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Dissolved Oxygen-And Temperature-Dependent Simulation of the Population Dynamics of Moon Jellyfish (*Aurelia coerulea*) Polyps

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Abstract: As the extent of hypoxia in coastal waters increases, the survivorship of jellyfish polyps relative to that of competing sessile organisms often increases, enabling them to reproduce more prolifically, leading to a medusa bloom in the following year. Quantifying the population of polyps can be used to predict when these blooms will occur. We used a time-delayed logistic equation to quantify the response to variable dissolved oxygen (DO) concentrations and temperatures in a population of moon jellyfish (*Aurelia coerulea*) polyps on substrates that carried competing sessile organisms. The availability of substrate depends on the DO threshold for each competitor, and substrates only become available to the polyps during hypoxic periods. We used the median sublethal concentration (SLC_{50}) thresholds of hypoxia for different groups of benthic organisms to calculate the DO-dependent survivorship of *A. coerulea* polyps competing on the substrate. Since the median lethal time (LT_{50}) for cnidarians is close to 240 h, we chose a 10-day delay in the time-delayed logistic equation. The carrying capacity is determined every 10 days depending on DO concentrations and temperature. The polyps reproduce by budding at a temperature-dependent rate after settling on the substrate during the hypoxic period, and thus, the annual polyp reproduction rate is determined by multiplying the temperature-dependent budding rate by the DO-dependent survivorship. The duration of hypoxia is a key factor determining the polyp population, which can increase more as the duration of hypoxia increases. Modeling simulations were compared to observed data. In this model, the DO and temperature distribution data make it possible to quantify variations in the population of the *A. coerulea* polyps, which can be used to predict the abundance and appearance of medusa the following year.

Keywords: *Aurelia coerulea* polyp; dissolved oxygen; temperature; hypoxia; logistic equation

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1. Introduction

Hypoxia in coastal waters is expected to increase because of eutrophication, climate change, stratification pattern change, and oxygen solubility [1,2]. According to many reports, both the intensity and duration of hypoxia are increasing [3,4], while the number of coastal sites where hypoxia has been reported has increased exponentially at 5.54% per year [5].

Hypoxia profoundly affects the abundance and distribution of marine species in coastal waters [6–8]. The reduced growth and increased mortality of mussels caused by hypoxia has implications at the ecosystem level because of their functions of water column filtration and benthic–pelagic coupling [6]. In coastal systems, vertical and horizontal distributions of organisms follow oxygen gradients and discontinuities, and migratory behavior is constrained in response to oxygen availability [8]. During hypoxic periods, organisms such as cnidarians that have a high tolerance for low dissolved oxygen (DO) concentrations dominate the substrate [5].

Hypoxia usually begins at a DO concentration ≤ 2 mg O_2 L^{-1} [9]; however, the criteria for classifying the responses of DO-dependent ecosystems as hypoxic are somewhat ambiguous. There are some ecosystem-related DO thresholds, such as the median lethal time (LT_{50}), which represents the time interval at which 50% of a given population dies after exposure to low DO levels, and the median sublethal concentration (SLC_{50}), which represents the O_2 concentration at which 50% of the organisms in a given population exhibit sublethal responses, such as forced migration and reduced presence in otherwise suitable habitat [5].

The hypoxia tolerance threshold is species- and stage-specific and may have a significant effect on both benthic and pelagic species at both individual and population levels [5,10]. Jellyfish polyps can survive and even reproduce exponentially under hypoxic conditions [11]. Different species cannot coexist if they have identical niches, because the species that is a better competitor will always exclude its competition from the area [12].

During hypoxic seasons, moon jellyfish (*Aurelia coerulea*) polyps can be excellent competitors against other sessiles with lower SLC_{50}. However, during other seasons and under normal DO conditions, organisms with a higher competitive hierarchy appear on the substrate [13,14]. In these circumstances, although the polyps are able to reproduce by budding, they do not have sufficient space on the substrate to do so because of the presence of many other high-level competitors.

After settling on the substrate, polyps reproduce asexually at a rate that depends on the temperature, yielding more polyps at higher average sea surface temperatures SSTs in the coastal zone, which have been increasing globally [15,16] by approximately 0.13 °C per decade over the past 100 years [17].

DO concentrations and water temperature are the key conditions for the survivorship and reproduction of jellyfish polyps competing on coastal substrates [11,18]. In hypoxic coastal waters where food is sufficient, such as in eutrophic areas, the population of *A. coerulea* polyps increases under ambient temperatures. With prolonged periods of hypoxia, the survivorship of *A. coerulea* polyps increases and polyps reproduce more prolifically, leading to a medusa bloom in the following year [19,20].

The annual distributions of DO and temperature were used to establish an equation to simulate population variations of polyps in competing substrates. This model can be used to quantify the population of polyps and predict the time when medusa will occur in the following year. We suggest a model that describes the polyp population dynamics on a substrate in competition with other sessile organisms depending on the dissolved oxygen (DO) concentration and temperature. The model was applied to the polyp experiment in Tokyo Bay, Japan, 2001, where the DO data were available from field observations [13]. The temperature-dependent population growth rate was approximated from laboratory experimental data [21].

2. Methods

The present polyp population, $x(t)$, depends on the population before τ time, $x(t - \tau)$, which influence of the population on the carrying capacity requires time in order to create additional survivorship depending on environmental conditions [22]. The carrying capacity is determined every delay time depending on DO concentrations and temperature. Since the LT_{50} of cnidarians is in the range of 232 ± 114 h [5] we used a 10-day delay time in the dynamic equation. The Equation (1) gives 10-day unit variation of the population of *A. coerulea* polyps with DO and temperature.

To express the rapid change of survivorship at near hypoxia conditions we used a sigmoid function with an inflection point at hypoxic DO concentrations, which generates the DO-dependent survivorship value of *A. coerulea* polyps. This was constructed using the SLC_{50} data of mollusks and cnidarians from Vaquer-Sunyer and Duarte [5].

2.1. Model

We used a dimensionless, time-delayed, logistic equation with a time-dependent carrying capacity, expressed as,

$$x'(t) \;=\; x(t) - \frac{x^2(t)}{y(x)} \tag{1}$$

where $x(t)$ represents the normalized polyp population unit [22,23]. The effective carrying capacity $y(x)$ depends on the population at an earlier time, τ,

$$y(x) = y(x(t-\tau)) = \alpha + \gamma(O_2, T, t-\tau)\, x(t-\tau)$$

The constant α represents the dimensionless basic carrying capacity, whereas $\gamma(O_2, T, t-\tau)$ represents the reproduction rate dependent on dissolved oxygen and temperature at an earlier time,

$$\gamma(O_2, T, t-\tau) = \;\beta(t-\tau)\times\, h(t-\tau),$$

where $\beta(t)$ represents the annual survivorship depending on DO and h(t) represents the annual reproduction rate depending on temperature.

The carrying capacity over the time interval, $0 \le t < \tau$,

$$y(x(t\;=0)) = \alpha + \gamma(O_2, T, t\;=0)\; x(t\;=0)$$

Thus, the present carrying capacity depends on the environmental condition of the substrate and the population of polyps at time $t = 0$.

By denoting

$$x(t\;=0) = x_0$$

and

$$y(x(t\;=0)) = \;y_0 = \alpha + \gamma(O_2, T, t\;=0)x_0,$$

the solution for Equation (1) is

$$x(t) = \frac{x_0 y_0 e^t}{y_0 + x_0(e^t - 1)}.$$

This equation gives the population size of *A. coerulea* polyps over the time intervals, $0 \le t < \tau, \tau \le t < 2\tau, \ldots, (n-1)\tau \le t < n\tau$. The parameters used for the simulations of the population dynamics are summarized in Table 1.

Table 1. Summary of the parameters used in the construction of a model of the population dynamics of *Aurelia coerulea* polyps.

Parameter	**Definition**	**Comments**
α	Basic carrying capacity	Dimensionless unit. Set to one unit
$\beta(O_2)$	Survivorship depending on DO	Values closer to 1 represent better conditions for polyps
$\beta(t)$	Annual DO dependent survivorship	Annual survivorship $0 < \beta(t) < 1$
$h(T)$	Reproduction rate depending on temperature	Assuming food and other conditions are satisfied.
h(t)	Annual temperature-dependent reproduction rate	Assuming food and other conditions are satisfied

Table 1. *Cont.*

Parameter	Definition	Comments
$\gamma(O_2, T, t)$	Reproduction rate depending on DO, temperature, and time	Annual reproduction rate $\gamma(O_2, T, t) = \beta(t) * h(t)$
$y(x(t-\tau))$	Effective carrying capacity	Carrying capacity depending on the population at time $t - \tau$
y_0	Effective carrying capacity	Constant carrying capacity over the time intervals
τ	Time delay	Feedback time, set to 10 days
$x(t)$	Normalized population	Normalized polyp population unit
$x_0 = x(t-\tau)$	Polyp population for $t < \tau$	Polyp population size before feedback [1] to the present

[1] feedback: the effect of dissolved oxygen and temperature on the surrounding waters.

2.2. Algorithm

1. The initial polyp population size x_0 was set to one unit;
2. The basic carrying capacity α was set to one unit;
3. The DO-dependent survivorship of the polyps was estimated through the sigmoid function: $\beta(O_2)$;
4. The annual survivorship curve, $\beta(t)$, was constructed;
5. The temperature-dependent reproduction rate was estimated through the interpolating function: $h(T)$. It is constructed by fitting a curve to the experimental data;
6. The annual reproduction rate curve, $h(t)$, was constructed;
7. The annual reproduction rate polyp was calculated: $\gamma(O_2, T, t) = \beta(t) \times h(t)$;
8. The population units of polyps over a 1-year period were evaluated using a delay dynamic Equation (1).

2.3. Dissolved Oxygen-Dependent Polyp Survivorship

In the inner Tokyo Bay, the dominant sessile organisms that are found when the DO is above 2 mg O_2 L^{-1} are mollusks, such as *Mytilus galloprovincialis*, *Crassostrea gigas*, *Perna viridis*, and *Xenostrobus securis*, and crustacean barnacles [13]. In summer, when the bottom waters reach DO concentrations below 2 mg O_2 L^{-1}, many empty spaces become available on the substrate. This enables the scyphozoan *A. coerulea* polyps to take over the empty substrate. The population of *A. coerulea* polyps can increase by reproduction at these low DO levels. Survivorship ranges between $0 \leq \beta(O_2) \leq 1$. As the value approaches 1, the *A. coerulea* polyps become dominant, while for values close to 0, the polyps become hard to find.

To simulate the population of *A. coerulea* polyps, survivorship on the substrate was generated using the SLC_{50} criteria. Since the SLC_{50} of crustaceans is relatively high (Table 2), other benthic organisms were not commonly found on the substrate when the DO level was lower than 2 mg O_2 L^{-1}. Focusing on two species of mollusks and cnidarians, we set up the survivorship of the *A. coerulea* polyps as 0.1 for the 90th percentile of mollusk SLC_{50}, which meant that when 90% of mollusks reside on the substrate, only 10% was available for *A. coerulea* polyps. At 1.99 mg O_2 L^{-1}, 50% of the mollusks move to other places, giving the polyps a 50% chance of surviving. At 0.91 mg O_2 L^{-1}, the survivorship was set up as 0.9 when we referred to the 90th percentile of cnidarians, while at 0.6 mg O_2 L^{-1}, it was set up as 0.95 at the 95th percentile by assuming the SLC_{50} of cnidarians followed a normal distribution. Table 3 shows the resulting value of $\beta(O_2)$ for various DO concentrations.

Table 2. Median sublethal concentrations (SLC_{50}, mg O_2 L^{-1}) and the 90th percentile thresholds for hypoxia in Crustacea, Mollusca, and Cnidaria provided by Vaquer-Sunyer and Duarte [5].

Organisms	**SLC_{50} (mean ± S.E.) (mg O_2 L^{-1})**	**N**	**90th Percentile**	**Standard Deviation**
Crustaceans	3.21 ± 0.28	30	5.0	1.53
Mollusks	1.99 ± 0.16	28	2.83	0.85
Cnidarians	0.69 ± 0.11	19	1.43	0.48

S.E.: standard error of the mean, N: number of observations.

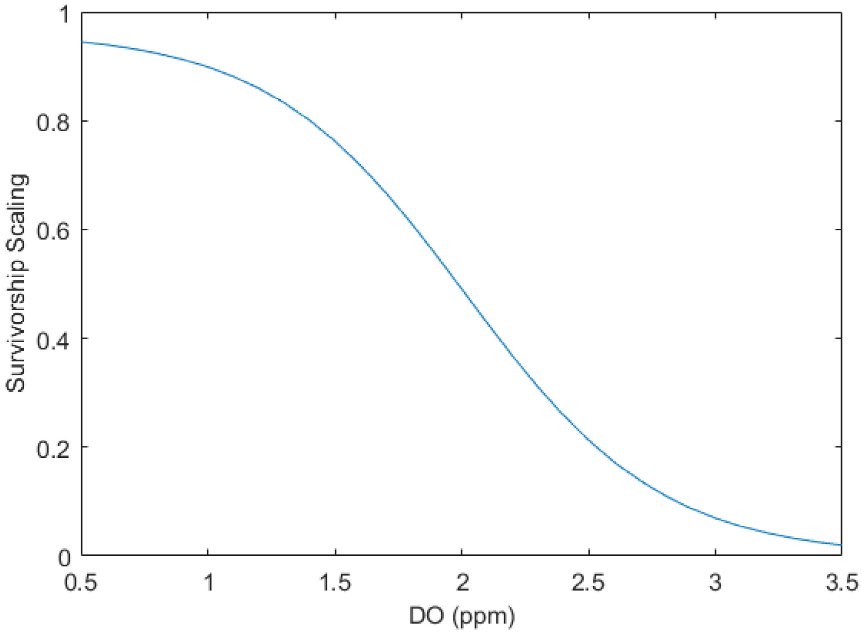
Table 3. Survivorship $\beta(O_2)$ of *Aurelia coerulea* polyps at different dissolved oxygen concentrations; estimated using the median sublethal concentration (SLC_{50}) of mollusks, which would competitively occupy the substrate that would otherwise be available to cnidarians.

O_2 Concentration (mg O_2 L^{-1})	**2.83**	**1.99**	**0.91**	**0.60**
$\beta(O_2)$	0.10	0.50	0.90	0.95

The sigmoid function was constructed by curve fitting the data in Table 3, which generates the survivorship. Figure 1a shows the DO-dependent survivorship curve:

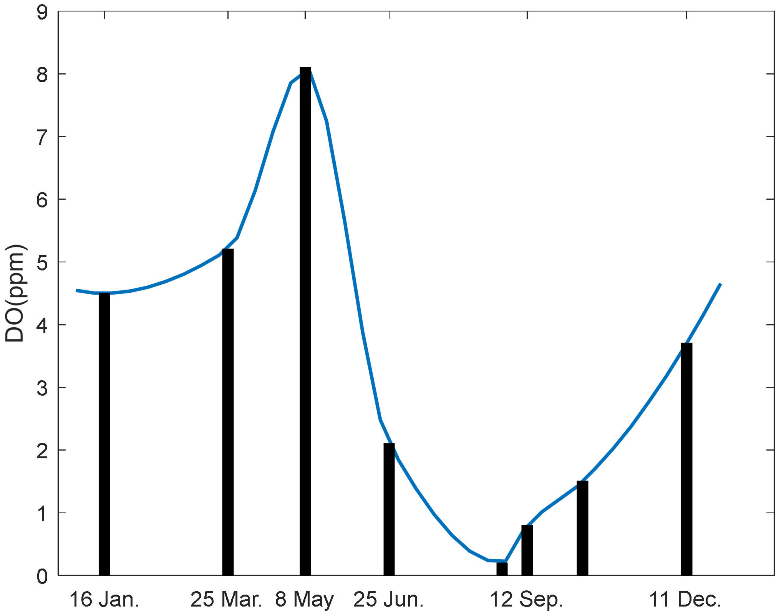
$$\beta(O_2) = \frac{1}{1 + e^{(2.118 \times O_2 - 4.215)}}, \tag{2}$$

where O_2 represents the concentration of dissolved oxygen.



(**a**)

Figure 1. *Cont.*



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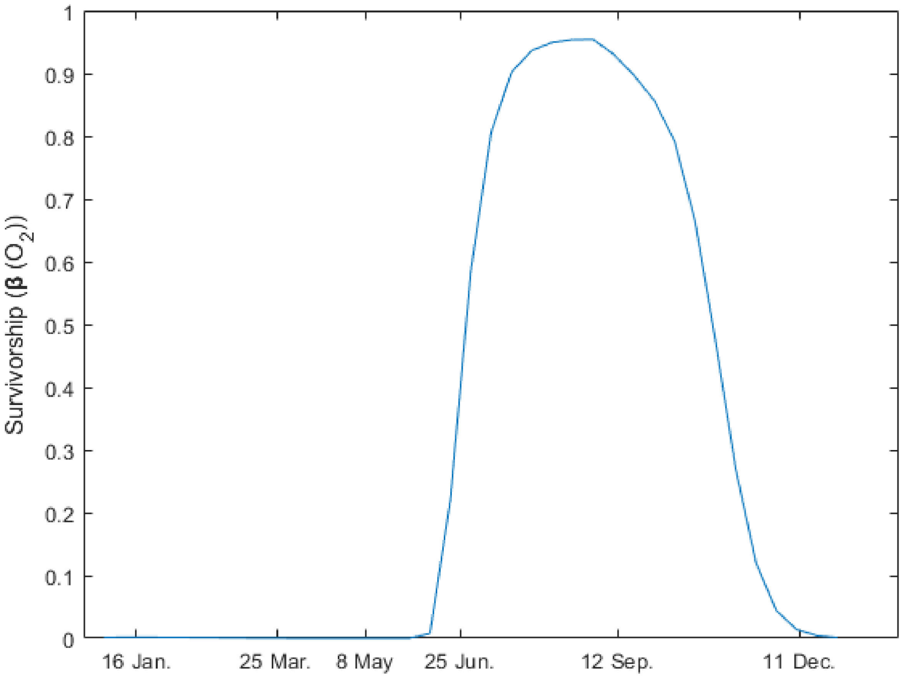

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Figure 1. (**a**) Survivorship generating function, $\beta(O_2)$, of *Aurelia coerulea* polyps; (**b**) dissolved oxygen concentrations observed at Tokyo Inner Bay in 2001 at 4 m depth [bar] [13] and the interpolated curve; (**c**) the annual survivorship curve, $\beta(t)$, constructed by inserting the DO data into the survivorship generating function.

The inflection point appeared near 2 mg O_2 L^{-1}, where the survivorship was 0.5 (Figure 1b). The survivorship increased up to 0.9 near 0.91 mg O_2 L^{-1} and decreased to 0.1 near 2.83 mg O_2 L^{-1}.

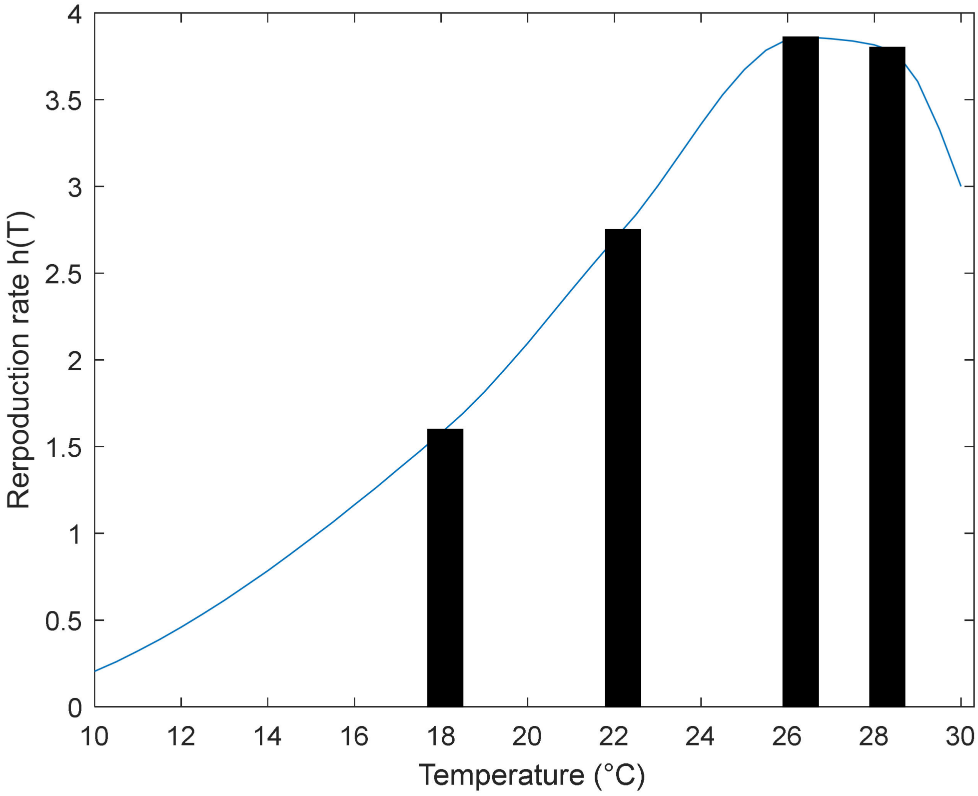
It was used to estimate the DO-dependent survivorship of the polyps. The annual DO-dependent survivorship curve, $\beta(t)$ (Figure 1c), was calculated by inserting the annual DO data (Figure 1b) into Equation (2).

2.4. Temperature-Dependent Polyp Reproduction Rate

The hypoxic period began near mid-June and ended near mid-October (Figure 1b). During this period, the polyp survivorship increased rapidly (Figure 1c). During the hypoxic period, the polyps had a high chance of residing on the substrate and reproducing asexually by budding. The reproduction rate mainly depended on temperature.

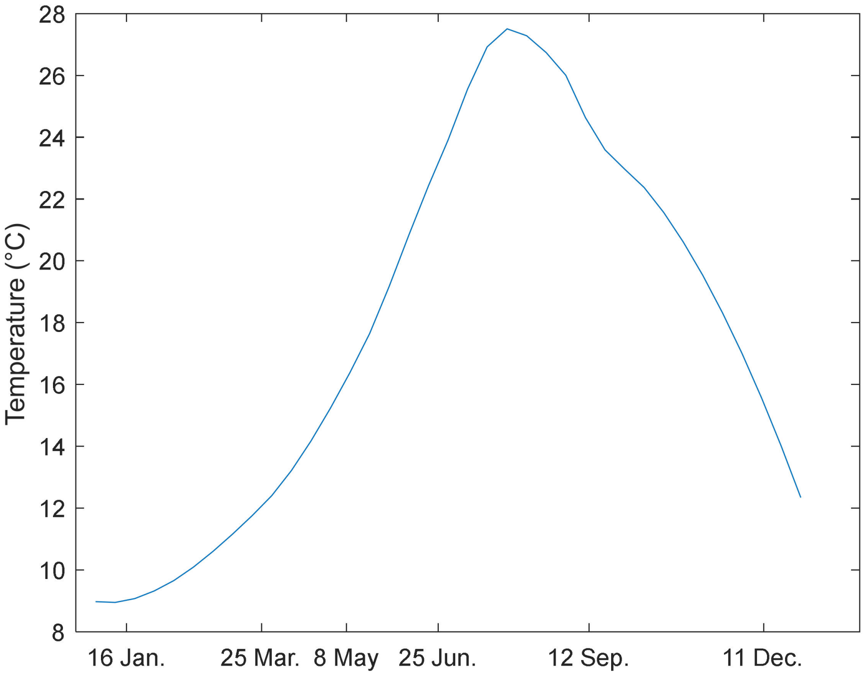
The temperature-dependent reproduction rate of polyps, $h(T)$ in Figure 2a, was constructed by fitting a curve to the experimental data from Han and Uye [21]. The data were rescaled to 365 days after adding the number of directly budded and stolonic budded polyps. Then the annual reproduction rate, $h(t)$, was calculated by inserting the annual temperature data to h(T).

Figure 2b shows the annual temperature in Tokyo Bay in 2011 [13]. The annual reproduction rate showed that, during the hypoxic period from mid-June to mid-October, the annual reproduction rate was more than 200% after adding the number of directly budded and stolonic budded polyps, with values close to 400% in July and August (Figure 2c).



(**a**)

Figure 2. *Cont.*



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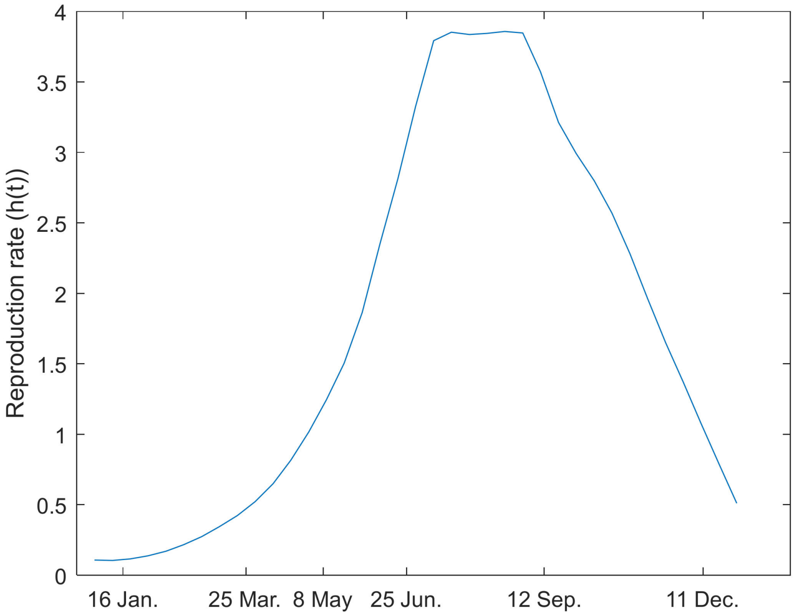

(**c**)

Figure 2. (**a**) Temperature-dependent annual reproduction rate year, $\mathrm{h}(\mathrm{T})$, constructed by fitting the curve to the data [bar] [21] which are rescaled to 365 days after adding the number of directly budded and stolonic budded polyps in the experiment of Han and Uye [21]; (**b**) annual temperature in Tokyo Bay, 2011 [13]; (**c**) annual reproduction rate, $\mathrm{h}(\mathrm{t})$, constructed by inserting the annual temperature distribution to $\mathrm{h}(\mathrm{T})$.

3. Results

Figure 3b shows the population of polyps over a 1-year period calculated using Equation (1), which was similar to the observed data of Ishii and Katsukosh [13] in Figure 3a.

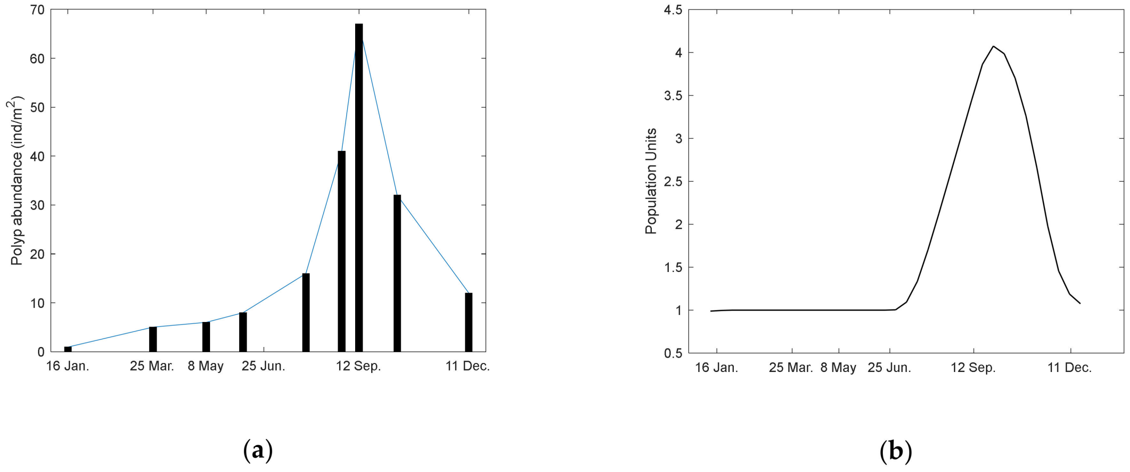

Figure 3. (**a**) Observed *Aurelia coerulea* polyp abundance [bar] [13] and the interpolated curve. (**b**) simulated polyp population.

We modified the data to simulate the population size when hypoxia duration was changed. The modified distribution is the solid line in Figure 4a, in which hypoxia occurs 1 month earlier and lasts longer. The population started to grow 1 month earlier and became much larger (solid line in Figure 4b).

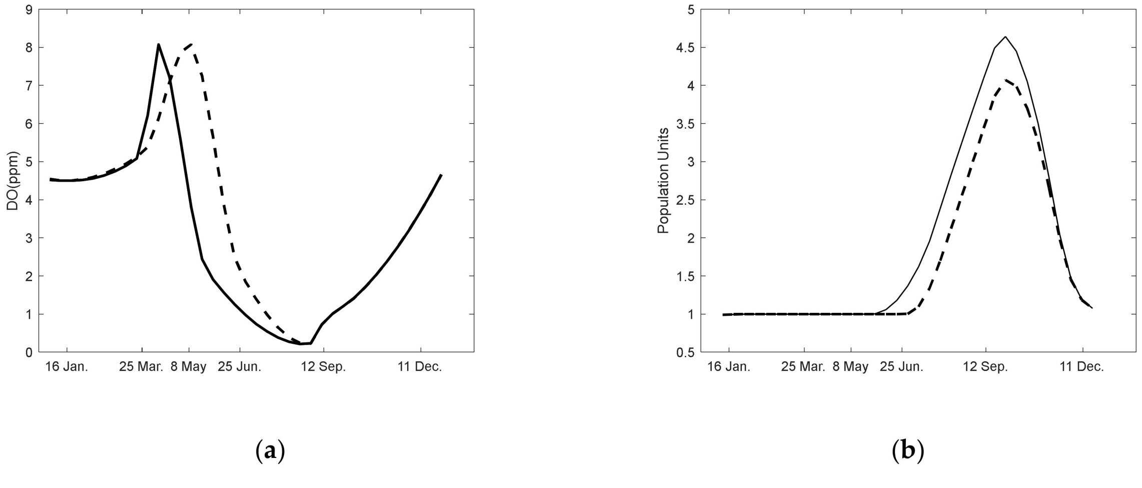

Figure 4. (**a**) Modified dissolved oxygen (DO) distribution to simulate hypoxia occurring one month earlier and for longer (solid line). (**b**) The population of *Aurelia coerulea* polyps for two cases of annual DO distributions. The solid line represents the simulated polyp population. If the hypoxia occurs earlier and lasts longer the population starts to grow earlier and becomes larger.

4. Discussion

We constructed a mathematical model to quantify the variation in the population of *A. coerulea* polyps on substrates on which they compete with other sessile organisms in terms of DO and temperature distribution. This model can be used to predict the abundance and appearance dates of *A. coerulea* in the following season. The model can be extended easily to include various environmental parameters.

4.1. Survivorship of Polyps Depends on the Thresholds of Hypoxia

Hypoxia is a key parameter to diagnose the marine ecosystem balance. Based on the observed data of Ishii and Katsukosh [13], the *A. coerulea* polyps were not commonly found on the substrate at a DO concentration of 4 mg O_2 L^{-1}, as they were inferior competitors compared to sessile organisms such as *M. galloprovincialis*. During a hypoxic period, *A. coerulea* polyps have a more distinct niche in the habitat in competition with other sessile organisms. When DO concentrations are close to 2 mg O_2 L^{-1}, usually referred to as hypoxia, many competing sessile organisms leave their habitat [5], which allows the *A. coerulea* polyps to remain and expand on the substrate through budding. Hypoxia in coastal waters can directly affect the survivorship of benthic organisms by inducing the formation of sublethal stress, leading to reduced growth and reproduction, forced migration, reduction of suitable habitats, and disruption of life cycles [1,24]. To quantify this sublethal stress, the median sublethal concentration, denoted by SLC_{50}, is used as the reference, which means that 50% of the species experience sublethal stress levels. Cnidarians such as *A. coerulea* have a low SLC_{50}, so their survivorship is very high in hypoxic waters, enabling them to be one of the best competitors. Hence, the DO concentration is a key factor for polyps to settle on substrates.

4.2. Effects of Hypoxia Appears Some Time Later

With extension of the hypoxic period, the ecosystem is expected to be more disturbed, species by species, depending on the tolerance of hypoxia [5]. The DO concentration can change in a matter of minutes and varies with seasons [25]. We used a 10-day delay time of the cnidarians' LT_{50}, which is in the range of 232 ± 114 h [5]. However, more precise data of the LT_{50} for the *A. coerulea* polyp and its competitors on the substrate are needed to simulate this more accurately.

4.3. Reproduction Until the Recovery of Normoxia

Recovery may follow hysteresis paths. After the DO levels recovered, the benthos did not fully recolonize the substrate for two months [26]. Hence, transient recovery process from DO changes cannot affect the growth of a polyp population. The population of *A. coerulea* polyps can be further increased by extending the duration of hypoxia. Therefore, the length of the hypoxic period is another major factor for estimating the population size of *A. coerulea* polyps.

4.4. Other Factors to Account for the Population of Polyps

In addition to the DO and temperature information, various environmental factors can be included in the model, but substrate preference is not considered in this model. It is necessary to consider new recruitments to estimate the population of polyps in a year. The effects of food are not counted. We focused on the substrate competition of *A. coerulea* against other species.

5. Conclusions

Variations in polyp populations have been quantified as a function of DO concentration and temperature. We constructed a substrate competition model describing the population variation of *A. coerulea* polyps depending on the DO concentration and temperature. This model is mainly based on the relative thresholds of hypoxia for benthic organisms.

The duration of hypoxia is a key factor determining polyp survivorship and population of *A. coerulea* polyps, which can increase more as the duration of hypoxia increases. After hypoxia has reached a level that is conducive to the polyps being dominant on the substrate, we estimated the population of polyps in terms of budding rate, which depends on the temperature.

With a 10-day delay time we were able to indicate that the environmental impact on polyp survival appeared after 10 days. We simulated 10-day unit variation of the population of *A. coerulea* with DO and temperature. The simulated population distributions of polyps were very close to the actual observed data. The dissolved oxygen and temperature distribution data made it possible to quantify the population variation of the *A. coerulea* polyps during the year.

This model can be easily extended to include various environmental parameters. If the population of some species changes due to environmental conditions, the carrying capacity can be increased or decreased, which has a delayed effect on the population at some later timer. This method can be also applied to population changes of many species due to environmental changes.

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