how kelp compete with phytoplankton, we did another simulation where kelps were allowed to drift with phytoplankton in the advective flow (no anchoring of kelp) (Fig. 4). We found that with advection, kelps accumulate less biomass (Fig. 4c) than in an anchoring simulation (Fig. 3c). In this advection situation (Fig. 4), the trend in kelp growth (Fig. 4b) and biomass (Fig. 4c) is similar to that of phytoplankton, but the magnitude of these values is less than that of phytoplankton. This is because kelp's nutrient uptake is less efficient [14], and the growth of kelp is slower compared to that of phytoplankton. Thus, the advection simulation shows that kelp cannot outcompete phytoplankton because it is very difficult for them to accumulate biomass when they move with water currents.

The comparison between these two simulations suggests that anchoring is a key niche feature of kelp. Here, anchoring or not is the only difference between these two simulations. In the anchoring simulation (Fig. 3), kelp have more nitrogen-containing biomass near

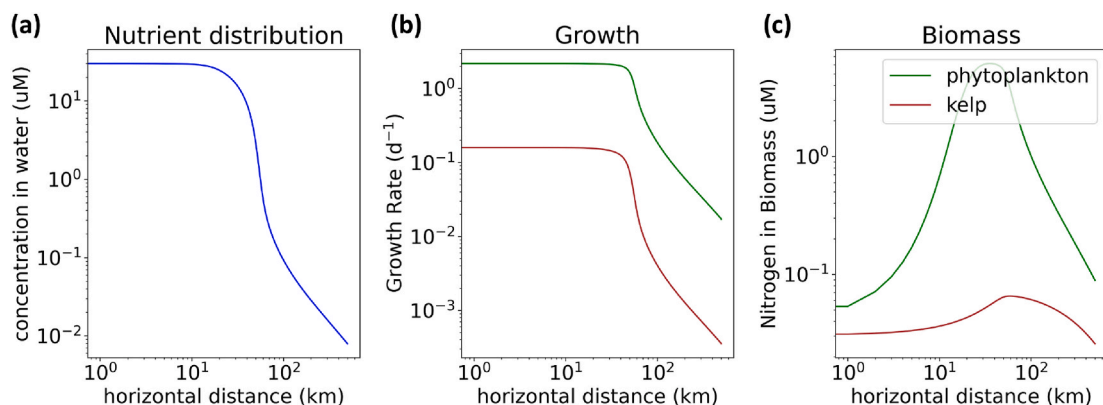


Fig. 4. Simulation results with kelp advection: nutrient distribution (a, the blue line), growth rate comparison (b) between phytoplankton (the green line) and kelp (the brown line), and biomass nitrogen comparison (c).

the coast compared to phytoplankton, whereas this is not the case for the advection simulation (Fig. 4b and c). Kelps stay near the coast and accumulate there for years and finally become foundation species [33] and form coastal kelp forest ecosystems to provide habitats [34].

3.2.2. Effect of water speed

Off-shore water moves the phytoplankton away from the shore, hindering the biomass accumulation of phytoplankton and promoting the advantage of kelp. In reality, water movement can change with global change as well as some abnormal conditions, such as El Niño and La Niña [35]. Under a slower water speed condition, observed phytoplankton biomass peaks occur near shore [36]. Here we simulate the water speed change (with kelp anchored to the seafloor) and discuss the value range in which it is insufficient for kelp's advantage.

In our simulation results, kelp's advantage can gradually be eliminated with the decrease in initial water speed (U_0). When U_0 is around 0.026 m/s, near-shore phytoplankton biomass equals kelp biomass. When U_0 exceeds this boundary value, kelp can outcompete phytoplankton (Fig. 3). When U_0 is smaller than 0.026 m/s, the phytoplankton can outcompete (Fig. 5b and c). In this slower water speed simulation (Fig. 5), nutrient concentration (Fig. 5a) and growth rate (Fig. 5b) changing trends are the same as in the above simulations. As for biomass (Fig. 5c), phytoplankton reaches the peak near shore, and it is always larger than kelp. These results show a potential pattern of how the competitive relationship changes with abnormal conditions.

3.2.3. Possible effect of El Niño and La Niña

El Niño and La Niña events are abnormal conditions in the Pacific Ocean, which can influence weather conditions, water temperature, and movement [37]. These larger ocean processes can influence the health and growth of kelp forests [35]. Previous researchers reported the effect of El Niño and La Niña in Point Loma. In the 1988–1989 La Niña period, the experimental kelp density increased dramatically, while in the 1993 El Niño period, the density was low [38]. Similarly, our simulated result (Figs. 3 and 5) may also provide a potential pattern of how ENSO (El Niño-Southern Oscillation, including El Niño and La Niña) events influence kelp. During the El Niño condition, the trade wind system in the Pacific can be decreased, and the upwelling near the eastern coast of the Pacific can also be weakened [39], which in our model, can be considered as the slower water movement condition (Fig. 5) and the abundance of kelp might decrease. While in La Niña conditions, the trade wind can be stronger, and the upwelling in the eastern Pacific can be stronger, which could lead to nutrient-rich and strong water movement conditions. In our model, we can consider La Niña conditions as the stronger water movement (Fig. 3) conditions and kelp abundance is higher. In this case, our model provides an explanation for the effect of ENSO on kelp forests.

3.2.4. The mechanism of how kelp acquire an ecological niche

Here we can come to a mechanism of how kelp acquire their ecological niche (Fig. 6) based on our simulated results. In upwelling oceans, nutrient concentration is higher near shore while lower in the open ocean. Kelp and phytoplankton co-exist but occupy different ecological niches (also called niche differentiation). Phytoplankton advect offshore with water movement and accumulate in lower nutrient areas. But for kelp, although they have a lower nutrient affinity, anchoring helps them remain in the near-shore high-nutrient areas, which can facilitate their nutrient uptake and enable them to reach a higher growth rate and accumulate biomass. As a result, kelp occupies the near-shore high-nutrient areas, while phytoplankton is more abundant in the lower-nutrient areas. Faster water speed can increase the differentiation, and slower water speed will decrease it.

3.2.5. Sensitivity test for other parameters

In our model, we considered several essential parameters related to the ocean environment and the physiology of kelp and phytoplankton, including initial water speed, initial nutrient concentrations, the remineralization fraction, maximum growth rates,

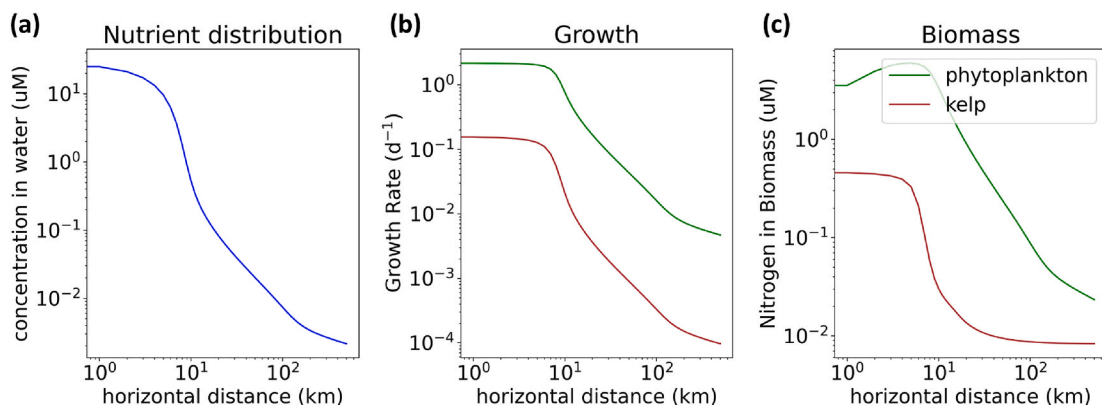


Fig. 5. Simulation results with slower water movement: nutrient distribution (a, the blue line), growth rate comparison (b) between phytoplankton (the green line) and kelp (the brown line), and biomass nitrogen comparison (c).

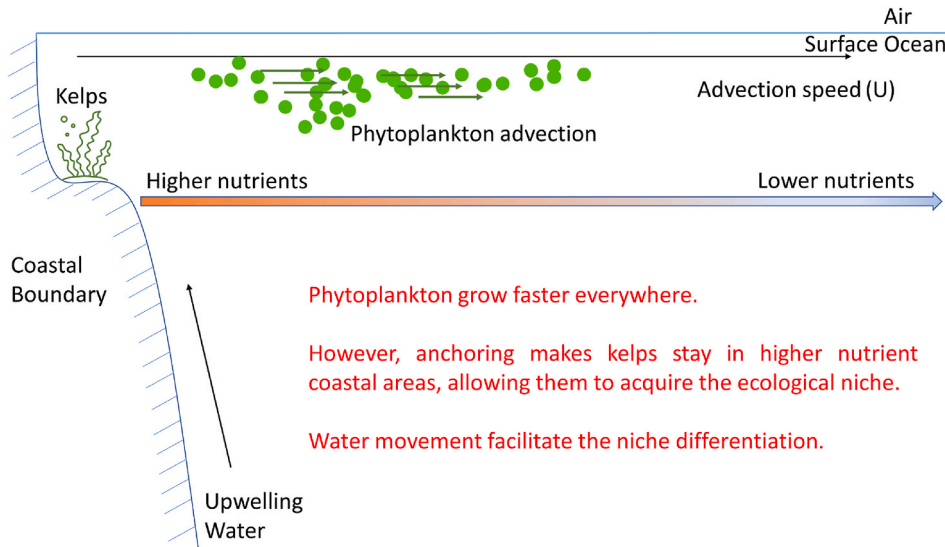


Fig. 6. The summary of how kelps acquire their niche. Black arrows mean water movement (upwelling and movement with the wind). The blue curve with slashes means the coastal boundary. Green dots mean phytoplankton. The dark green grass means kelp. Green arrows show how phytoplankton occupy low-nutrient areas.

half-saturation concentrations, mortality rates, and the amplitude of oscillation. We increased the values in these parameters by 10 %. We calculated the increased or decreased percentages of outputs, including total nutrients and total biomass of kelp and phytoplankton, from the boundary to 500 km in the open ocean. This sensitivity test method follows the approach used in a previous modeling study [40].

Fig. 7 shows that total nutrient concentration is more sensitive to initial nutrient concentrations ($N_{nut_initial}$), initial water speed (U_0), and maximum growth rate for phytoplankton (μ_{phyto}). $N_{nut_initial}$ and U_0 have positive effects since higher $N_{nut_initial}$ can directly increase the nutrient concentration, and higher U_0 can bring more nutrients with upwelling. In contrast, μ_{phyto} has a negative effect because faster growth of phytoplankton can cause more nutrient uptake and decrease nutrient concentration.

Total phytoplankton biomass is more sensitive to remineralization fractions (φ), initial water speed (U_0), and maximum growth rate for phytoplankton (μ_{phyto}). A 10 % increase of φ and U_0 , leads to an increase in phytoplankton biomass, while a 10 % increase of μ_{phyto} results in a decrease. This might be because higher φ can increase nutrients remineralized from dead kelp and phytoplankton, and higher U_0 can increase nutrient upwelling from the bottom water – both of which can facilitate the growth of the phytoplankton. In contrast, although an increased μ_{phyto} can increase the growth rate of phytoplankton at the beginning, by the end of the 1-year simulation, as the nutrient depletion becomes significant and phytoplankton biomass is lost with advection, the biomass of phytoplankton decreased.

Total kelp biomass is more sensitive to U_0 , μ_{phyto} , and maximum growth rate for kelp (μ_{kelp}). A 10 % increase in U_0 promotes

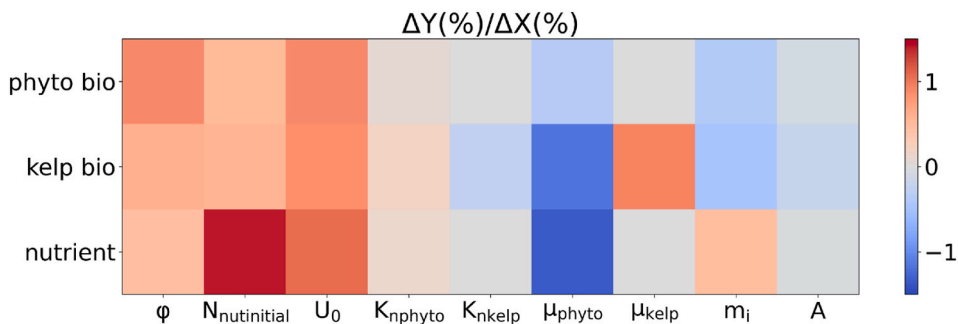


Fig. 7. Sensitivity test results for increased tested parameters (in X axis) by 10 %. Color mesh indicates the change in the model output (Y axis) based on a 10 % change in each parameter (X axis). The output in the Y axis includes total phytoplankton biomass (phyto bio), total kelp biomass (kelp bio), and total nutrient concentration from the boundary to the 500 km in the open ocean. X axis represents different tested parameters, including φ (remineralization fraction), $N_{nut_initial}$ (initial nutrient concentration), U_0 (initial water speed), K_{n_phyto} (half saturation concentration of N for phytoplankton), K_{n_kelp} (half saturation concentration for kelps), μ_{phyto} (maximum growth rate for phytoplankton), μ_{kelp} (maximum growth rate for kelp), m_i (mortality), A (the amplitude of oscillation). The color means $\Delta y (\%) / \Delta x (\%)$.

nutrient upwelling, which can support kelp growth and lead to an increase in total kelp biomass. Higher (μ_{kelp}) can facilitate the growth of kelp. Although it will also decrease nutrient concentration, kelp has a low turnover rate and can accumulate in the anchored area, resulting in an increase in total kelp biomass. With a 10 % increase of μ_{phyto} , biomass significantly decreases. Since μ_{phyto} has the largest negative effect on kelp biomass, indicating that the competition between kelp and phytoplankton is important to be considered

In conclusion, the different parameters we mentioned above can have various influences on different outputs. Water speed and maximum phytoplankton growth rate can have a relatively obvious impact on all three outputs. Figs. S1–S5 shows that the variation of all the relatively sensitive parameters we include here won't influence the distribution patterns of kelp and phytoplankton, which means that our conclusion from this study is robust.

4. Comparison to previous studies

4.1. Distribution of kelp

Kelp forests are distributed in upwelling regions of the coastal ocean, particularly in shallow, rocky subtidal zones [41]. According to some previous modeling studies, their abundance decreases with distance from the coast. Depth, temperature, and nutrients can all influence their distribution [42]. In addition, Young et al., 2016 [43] found that the biomass of kelp in the patch has a positive relationship with kelp's persistence, which is consistent with our study. We found that the accumulation of biomass in the kelp community could facilitate the kelp to acquire their niche, which is based on the anchoring of kelp. Satellite-based analyses by Wanner et al. [44] reported that the giant kelp populations fluctuated near shore and their dispersal affected by wave disturbance.

4.2. Distributions of phytoplankton

As for phytoplankton, in a previous observation near the Oregon coast, researchers found that the abundances of small-sized phytoplankton, and especially of coccoid cyanobacteria, were low in high-nutrient, high-chlorophyll shelf waters, which are consistent with our modeling results under the kelp anchoring condition, near the boundary, where the biomass of phytoplankton is lower with higher nutrient concentrations [45]. In another study [46], researchers reported that near-shore phytoplankton concentrations varied with mesoscale nearshore hydrographic conditions, including processes related to currents and winds. The inconsistent results might be due to our model's simplification: we didn't consider the vertical structures or the light availability (we just considered the surface and the light is abundant). We need to consider more complex processes.

4.3. Relationships between kelp and phytoplankton

Based on the hypothesized competition between phytoplankton and kelp, some studies have considered them as two important biological factors within models [8]. Previous studies have also reported the influence of phytoplankton blooms on kelps and the potential benefits of kelp cultivation on controlling harmful algae blooms [47]. In a recent study of aquaculture, researchers found that the bloom of dinoflagellates could notably damage kelp cultivation, as indicated by experimental and satellite data [48], which is consistent with our observed competitive patterns between kelp and phytoplankton. Similarly, in Northern Ireland, a data-based modeling study [49] also found that the increase of phytoplankton could decrease the productivity of kelp farming. However, in addition to competition, researchers found that kelp and phytoplankton may have a synergistic bioremediation effect on oyster farming [50]. More environmental factors were also considered when studying competitive patterns. For example, in Chen et al., 2024 [51], researchers mentioned that additional nutrients limit kelp growth in the ocean, which would likely reduce kelp primary production and increase competition between kelp and phytoplankton. Additionally, based on global kelp data, a recent modeling study has developed a tool to explore kelp's niche [52]. There, they also considered nitrate concentration, water movement, and wind speed as important environmental factors, just as our model does. So far, most previous studies have focused more on the competition phenomenon than the factors that promote co-existence in coastal areas. Compared with these previous studies, our simulation results highlight the importance of advection and explain niche differentiation of kelp and phytoplankton.

5. Limitations and future directions

5.1. Other biotic factors

In our model, we considered a normal condition: water movement speed is seasonal, and kelp mortality is stable. However, many studies have reported that with global change, the mortality of kelp has increased because they are sensitive to abiotic factors [53]. Kelp can be very easily influenced by abnormal conditions such as extreme flooding and reduced salinity [54]. In addition, kelp distribution is also influenced by grazers, predominantly sea urchins [55]. Sea urchins can, under certain circumstances, form “destructive grazing fronts” and remove all kelps from an area from 10s of meters to 1000s of kilometers [56]. Future approaches might include ‘patchy’ grazing impacts, for example, since sea urchins are the primary grazers of kelp. If we increase the abundance of sea urchins in the kelp patch, the kelp abundance will decrease, and their distribution pattern will shift. Due to grazing impact, the competition pattern of kelp and phytoplankton may also change. In the future, it will be essential to explore questions such as: How does sea urchin grazing promote the dominance of phytoplankton? How does the sea urchin grazing influence the persistence and

recovery of kelp beds?

5.2. Abiotic factors

In this model, we didn't consider additional environmental drivers related to global change, which can be incorporated into this model framework to enhance predictability. For example, under global warming, thermal stress can eventually lead to mortality and consequent population-level effects in kelp forests, including decreased abundance, altered size structure, local extirpation, and range contractions [57]. The distribution pattern of kelp forests might shift towards the poles. Besides, marine heat waves, which have been reported to enhance the competitive advantages of harmful algal blooms against kelp [58], could also be considered in the future for the prediction of competition patterns. Increasing the pH will decrease the concentration of carbonate or bicarbonate in the water and also influence enzyme activities inside kelp [59] and phytoplankton [60]. Light could influence the photosynthesis processes of kelp and phytoplankton. In the future, to make this model more accurate, both biotic and abiotic effects we mentioned above could be incorporated, including grazing pressure, light, temperature, and pH. If we need to use this model locally, detailed physical ocean data and processes, including eddies and tides and local fishery background, could also be considered to make this model more applicable in some specific areas.

As a spatial and temporal dynamic model, our model can be widely used in upwelling kelp forest regions to predict their distribution and dynamics. The parameters used in our model will likely need to be changed to match the local physiologies of kelp and phytoplankton across different kelp forest regions of the global ocean. Since our simulation results could be related to ENSO, our model can be a reference for future climate change effects on kelp.

6. Conclusion

Our coastal ecological model simulation in upwelling areas uncovers an important aspect of the ecological niche of kelps. By predicting the dynamics of kelp and phytoplankton growth as well as their distribution, we found that near the coastal area, kelp can accumulate larger biomass than phytoplankton. This is because they anchor and do not directly compete with the phytoplankton for nutrients. Kelps are able to acquire nutrients and accumulate biomass in a fixed site for years to form kelp forests. And slower water speed can eliminate kelp's advantage, which may explain the effect of ENSO. Our study simulates the ecological niche differentiation of kelp and phytoplankton, highlighting the strength of kelp near the coastal area. Our study can be a reference for future in situ measurements. By including basic processes and obtaining reasonable results, it can also become the basis for future coastal models.

CRedit authorship contribution statement

Meng Gao: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Resources, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Allen J. Milligan:** Writing – review & editing, Writing – original draft, Validation, Resources, Methodology, Investigation, Conceptualization. **Curtis Deutsch:** Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Resources, Methodology, Investigation, Data curation, Conceptualization. **Keisuke Inomura:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.heliyon.2026.e44523>.

Data availability

We used Python 3.8 to simulate our model. The datasets generated and/or analyzed during the current study are available in the [Kelp vs phytoplankton] repository, [<https://doi.org/10.5281/zenodo.8062161>].

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