Simulating Marine Life Survival Under Climate-Induced Environmental Stress : An Agent-Based Modeling Approach

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Abstract*—In the current era, marine ecosystems are facing major threats from climate change, this includes rising in temperature, ocean acidification, and deoxygenation. Understanding how these threats affect marine life is crucial for survival and preservation of it. This paper introduces an agent-based model that simulates the marine ecosystem dynamics under various climate scenarios. Our model incorporates three trophic levels: phytoplankton (primary producers), zooplankton (primary consumers), and fish (secondary consumers), each with their own physiological responses to environmental stressors. Our model tracks and simulates population dynamics, spatial distribution, and ecosystem health in three different environments, stable, gradual, and extreme conditions. Result shows that population of fish are vulnerable to environmental stress, with the potential of extinction between 50 and 200 simulation timesteps. The model shows that even moderate environmental changes can lead to major ecosystem collapses. Our results give clear insights into how resilient marine ecosystems are and can help guide climate adaptation efforts.

***Keywords*—agent-based modeling, marine ecosystems, climate change, environmental stress, population dynamics**

I. Introduction

Climate change presents significant threats to marine biodiversity. The primary stressors impacting marine ecosystems include rising sea surface temperatures, ocean acidification due to decreasing pH levels, and reduced oxygen concentrations (deoxygenation) [1]. Although these environmental changes may appear small, they significantly challenge the adaptive capacity of marine organisms [2].

The structure of marine food webs makes them highly susceptible to environmental disturbances. Phytoplankton, as primary producers, support zooplankton, which in turn sustains fish and higher-level consumers [3]. Disruptions at any trophic level can propagate through the ecosystem, potentially resulting in population declines and biodiversity loss [4].

Most aquatic model systems traditionally assume closed environments and lack spatial structure, often relying on mean-field approximations for environmental variables. This contrasts with field experiments that incorporate spatial heterogeneity and open-system dynamics [5]. Agent-based modeling (ABM) provides an effective alternative by representing individual organisms as autonomous agents that follow specific behavioral rules, allowing system-level patterns to emerge from their interactions [6].

Recent applications of agent-based modeling (ABM) in marine ecology have shown its effectiveness in simulating fish responses [7], predator–prey interactions [8], and habitat selection [9]. However, few studies have combined multiple environmental stressors with multi-trophic ecosystem dynamics to evaluate the impacts of climate change on marine biodiversity.

This study investigates a central ecological question: *How do climate-related environmental stressors affect the stability of marine ecosystems and the survival of species across multiple trophic levels?* The primary contributions of this work are outlined as follows:

- Development of an agent-based model that includes three trophic levels, each with physiological mechanisms that respond to environmental stress.
- The incorporation of multiple climate-induced stressors, namely ocean temperature, acidity (pH), and deoxygenation by taking into account spatial distribution of organisms and environmental variables in the ecosystem.
- Quantitative analysis of ecosystem resilience under various climate change scenarios.
- Identification of critical thresholds that may lead to ecosystem collapse.

II. Methodology

A. Model Architecture

Our agent-based model simulates a marine ecosystem using a two-dimensional grid representing horizontal space (x-axis) and depth (y-axis). The model incorporates three primary components: the environment module, agent classes, and simulation dynamics.

Environment Module: The environment maintains spatial distributions of temperature, pH, oxygen concentration, and light availability. Environmental gradients reflect realistic marine conditions, with temperature and oxygen decreasing with depth, and light declining exponentially according to Beer's Law [10] :

$$I(Z) = I_o \times e^{(-k \times z)} \tag{1}$$

$I(Z)$ is the light intensity at depth Z, I_o is the surface light intensity, and k is the light attenuation coefficient. The value of k varies depending on water clarity and constituents.

Agent Classes: Three agent types represent key trophic levels:

- Phytoplankton: Stationary primary producers utilizing photosynthesis
- Zooplankton: Mobile primary consumers feeding on phytoplankton
- Fish: Mobile secondary consumers feeding on zooplankton

B. Agent Behaviors and Physiology

Each agent class implements species-specific physiological responses and behavioral strategies:

1) Phytoplankton Agents

Phytoplankton agents represent light-dependent primary producers in the marine ecosystem model. Their energy acquisition and behavior are governed by well-established physiological and ecological principles, adapted for agent-based modeling.

a) Photosynthesis and Energy Gain

Energy gain through photosynthesis is modeled using the scientifically established Jassby & Platt (1976) photosynthesis-irradiance model, which represents the gold standard for modeling phytoplankton photosynthetic responses to light availability [11]. The photosynthesis rate follows

$$E_{gain} = P_{max} \times \tanh\left(\frac{\propto \times I}{P_{max}}\right) \quad (2)$$

Said equation is upadated to take into account Temperature, pH, and other variables. The current implemented equation is as follows :

$$E_{gain} = P_{max} \times \tanh\left(\frac{\propto \times I}{P_{max}}\right) \times T_{factor} \times N_{factor} \times Efficiency \quad (3)$$

where :

Photosynthesis Parameters:

- P_{max} : maximum photosynthetic rate, representing the light-saturated photosynthetic capacity
- $\propto$: initial slope of the photosynthesis-irradiance curve (photosynthetic efficiency), representing the quantum yield at low light
- I : irradiance, converted from normalized light levels using typical surface irradiance values (2000)

Environmental Modifiers:

Temperature Response Factor (T_{factor}): The temperature response follows the Q_{10} relationship, which describes how biological reaction rates change with temperature [12]

$$T_{factor} = Q_{10}^{\frac{T-T_{opt}}{10}}, Q_{10} = 2.0, T_{opt} = 20°C \quad (4)$$

Where Q_{10} = 2.0 represents the rate doubling per 10°C increase (typical for biological processes), T is the current temperature (°C), and $T_{optimal}$= 20°C [13] is the optimal temperature for marine phytoplankton photosynthesis.

Note on pH Effects : While the broader literature suggests that pH may influence photosynthetic rates, particularly under conditions of ocean acidification, this model currently incorporates pH indirectly through its contribution to environmental stress rather than as a direct modifier of energy gain. Future extensions may integrate a dedicated pH_{factor} term to more explicitly represent species-specific pH sensitivity and CO_2 enhancement effects [14].

Additional factors :

- N_{factor} : nutrient limitation factor (0.9), representing typical marine nutrient availability
- $Efficiency$: energy conversion efficiency (0.85), representing the fraction of photosynthetic products converted to usable cellular energy

b) Movement and Vertical Migration

Motile phytoplankton agents adjust their vertical position to optimize light absorption and nutrient acquisition by performing diel vertical migration when energetically viable. Agents ascend during daylight hours to photosynthesize and descend to nutrient-rich depths under low surface nutrient conditions, mimicking observed natural behavior. [15]. Non-motile or energy-depleted cells passively sink due to gravity, whereas motile phytoplankton may override this behavior by actively migrating in response to vertical light gradient.

c) Reproduction and Mortality

When energy exceeds a threshold and stress levels are minimal, phytoplankton is divided by binary fission. Each daughter inherits parent traits with small Gaussian variation, introducing population diversity.

2) Zooplankton Agents

Zooplankton agents represent actively swimming organisms that consume organic material, modeled after marine copepods. They forage for phytoplankton by filtering surrounding water, simulating clearance-based feeding behavior where feeding efficiency depends on prey density and quality. Behavioral decisions are governed by physiological conditions such as hunger and environmental stress, along with external stressors like temperature, oxygen concentration, pH, and the presence of predators or prey.

Physiological processes include temperature-dependent metabolism [16] modeled using the Q_{10} principle, which reflects the biological tendency for metabolic rates to approximately double for every 10°C rise in temperature (Q_{10} = 2.0) [17]. Reproduction occurs probabilistically and is influenced by age, energy reserves, and environmental stress. Agents also exhibit diel vertical migration (DVM) [18], a daily behavioral rhythm in which they ascend to surface waters at night to feed and descend during the day to evade visually hunting predators.

When predators are nearby, zooplankton relocate using an escape trajectory determined by a "threat-weighted" influence, giving greater importance to closer predators. They may also form aggregations (schooling) when local population density conditions are favorable. Their movement behavior is guided by a scoring system that combines multiple spatial factors including food abundance, environmental quality, and predator presence. Mortality results from natural aging, stressful environmental extremes (e.g., high temperatures or low oxygen), and energy depletion.

The model is grounded in ecological observations and empirical studies [16 - 18], enabling realistic simulation of mid-trophic level dynamics in marine food webs.

3) Fish Agents

Fish agents represent the apex predators in the marine ecosystem model, implementing sophisticated physiological and behavioral mechanisms based on marine fish biology research. The implementation incorporates species-specific thermal tolerances, hypoxia sensitivity, and complex behavioral strategies including behavioral thermoregulation and habitat selection.

a) Temperature Response and Thermal Tolerance

Fish agents exhibit species-specific thermal preferences with three distinct types: polar, temperate, tropical. These ranges reflect observed thermal niches of marine fish communities [19]. Critical thermal limits for each type are modeled based on experimentally derived upper and lower thermal tolerance thresholds, capturing species-specific survival ranges under temperature stress. Metabolic rate adjustments follow Q_{10}.

b) Oxygen Requirements and Hypoxia Tolerance

Oxygen requirements are modeled using species-specific critical oxygen thresholds derived from established datasets on hypoxia tolerance in marine fish [24]. When oxygen levels drop below critical levels, fish are unable to sustain their normal metabolic functions, resulting in elevated energy costs and physiological stress. Lethal thresholds are defined based on oxygen concentrations that cause acute mortality, as observed in experimental studies. Below these levels, the model simulates the shift to less efficient anaerobic metabolism

c) PH Tolerance and Ocean Acidification Effects

Fish agents exhibit narrow pH tolerances, as evidenced by significant impairment of multiple critical life processes—including survival, growth, calcification, and behavior—at CO2 concentrations representing relatively modest departures from current ocean chemistry [25]. pH stress contributes to the total environmental stress calculation through multiple pathways, including direct neurological effects and indirect impacts on resource availability and species interactions [26].

d) Feeding Behavior and Predation

Hunting behavior incorporates search efficiency, handling time per prey, and capturing success rates as key components of predatory performance. Energy gain from zooplankton prey varies depending on prey condition, with assimilation efficiency reflecting typical marine fish digestive efficiency. Hunting success varies with environmental conditions, as temperature changes can impair predation efficiency by affecting the physiological and behavioral performance of predators.

e) Reproduction

Reproduction follows hyperallometric scaling relationships where larger fish invest disproportionately more energy in reproduction [23]. The model implements variable energy thresholds and costs per spawning event, with maturation occurring after reaching minimum age and reproductive senescence beginning in later life stages.

Batch spawning and seasonal reproduction are implemented with species-specific spawning intervals, reflecting the diverse reproductive strategies observed in marine fish communities [22]. Spawning requires low environmental stress levels and suitable temperatures, consistent with observations that fish reproduction is highly sensitive to environmental conditions [21].

f) Thermoregulation

Fish agents implement behavioral thermoregulation through vertical and horizontal movements to optimize body temperature [27]. Thermoregulatory behavior is triggered when thermal stress exceeds threshold levels, with agents actively seeking temperatures within their thermal preference range.

g) Habitat Selection and Migration

Habitat quality assessment integrates multiple environmental factors with species-specific weightings emphasizing temperature and oxygen availability over pH effects. Migration behavior is triggered when environmental stress exceeds species-dependent thresholds, leading to active search for better habitat. This reflects observed fish distribution shifts in response to sea temperature increases, with species showing significant northward movement correlated with warming trends [20].

h) Mortality

Mortality results from several mechanisms operating at different timescales: acute mortality from lethal environmental conditions, chronic stress-induced mortality under prolonged adverse conditions, age-related senescence mortality increasing in later life stages, and energy depletion mortality when energy reserves approach zero.

i) Lifespan

Maximum lifespan varies substantially among modeled species, representing the diversity of marine fish life histories from short-lived to long-lived species. This variation enables the model to capture different life history strategies and their responses to environmental change.

C. Environmental Stress Modeling

Environmental stress for each agent is computed using the deviation of current environmental conditions from the species-specific optimal range. Specifically, stress is calculated as the sum of the normalized differences between current and optimal values of key environmental parameters, such as temperature, pH, and oxygen:

$$Stress = \sum \frac{|Param_{current} - Param_{optimal}|}{Tolerance_{range}} \quad (5)$$

This stress metric directly influences key biological functions, including metabolic energy expenditure, reproductive success, and mortality rates. Each agents in the model is assigned unique optimal environmental values and tolerance thresholds, which are derived from established marine biology studies.

D. Implementation

Link to github:

https://github.com/MarvelPangondian/Tugas-Besar-IF3211.git

The marine ecosystem simulation was implemented as a modular, extensible agent-based system using Python. The system is composed of four main components: the environment module, agent classes, simulation engine, and an interactive visualization interface. These components collectively model ecological dynamics, environmental stress, and population interactions under various climate scenarios.

1) Environment Module

The Environment class initializes a two-dimensional grid representing spatial heterogeneity in temperature, pH, oxygen, and light. Environmental gradients are created by decreasing temperature and oxygen levels with depth, and by applying exponential decay to light intensity based on Beer's Law. Spatial noise is also added using Gaussian distributions to simulate natural environmental variability.

Three climate scenarios are supported:

- Stable: Default parameters remain constant over time.
- Warming: Simulates gradual increases in temperature with slight decreases in pH and oxygen.
- Extreme: Models more rapid environmental degradation across all parameters.

At each simulation step, the environment updates itself based on the selected scenario and records statistics such as average temperature, pH, and oxygen.

2) Agent Design

Three distinct agent classes, Phytoplankton, Zooplankton, and Fish are implemented by inheriting from an abstract base class Agent. Each agent operates autonomously, executing behaviors based on local environmental conditions and internal states such as energy, age, and stress level.

a) Phytoplankton

Phytoplankton agents are non-motile and perform photosynthesis using a light-dependent growth model based on Jassby & Platt's (1976) formulation.

The implementation includes environmental modifiers:

- Temperature effect: Based on the Q_{10} coefficient, enhancing photosynthesis up to an optimal temperature.
- pH effect: Modeled as a Gaussian curve centered at optimal pH, with additional enhancement for moderate acidification.
- Light and nutrient factors: Irradiance is computed from the environmental light matrix, and nutrient availability is represented by a constant modifier.

Photosynthetic energy gain increases the agent's energy, which contributes to growth and reproduction. Reproduction is modeled through binary division if energy and age criteria are met.

b) Zooplankton

Zooplankton agents are mobile consumers that actively search for phytoplankton within a defined hunting radius.

Their behavior is governed by:

- Feeding: Energy is gained by consuming phytoplankton at the same grid cell, up to a maximum number of meals per step.
- Seeking: If no food is available locally, agents move toward the closest detected phytoplankton.
- Avoidance: If nearby fish are detected, zooplankton attempt to move away from them.

Zooplankton reproduction depends on energy reserves, age range, and environmental stress tolerance.

c) Fish

Fish represent top predators in the simulation. Their behavior is the most complex, involving:

- Hunting: Fish consume zooplankton at their current location, with probabilistic success and energy reward.
- Prey Seeking: Fish scan their surroundings for zooplankton density and move toward areas with higher prey concentrations.
- Schooling: Fish can move toward nearby conspecifics to form loose groups, enhancing survival likelihood.
- Migration: If local environmental stress exceeds a threshold, fish seek optimal environmental conditions within a search radius.

Fish reproduction and survival are strongly influenced by temperature, oxygen, and pH, making them highly sensitive to climate-induced stressors.

3) Simulation Engine

The *MarineEcosystemSimulation* class manages the core logic of the simulation. Key tasks include:

- Initializing environment and agents based on a SimulationConfig.
- Iterative update loop where, at each time step:
- The environment is updated.
- Agents are shuffled and individually updated.
- Dead agents are removed.
- Spatial and statistical data are logged.

The simulation records metrics at each step including population sizes, energy levels, average stress, diversity indices (e.g., Shannon Index), and total biomass. This enables post-simulation analysis and visualization.

4) Visualization and Interface

The simulation is integrated into an interactive Streamlit web interface through the MarineEcosystemInterface class. Users can:

- Configure environmental and biological parameters.
- Run or reset simulations.
- Visualize real-time outputs including:
- Population dynamics
- Energy and stress trends
- Environmental changes
- Spatial agent distributions
- Compare multiple scenarios (e.g., stable vs. extreme) using side-by-side plots.

III. Result and Discussion

A. Ecosystem Stability and Collapse Dynamics

1) Ecosystem Persistence Under Climate Stress

The model revealed dramatic differences in ecosystem persistence across climate scenarios (Fig. 1). Under stable environmental conditions, the ecosystem maintained complex dynamics for 228 time steps before eventual collapse. Progressive environmental deterioration significantly reduced ecosystem resilience, with warming scenarios triggering collapse at step 98 (57% reduction in persistence), and extreme scenarios causing rapid collapse at step 52 (77% reduction in persistence). These results demonstrate clear threshold effects where environmental stress intensity directly correlates with ecosystem stability duration.

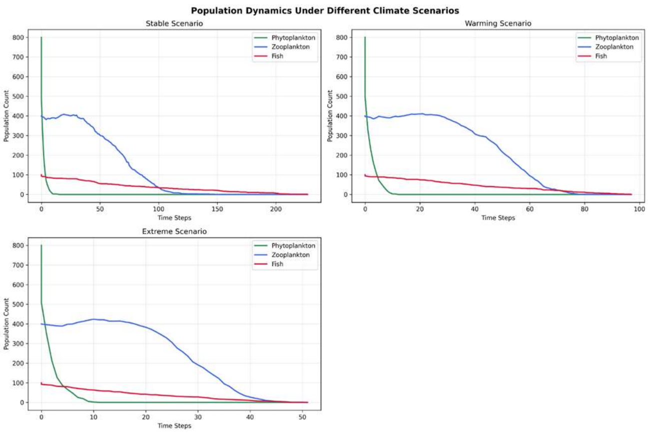

Fig. 1. Population dynamics under different climate scenarios

2) Collapse Pattern Analysis

All scenarios eventually led to complete ecosystem collapse, indicating the severity of multi-stressor impacts on simplified marine food webs. However, the timing differences reveal important insights into ecosystem vulnerability thresholds. The stable scenario's extended persistence (228 steps) suggests the baseline ecosystem configuration can maintain complex dynamics under optimal conditions, while the accelerated collapse under climate stress scenarios (98 and 52 steps respectively) demonstrates exponential vulnerability increases with environmental deterioration.

B. Environmental Threshold Identification and Species-Specific Responses

1) Critical Environmental Limits

Threshold analysis identified critical environmental limits for ecosystem survival (Fig. 2). All species showed critical survival thresholds at 18°C, indicating that despite behavioral adaptations, temperatures beyond this threshold trigger rapid population declines. Similarly, pH thresholds of 6.8 and oxygen thresholds of 2.0 mg/L represent critical limits for ecosystem persistence across all trophic levels.

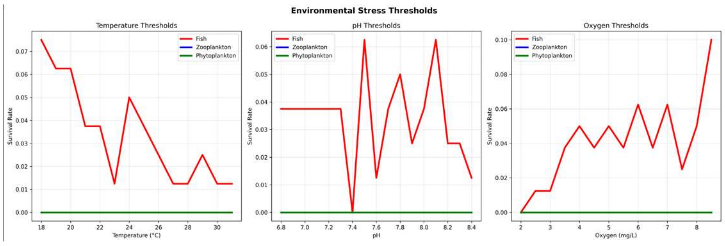

Fig. 2. Stress thresholds

2) Localized Vulnerability Thresholds Under Extreme Conditions

The identification of threshold values in localized simulations highlights critical environmental limits beyond which marine species cannot maintain viable populations. While not globally universal, these thresholds indicate potential ecosystem tipping points under specific regional or experimental conditions, where environmental stressors simultaneously compromise survival across multiple trophic levels.

C. Direct Physiological Vulnerability

1) Stress-Specific Vulnerability Patterns

Systematic tests under isolated environmental stressors revealed that species vulnerability is not fixed but varies depending on the type and severity of stress (Fig. 3). Under mild conditions (22 °C, pH 7.9, oxygen 6.0 mg/L), phytoplankton were the most vulnerable, with only 14.6% survival. In contrast, zooplankton (54.0%) and fish (53.3%) showed similar and higher resilience.

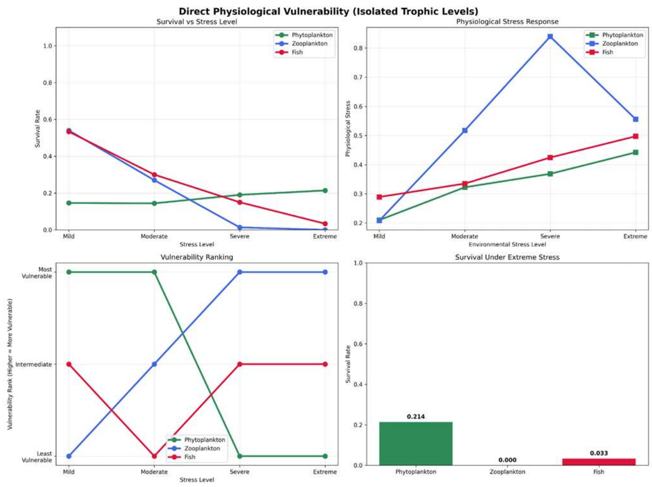

Fig. 3. Vulnerability analysis

2) Vulnerability Reversal at High Stress

Under extreme stress conditions (28 °C, pH 7.3, oxygen 3.0 mg/L), a reversal was observed. Zooplankton exhibited complete mortality (0% survival), becoming the most vulnerable group. Phytoplankton showed increased resilience (21.4%), and fish maintained intermediate survival (3.3%). These results indicate that intermediate trophic levels, such as zooplankton, may be more susceptible under high-stress multi-factor conditions, while primary producers and top predators may employ different survival strategies.

3) Species-Specific Stress Responses

Quantitative stress analysis showed varying physiological responses across trophic levels. Zooplankton had the sharpest stress increase, from 0.208 (mild) to 0.556 (extreme), indicating low tolerance margins. Fish displayed moderate stress growth (0.289 to 0.497), while phytoplankton stress levels remained relatively stable (0.210 to 0.442), suggesting more consistent tolerance to environmental change.

D. Model Validation and Ecological Realism

The model successfully reproduced several key patterns observed in marine ecosystems under climate stress:

1) Trophic cascade dynamics

Different collapse timing across scenarios reflected food web dependencies (Fig. 1)

2) Stress-dependent vulnerability

Vulnerability hierarchies shifted with environmental stress intensity (Fig. 3)

3) Threshold-driven responses

Ecosystem persistence showed non-linear responses to environmental stress (Fig. 2)

Results challenge the traditional fixed hierarchy assumption (fish > zooplankton > phytoplankton vulnerability) and support theory of context-dependent vulnerability patterns, .

IV. Conclusion

This agent-based modeling study addresses the central ecological question of *how climate-related environmental stressors affect marine ecosystem stability and species survival across multiple trophic levels*. Our findings demonstrate that climate stressors profoundly destabilize marine ecosystems through exponential resilience decline, with ecosystem persistence times decreasing from 228 steps (stable) to 52 steps (extreme scenarios), representing a 77% reduction in stability under severe climate stress.

Regarding species survival across trophic levels, this research reveals fundamentally different patterns than traditionally assumed. Rather than fixed vulnerability hierarchies, we demonstrate context-dependent vulnerability patterns. Under mild stress, phytoplankton is most vulnerable (14.6% survival), while under extreme conditions, zooplankton become most susceptible (0% survival) due to high metabolic demands and limited escape mechanisms.

This research contributes to growing evidence that marine ecosystem responses to climate change are fundamentally non-linear, context-dependent, and characterized by critical threshold effects. The agent-based modeling framework provides a valuable tool for exploring complex ecosystem dynamics and supports evidence-based development of climate adaptation strategies for marine resource management.

For future research, model enhancement should prioritize evolutionary adaptation and expanding food web complexity.

References

[1] O. Hoegh-Guldberg and J. F. Bruno, “The Impact of Climate Change on the World’s Marine Ecosystems,” *Science*, vol. 328, no. 5985, pp. 1523–1528, Jun. 2010, doi: 10.1126/science.1189930.

[2] K. E. Limburg, D. Breitburg, D. P. Swaney, and G. Jacinto, “Ocean Deoxygenation: A Primer,” *One Earth*, vol. 2, no. 1, pp. 24–29, Jan. 2020, doi: 10.1016/j.oneear.2020.01.001.

[3] A. J. Richardson, “In hot water: zooplankton and climate change,” *ICES Journal of Marine Science*, vol. 65, no. 3, pp. 279–295, Apr. 2008, doi: 10.1093/icesjms/fsn028.

[4] M. L. Pace, J. J. Cole, S. R. Carpenter, and J. F. Kitchell, “Trophic cascades revealed in diverse ecosystems,” *Trends in Ecology & Evolution*, vol. 14, no. 12, pp. 483–488, Dec. 1999, doi: 10.1016/S0169-5347(99)01723-1.

[5] M. Bulling, P. White, D. Raffaelli, and G. Pierce, “Using model systems to address the biodiversityecosystem functioning process,” *Mar. Ecol. Prog. Ser.*, vol. 311, pp. 295–309, Apr. 2006, doi: 10.3354/meps311295.

[6] D. L. DeAngelis and W. M. Mooij, “Individual-Based Modeling of Ecological and Evolutionary Processes,” *Annu. Rev. Ecol. Evol. Syst.*, vol. 36, no. 1, pp. 147–168, Dec. 2005, doi: 10.1146/annurev.ecolsys.36.102003.152644.

[7] K. Rossington and T. Benson, “An agent-based model to predict fish collisions with tidal stream turbines,” *Renewable Energy*, vol. 151, pp. 1220–1229, May 2020, doi: 10.1016/j.renene.2019.11.127.

[8] E. McCauley, W. G. Wilson, and A. M. de Roos, “Dynamics of Age-Structured and Spatially Structured Predator-Prey Interactions: Individual- Based Models and Population-Level Formulations,” *The American Naturalist*, vol. 142, no. 3, pp. 412–442, 1993.

[9] S. F. Railsback and B. C. Harvey, “Analysis of Habitat-Selection Rules Using an Individual-Based Model,” *Ecology*, vol. 83, no. 7, p. 1817, Jul. 2002, doi: 10.2307/3071767.

[10] T. G. Mayerhöfer, S. Pahlow, and J. Popp, “The Bouguer-Beer-Lambert Law: Shining Light on the Obscure,” *ChemPhysChem*, vol. 21, no. 18, pp. 2029–2046, Sep. 2020, doi: 10.1002/cphc.202000464.

[11] A. D. Jassby and T. Platt, “Mathematical formulation of the relationship between photosynthesis and light for phytoplankton,” *Limnology & Oceanography*, vol. 21, no. 4, pp. 540–547, Jul. 1976, doi: 10.4319/lo.1976.21.4.0540.

[12] E. Marañón, P. Cermeño, M. Huete-Ortega, D. C. López-Sandoval, B. Mouriño-Carballido, and T. Rodríguez-Ramos, “Resource Supply Overrides Temperature as a Controlling Factor of Marine Phytoplankton Growth,” *PLoS ONE*, vol. 9, no. 6, p. e99312, Jun. 2014, doi: 10.1371/journal.pone.0099312.

[13] R. W. Eppley, "Temperature and phytoplankton growth in the sea," *Fishery Bulletin*, vol. 70, pp. 1063–1085, 1972

[14] G. Tilstone, B. Šedivá, G. Tarran, R. Kaňa, and O. Prášil, “Effect of CO2 enrichment on phytoplankton photosynthesis in the North Atlantic sub-tropical gyre,” *Progress in Oceanography*, vol. 158, pp. 76–89, Nov. 2017, doi: 10.1016/j.pocean.2016.12.005.

[15] K. Wirtz, S. L. Smith, M. Mathis, and J. Taucher, “Vertically migrating phytoplankton fuel high oceanic primary production,” *Nat. Clim. Chang.*, vol. 12, no. 8, pp. 750–756, Aug. 2022, doi: 10.1038/s41558-022-01430-5.

[16] D. R. Heinle, “Temperature and Zooplankton,” *Chesapeake Science*, vol. 10, no. 3/4, p. 186, Sep. 1969, doi: 10.2307/1350456.

[17] T. Ikeda and E. Fay, “Metabolic activity of zooplankton from the Antarctic Ocean,” *Mar. Freshwater Res.*, vol. 32, no. 6, p. 921, 1981, doi: 10.1071/MF9810921.

[18] S. M. Bollens and B. W. Frost, “Predator-induced diel vertical migration in a planktonic copepod”.

[19] N. L. Payne *et al.*, “Fish heating tolerance scales similarly across individual physiology and populations,” *Commun Biol*, vol. 4, no. 1, p. 264, Mar. 2021, doi: 10.1038/s42003-021-01773-3.

[20] A. L. Perry, P. J. Low, J. R. Ellis, and J. D. Reynolds, ‘Climate Change and Distribution Shifts in Marine Fishes’, *Science*, vol. 308, no. 5730, pp. 1912–1915, Jun. 2005, doi: 10.1126/science.1111322.

[21] N. W. Pankhurst and P. L. Munday, ‘Effects of climate change on fish reproduction and early life history stages’, *Mar. Freshwater Res.*, vol. 62, no. 9, p. 1015, 2011, doi: 10.1071/MF10269.

[22] S. K. Lowerre-Barbieri, K. Ganias, F. Saborido-Rey, H. Murua, and J. R. Hunter, ‘Reproductive Timing in Marine Fishes: Variability, Temporal Scales, and Methods’, *Marine and Coastal Fisheries*, vol. 3, no. 1, pp. 71–91, Jan. 2011, doi: 10.1080/19425120.2011.556932.

[23] S. K. Lowerre-Barbieri, K. Ganias, F. Saborido-Rey, H. Murua, and J. R. Hunter, ‘Reproductive Timing in Marine Fishes: Variability,

Temporal Scales, and Methods', *Marine and Coastal Fisheries*, vol. 3, no. 1, pp. 71–91, Jan. 2011, doi: 10.1080/19425120.2011.556932.

[24] R. Vaquer-Sunyer and C. M. Duarte, 'Thresholds of hypoxia for marine biodiversity', *Proc. Natl. Acad. Sci. U.S.A.*, vol. 105, no. 40, pp. 15452–15457, Oct. 2008, doi: 10.1073/pnas.0803833105.

[25] C. Cattano, J. Claudet, P. Domenici, and M. Milazzo, 'Living in a high CO_2 world: a global meta-analysis shows multiple trait-mediated fish responses to ocean acidification', *Ecological Monographs*, vol. 88, no. 3, pp. 320–335, Aug. 2018, doi: 10.1002/ecm.1297.

[26] I. Nagelkerken and P. L. Munday, 'Animal behaviour shapes the ecological effects of ocean acidification and warming: moving from individual to community-level responses', *Global Change Biology*, vol. 22, no. 3, pp. 974–989, Mar. 2016, doi: 10.1111/gcb.13167.

[27] F. Amat-Trigo, D. Andreou, P. K. Gillingham, and J. R. Britton, 'Behavioural thermoregulation in cold-water freshwater fish: Innate resilience to climate warming?', *Fish and Fisheries*, vol. 24, no. 1, pp. 187–195, Jan. 2023, doi: 10.1111/faf.12720.