Nutrients and the food web

Dad: Why do we usually catch fish where you usually take us, whereas Charlie often brings nothing home?

Photo by Quang Nguyen Vinh: https://www.pexels.com/photo/photo-of-people-catching-fishes-2150362/

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Storyline

Phytoplankton are microscopic, unicellular photosynthetic organisms that drift with the currents and inhabit the surface illuminated layers of every sea and ocean. They ensure the growth of the species used as seafood and account for nearly as much as all the photosynthesis that takes place in all the forests and grasslands of terrestrial ecosystems. Phytoplankton need light, carbon, and nutrients (e.g. nitrate, ammonium or phosphate salts) to build new biomass. While light is abundant near the surface and decreases with depth, nutrients are plentiful in deep waters and tend to be scarce near the surface. Nutrients reach the surface through freshwater discharge, atmospheric deposition, and physical processes promoted by blowing winds which move up deep and nutrient-rich water. That is why phytoplankton is generally more abundant at high latitudes and in coastal areas than in the open tropical and subtropical ocean. In surface, well-illuminated waters, the growth of phytoplankton may become limited if a given nutrient is scarce, which in turn will have an impact on the marine food webs. Nutrient limitation, which can be experimentally assessed using relatively simple bioassays, is common in marine ecosystems. A different trophic organization emerges when phytoplankton is dominated by large or small cells, which in turn largely depends on the availability of nutrients. Large food chains, including many trophic levels between phytoplankton and top predators, are found in regions where nutrients are scarce, while shorter food chains occur in nutrient-rich regions, which has important implications for fisheries: shorter food chains are more efficient and sustain more seafood than the longer ones. Climate change may cause a decrease in marine primary production and in fish catches, yet such impacts are difficult to predict and will likely differ among oceanic regions.

The Microbiology and Societal Context

The microbiology: diversity and distribution of marine microalgae; environmental factors; nutrients; limitation; primary production; food chain. *Sustainability issues*: food; health; oceans; climate change.

Nutrients and the food web: The microbiology

1. **Phytoplankton: the green engines that sustain ocean life.** What do whales, crude oil and most of the oxygen we breathe have in common? They all owe their existence to marine phytoplankton: the ensemble of microscopic, unicellular photosynthetic organisms that drift with the currents and inhabit the surface, illuminated layers of every sea and ocean.

Phytoplankton (from the Greek words 'phyto', meaning plant, and 'plankton', meaning wanderer or drifter), include more than 25,000 species of both bacteria and eukaryotic (with nucleus) cells and, although they are extremely diverse in terms of evolutionary origin, morphology and size, they share a key feature: their ability to carry out photosynthesis, using the sun's energy to convert $CO₂$ into sugars and releasing oxygen as a by-product.

Photomicrograph showing phytoplankton (diatoms and dinoflagellates) cells from a coastal productive location. See size scale below the picture. Thick black line represents 100 µm. Taken from https://www.facebook.com/Planktonbook.

Photosynthetic organisms are autotrophs, also known as primary producers, and create the food that sustains the rest of the species in most marine and land ecosystems. We are most familiar with land plants, but not so much with the invisible, plant-like organisms of the phytoplankton. Yet every year they capture some 45 billion tons of carbon as CO_2 (45 x 10¹⁵ g C), which is nearly as much as all the photosynthesis that takes place in all the forests and grasslands of terrestrial ecosystems. Thus, the primary production by phytoplankton ultimately ensures the growth of the species used as seafood, such as fish, prawns or mussels.

2. **Role of phytoplankton carbon sequestration.** Part of the organic matter (the sugars, protein, fats that form biomass) produced by phytoplankton from $CO₂$ sinks away from the

surface, either directly in the form of dead cells, or indirectly as part of the remains of other organisms. The continuous 'rain' of settling particles (also called 'marine snow') carries organic carbon into the deep ocean, and decomposing organisms such as bacteria convert it again into $CO₂$ along the way. This so-called 'biological pump' transports carbon from the surface to the ocean's interior and contributes to storing $CO₂$ away from the atmosphere. A small fraction of the organic matter that settles on the bottom of the ocean escapes degradation by decomposing organisms and is buried in the marine sediments. Over millions of years, the transformation of this organic matter under high pressure and temperature results in the formation of oil reserves. *So, phytoplankton photosynthesis not only puts food on the table, but it also puts gas in the tank.*

3. **Phytoplankton were responsible for the Great Oxygenation Event (GOE) and transformed the atmosphere of planet Earth from anoxic to oxic.** We can realize the importance of marine phytoplankton and photosynthesis for the evolution of life on Earth by looking back in time. Before the emergence of the first O_2 -producing, photosynthetic blue-green bacteria some 3 billion years ago, there was no free oxygen (O_2) in the atmosphere. The release of O_2 from photosynthesis in the ocean, and its slow accumulation in the atmosphere over the next 2 billion years, resulted in the oxygenation of Earth, gave way to the ozone layer (which protects living beings from the Sun's ultraviolet radiation), and facilitated the evolution of animal life. The diminutive size of phytoplankton cells is no obstacle for their role as forces of planetary transformation and providers of resources.

4. **The phytoplankton growth conundrum: divergence of availability of the two essentials.** Photosynthetic organisms need more than light and carbon to build new biomass. They also need elements such as nitrogen and phosphorus to synthesize biomolecules like proteins and nucleic acids. These elements are obtained from nutrients (e.g. nitrate, ammonium or phosphate salts) that are dissolved in the surrounding water.

Vertical distribution of light, temperature and nutrients in the ocean. The upper mixed layer represents the layer where the mixing driven by the wind homogenizes vertical gradients of temperature and nutrients.

The challenge phytoplankton face constantly is that, whereas the light needed for growth is abundant near the surface and decreases fast with depth, the opposite is true of nutrients, which are also needed for growth, and are plentiful in deep waters but tend to be scarce near the surface.

5. The biological pump is responsible for the light-nutrient availability divergence. The reason nutrients are often depleted in surface waters (i.e. the euphotic layer, where sufficient light allows photosynthesis to take place) is that phytoplankton keep consuming them, and when organisms and particles sink to the deep ocean, they carry with them key elements that include nitrogen, phosphorus, silicon and iron. Thus, the surface ocean is constantly losing nutrients. As organic matter sinks and gets decomposed-recycled in deeper waters, it releases its nutrients, which is why the deep ocean is nutrient-rich.

The biological pump influences the distribution of nutrients. Taken from Käse and Geuer (2018)

6. **The pycnocline is a barrier to replenishment of nutrients in the ocean surface.** For phytoplankton to be able to photosynthesize and create new organic matter, nutrients from the deep must reach the surface. Nutrients also enter the surface through precipitation, dust deposition and runoff.

The upward transport of nutrients towards the euphotic layer is hampered by a physical barrier named the pycnocline. Warmer and less salty waters are less dense and lie on top of colder, saltier and denser waters. The pycnocline forms where the light waters high in the water column meet the heavy waters lower in the water column, and where there is a steep change in density over a few meters. If you ever swam in a mountain lake during summer - you do not need to think about salinity in this case - you probably felt the temperature difference between your feet and

your neck when you stand vertically inside the water. This illustrates the low mixing of warmer surface water with lower, colder water that is prevented by the pycnocline barrier, which is not only responsible for temperature differences in the water column, but also the poor upward transport of nutrients.

7. **Phytoplankton is more abundant in high latitudes and coastal waters than in the tropical open ocean.** Because of the differences between surface solar radiation between low and high latitudes, tropical surface waters are much warmer than polar surface waters and form steeper pycnoclines. This means that vertical mixing in the water column, and upward transportation of nutrients, is low in waters at low latitudes and higher in waters at high latitudes.

Global distribution of surface nitrate (from the World Ocean Atlas 2009) and chlorophyll-a concentration derived from remote sensing images (Aqua MODIS-NASA). Taken from Gledhill and Buck (2012).

This explains why when we look at the concentration of chlorophyll-a (a proxy for the amount of phytoplankton in the water, and which can be measured by satellites in space) in the surface ocean, we observe that, in general, chlorophylla is lower in tropical and subtropical regions, where nutrients at the surface are scarce.

8. **However, different physical processes can help nutrients to cross the pycnocline.** As an important ally, let´s focus on the wind. Wind blowing at the surface is a source of mechanical energy with the power to stir and mix water particulates and erode the pycnocline. Regional winds are also responsible for the rising of nutrient-replete deep waters to the surface in ocean and coastal upwelling regions, which stimulates phytoplankton growth. This explains why we observe

more chlorophyll at the surface of equatorial regions and the eastern boundaries of the large subtropical gyres (circular ocean currents).

Dark blue areas on the globe indicate main regions of coastal upwelling. The box is a scheme for the circulation of upwelling bays in the NW Iberian Peninsula, where winds blowing from the north cause the rising of nutrient -enriched deep waters. Taken from Broullón (2024).

9. **Mixing, upward transport of nutrients and phytoplankton growth are also seasondependent.** Especially at temperate and high latitudes, climate changes over the seasons also influence phytoplankton growth. During winter, strong winds increase mixing which erodes the pycnocline, so phytoplankton have plenty of nutrients. However, mixing also transports cells to deeper waters where light is low. Solar radiation during the summer intensifies the pycnocline, so light is abundant but nutrients are scarce. It is therefore during spring and autumn when phytoplankton cells meet the right conditions to flourish. Seasons are less evident in the tropics.

10. **Nutrient limitation is widespread and varies in time and space.** In surface, wellilluminated waters, the growth of phytoplankton will be limited if a given nutrient is scarce. It has been estimated that in more than 80% of the ocean there is nutrient limitation of phytoplankton abundance and photosynthetic activity all year round or during certain seasons. The limiting nutrient will be that which is supplied at the lowest rate compared with phytoplankton demand (the rate-limiting parameter/bottleneck/pinch-point: see also *Bottlenecks and rate-limiting parameters*, in the Critical Thinking MicroChats Gallery).

While phosphorus is frequently the limiting nutrient in freshwater lakes, nitrogen is generally the limiting element in the ocean. To make things more complex, the limiting nutrient in marine ecosystems varies in time and space, and several elements (e.g. nitrogen (N), phosphorus (P) and iron (Fe)) may simultaneously act as limiting factors, thus, co-limiting phytoplankton growth.

N is very abundant in the atmosphere as N_2 , but only a few prokaryotes are able to convert N_2 to accessible forms for phytoplankton, through the process named N_2 fixation. N_2 fixation is

an activity that requires a large amount of energy and Fe. In water bodies in which nitrogen is scarce due to consumption and strong density stratification, nitrogen fixers may grow and increase the amount of available N. Under these circumstances, P may then become limiting. Iron inputs to the ocean mostly originate from the continents, so Fe availability decreases with distance from coastlines. Iron supply in remote areas of the ocean (e.g. Southern Ocean, Equatorial Pacific) is therefore low and hence can also be limiting for phytoplankton growth.

11. **Impact of nutrient limitation on food chains.** If phytoplankton growth is reduced, then the trophic levels further up the food chain will be negatively impacted, as they will have less food available. Moreover, when phytoplankton grows under nutrient stress, their nutritional value may lower and, consequently, herbivore fitness and performance may also drop.

12. **But nutrients are sometimes available in excess.** Nitrogen excess in coastal ecosystems may result from fertilizers that enter via runoff from agricultural operations, and/or from human and animal waste effluents. An excess of N may eventually force a secondary limitation by P. These allochthonous inputs are highly variable both in space and in time, thus it is difficult to predict when an element may be limiting. The proper identification of which nutrient is limiting phytoplankton growth in marine ecosystems is critical not only for a better understanding of the ecology of planktonic communities but also for water and ecosystem management purposes.

13. **Impact of nutrient excess: eutrophication and formation of oxygen-minimum zones.** When nutrients are in excess, phytoplankton may grow fast and form extensive blooms – eutrophication – which ultimately may cause problems in ecosystem health. This is because ecological balances are perturbed: herbivore grazers are too few to consume the elevated phytoplankton biomass, which continues to increase until it runs out of nutrients, at which point much of it dies. Some blooms involve toxin-producing phytoplankton, the toxins of which can poison other inhabitants of the sea and hence also perturb ecological balances. Importantly, the dead biomass is used as food by bacteria which digest it using oxygen, much in the same way that we metabolise our food using oxygen. This results in a massive local consumption of oxygen, creating so-called oxygen minimum zones that no longer support oxygen-dependent forms of marine life forms, which die. Oxygen minimum zones are increasing in number and size and are negatively impacting fish stocks, and hence food security, and biodiversity. Toxic algal blooms additionally lead to prohibition of fishing because of toxin contamination of fish, further impacting the supply and security of food from the sea.

14. **Phytoplankton cell size, nutrient supply, and marine food chains.** Phytoplankton cells come in all sorts of shapes and sizes. The smallest cells are spherical and have a diameter of 0.5 micrometers (µm; one millionth of a metre), whereas the largest ones can reach lengths of hundreds of micrometers. In terms of volume, phytoplankton cell size spans a range of more than 9 orders of magnitude (from approximately 0.1 μ m³ to more than 100 million μ m³) – this is comparable to the difference in weight between a housefly and an elephant. Cell size strongly affects multiple aspects of phytoplankton ecology, including their ability to obtain nutrients and light, how fast they can grow, and how susceptible they are to being eaten by a predator or sinking out of the euphotic layer.

The smallest cells, thanks to their large surface to volume ratio, are capable of taking up nutrients even when they are present in vanishingly low concentrations. In contrast, large cells have a small surface to volume ratio (surface is proportional to the square of length, whereas volume is proportional to the cube of length) and therefore struggle to obtain nutrients in

nutrient-impoverished (oligotrophic) waters. Conversely, large size allows cells to take up nutrients fast when they are abundant, and to store them intracellularly. As a result, small cells dominate in oligotrophic regions such as the vertically thermally- and density-stratified tropical open ocean, whereas large cells contribute most of the phytoplankton biomass in nutrient-rich environments, such as those of coastal upwelling areas.

The relative abundance of small versus large phytoplankton cells has profound implications for the fate of primary production and the transfer of energy towards organisms occupying higher trophic levels, such as fish. Small phytoplankton cells are mostly grazed upon by other unicellular organisms that grow more or less at the same pace. In turn, many of these consumers are ingested by other unicellular grazers, which are then predated upon by the small crustaceans (so called mesozooplankton) that are food for fish. The result is a complex, long food web with numerous trophic levels.

A different trophic organization emerges when phytoplankton is dominated by large cells, such as diatoms or dinoflagellates shown in the Figure above. In these conditions, typical of coastal regions, phytoplankton tend to be consumed by mesozooplankton, such as copepods and krill, which are themselves eaten by fish. This type of food chain is therefore shorter, and transfers energy more efficiently from phytoplankton to fish.

An additional factor that affects trophic efficiency (the percentage of biomass produced in a trophic level that is passed on to the next) is temperature: in warm waters $(20^{\circ}C)$ animals spend more energy in sustaining their metabolism, which means that less energy is left available for transfer to the next trophic level.

The combined effects of phytoplankton cell size, trophic structure and temperature explain why different fishing areas deliver catches that are widely different (by a factor of up to 100) when their primary production may differ only by a factor of 4. Because fish catch is not a simple linear function of phytoplankton primary production, predicting the impacts of climate change on fisheries yield around the world remains a challenge.

15. **Impact of climate change on phytoplankton productivity***.* Global warming of the lower atmosphere due to anthropogenic greenhouse gas emissions is responsible for the increasing heat content, and thus temperature, of the upper oceanic layers, particularly in tropical and subtropical regions. The same process is also involved in ice sheets melting sea in polar areas, releasing massive amounts of freshwater into the surface layer. As explained above, both increasing surface temperature and decreasing salinity lead to a strengthening of the pycnocline (density gradient between the upper and subsurface layers), thereby reducing the amount of nutrients reaching the photic zone from below. Consequently, it has been predicted that in lowlatitude, oligotrophic regions marine primary production by phytoplankton, and the food chains/webs dependent upon it, including fish stocks, will decrease during the next decades. However, measurements conducted over the last 30 years in the subtropical North Pacific and North Atlantic have not found such decreases in primary production, perhaps because phytoplankton have become able to use the available nutrients more efficiently.

16. **Impact of climate change on fish catches.** The last IPCC (Intergovernmental Panel on Climate Change) report on Ocean and Cryosphere concludes that, based on mathematical models, ocean primary productivity is very likely to decline by 4-11% by the end of this century in the worst-case climate change scenario. This decreasing trend is expected to be more intense in tropical regions, where global primary production could be between 7 and 16% lower by 2100 relative to 1850-1900. By contrast, primary production is projected to increase in the Arctic and Southern Oceans regions, mainly due to reduced ice cover, and the increase in the vertical density

gradient as a result of freshwater inputs, both of which relax light limitation of phytoplankton growth in a nutrient-rich environment. The contrasting productivity response of different regions to ocean warming helps to explain that available records of global marine primary production, obtained from data of ocean color retrieved by satellites over the last 2-3 decades, show no clear temporal trends.

The IPCC report also concluded that the high spatial heterogeneity foreseen for the impact of climate change on the ecology of pelagic ecosystems would ultimately lead to sharp latitudinal differences in maximum fish catch potential by the end of the century under the worstcase scenario. These projections show that maximum fish catch potential may become smaller by 15% in low and medium latitudes, with the largest reduction expected for the tropical and subtropical Pacific along with the western coasts of tropical Africa and South America, where decreases greater than 30% are forecasted.

Projected changes in maximum fish catch potential under the worst-case scenario (RCP8.5) relative to the 2000s and the relative contribution of fish to the total animal sourced food of the human diet (From Bindoff et al., 2019).

17. **Fish catches will decrease most in regions with the highest dependency on fish-centric diets.** When the dependence of each country's diet on fish is compared with the projected change in fish catch potential (an activity proposed as pupil discussion exercise 4 below), a clear pattern emerges: those countries where the more intense decreases in fish catch potential are expected, mainly low latitude countries, largely coincide with those where the diet of the population is highly dependent on fish.

Relevance for Sustainable Development Goals and Grand Challenges

• **Goal 2. Zero Hunger** (*end hunger and malnutrition*, *ensure sustainable food production systems*). According to the last IPCC special report, the impacts of global warming on the ecology of marine pelagic ecosystems are expected to show a high spatial heterogeneity. Significant

changes are projected for the maximum fish catch potential by the end of the century, implying either decreases in the amount of fish that could be harvested from tropical and subtropical areas or increases in temperate and polar regions. If these projections are eventually confirmed, a concerning paradox would emerge. High latitude, developed countries where fish accounts for a small share of the population diet, might potentially obtain higher amounts of fish from the ocean. By contrast, low latitude, developing countries where the diet of their population is highly dependent on fish would likely experience important declines in fish captures, which might increase hunger and malnutrition in these countries and probably foster migration events.

• **Goal 14. Conserve and sustainably use the oceans, seas and marine resources** (*reduce marine pollution, protect marine ecosystems, sustainably manage fisheries, aquaculture and tourism*). Aquatic nutrient pollution as a result of agriculture, aquaculture, urban and industrial activity, mostly impact coastal seas through land run-off and may cause coastal eutrophication, with negative consequences for the ecosystem and human health associated with oxygen depletion or pathogen proliferation. Other human activities such as dredging or trawling also release nutrients to coastal areas. Overfishing also impacts nutrient fluxes both directly, by removing biomass, and indirectly, by modifying food webs. Therefore, it is essential to conserve and sustainably manage coastal and marine ecosystems to ensure their functioning, resilience and capacity to provide goods and services.

Potential Implications for Decisions

1. Individual

a. Eat less meat (this reduces the demand on fertilizers and the production of manure).

- b. Do not throw rubbish to water bodies and beaches.
- c. Reduce your carbon footprint to help slow climate change.

2. Community policies

a. Implement regular monitoring of coastal waters, groundwaters and subterranean

estuaries.

- b. Promote public outreach and awareness of marine conservation issues.
- c. Ensure proper management of domestic and industrial sewage.

3. National policies

- a. Implementation of national monitoring systems.
- b. Regulation of aquaculture.
- c. Regulation of dredging activity.
- d. Regulation of fisheries.
- e. Regulation of tourism and recreation activities.
- f. Protection of marine wildlife.
- g. Regulation of the use of fertilizers.
- h. Regulation of agricultural, industrial and urban run-off.
- i. Implementation of global change impact research programs.
- j. Development of a global change policy.

Pupil participation

1. **Class discussion about the role of mixing and nutrient availability on phytoplankton size-structure.** Imagine a two dimensional space where the x-axis represents mixing intensity and the y-axis represents nutrients availability. Discuss the location in this two-dimensional space of a) phytoplankton communities dominated by microplankton (> 20 μm cell size) or picoplankton (< 2 μm cell size), and b) phytoplankton communities collected in different marine ecosystems including: Galician coastal upwelling region, NW Mediterranean Sea, or tropical and subtropical regions.

Because the supply of nutrients into the euphotic zone is frequently determined by mixing, species adapted to high nutrient concentrations tend to be adapted, as well, to high mixing levels, and vice versa. The previous sections explained how under calm conditions, small and motile cells are better competitors for limiting nutrients due to their large surface to volume ratio and the increased nutrient supply to cells through swimming, respectively, whereas enhancement of nutrient uptake in turbulent environments is greatest for larger cells. Moreover, low mixing conditions also select for small cells as large and non-motile phytoplankton tend to sink rapidly in the water column if there is not enough mixing to maintain them suspended. The main sequence of phytoplankton size-classes will be expected to follow a diagonal from upper right (high mixing-high nutrient) to lower left (low mixing-low nutrient). Large (> 20 μm cell size) microplankton will be dominant in high mixing water rich in nutrients, whereas small (< 2 μm cell size) picophytoplankton will dominate in stratified waters where nutrients are scarce. Note that large cells (diatoms and dinoflagellates) dominate in nutrient-rich coastal upwelling samples, whereas small cells (cyanobacteria) are predominant in oligotrophic subtropical regions.

Dominance of microphytoplankton (diatoms and dinoflagellates), nano (2-20 μm cell size) and picophytoplankton, and exclusively picophytoplankton (cyanobacteria) in Galician coastal upwelling region, the Mediterranean Sea, tropical and subtropical regions and other regions versus vertical mixing (Kz, x-axis) and nitrogen availability (N supply, y-axis). Adapted from observations described in detail in Villamaña et al (2019).

2. **Online quiz: Which nutrient is limiting?** Nutrient limitation can be verified experimentally using enrichment experiments (also named nutrient bioassays) with natural plankton communities. The bioassays consist in adding different nutrients to a natural seawater sample containing the phytoplankton community and comparing the response of the phytoplankton in terms of abundance (using chlorophyll-a concentration as a proxy) or photosynthetic activity (measuring $CO₂$ fixation or $O₂$ production) in the nutrient-enriched sample with that in the control sample (the same natural sample which has not received any nutrient amendment). If after the addition of a certain nutrient the abundance or photosynthetic activity of phytoplankton increases, while no change is observed in a control, then it must be concluded that limitation by such nutrient existed. Testing more than one nutrient simultaneously may be necessary because, as explained in the previous sections, situations of colimitation (two or more nutrients are simultaneously limiting growth), secondary limitation (when the addition of one nutrient forces the limitation by a second nutrient), or independent limitation (when the addition of two nutrients causes a greater growth than the response caused by each of the single nutrients separately) are relatively common. After a brief explanation about how to experimentally assess nutrient limitation, the students can access this basic online quiz to learn how to interpret the results of nutrient bioassays.

<https://view.genial.ly/632b15b7040b860017f2ae76/interactive-content-quiz-formas-basico>

3. **Learn how countries more dependent on fisheries will be the most impacted by projected productivity declines.** In the previous sections, a large geographical heterogeneity in the impact of climate change on the world fish captures and also sharp differences in the dependence of each national society on fisheries was shown. This observation allows us to pose the question on whether the highest expected declines in fish captures are associated or not with countries where fisheries account for a significant share of both their diet and their economy.

To answer this question and further discuss the implications of the observed results, a data set is presented in the table below. This data set shows the values of two variables for a number of countries. The first variable indicates the expected change in potential fish catch as a result of climate change by the end of the century and is expressed as a percentage. The second variable refers to a composite index which indicates each nation's dependency index on fisheries, taking into consideration the effects of fisheries on food, economic and employment provision. The higher the value of this index the higher the dependency of the diet or economy of a given country on fisheries.

Percentage of potential fish catch change because of climate change by the end of the century and national dependency index for a selection of countries. This index combines the dependency on fisheries of a given country taking into consideration the effects of food, economic and employment provision. Data estimated from Figure 4 in Barange et al. (2014).

Using this data set, the students should first draw a X-Y plot representing the relationship between the two mentioned variables. Once the graph has been elaborated, the students would be asked to split into small groups and interpret the information derived from the figure.

 Relationship between the percentage of potential fish catch change as a result of climate change by the end of the century and the national dependency index on fisheries for a selection of countries.

The results show that tropical and subtropical countries where potential fish catch is expected to sharply decline coincide with those more dependent on fisheries. On the contrary, countries that are expected to experience significant increases in fish captures, mainly countries located in temperate or subpolar regions, show a low dependency on fisheries. The students will

be asked to relate these results with data on the GDP per capita of these countries and discuss their implications in the context of global social inequality, thus opening the opportunity to introduce the students to critical social issues for the XXI century such as food sovereignty, climatic migrations or the wider concept of equitable and inclusive ecological transition.

The evidence base, further reading and teaching aids

Webs links Plankton images and outreach <https://www.facebook.com/Planktonbook> **Down to the Deep - The Ocean's Biological Pump** <https://serc.carleton.edu/eslabs/carbon/6b.html> **Phytoplankton - The Ocean's Green Machines:** <https://serc.carleton.edu/eslabs/carbon/6a.html> **Phytoplankton and mixing** <https://www.youtube.com/watch?v=B28pMD8mTZ4> **Ocean Data Labs** <https://datalab.marine.rutgers.edu/data-explorations/> **Ocean Fertilization** <https://web.whoi.edu/ocb-fert/> **Upwelling** <https://svs.gsfc.nasa.gov/20019> **World Ocean Atlas 2009** <https://repository.library.noaa.gov/view/noaa/1259>

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Glossary

Acidification. The decrease of surface seawater pH resulting from the absorption by the ocean of the atmospheric $CO₂$ produced by human actions.

Aquaculture. Human activity that involves the cultivation of aquatic organisms under controlled conditions in artificial facilities or enclosing areas of natural aquatic ecosystems.

Autotroph. An organism able to synthesize new organic matter, such as sugars, fat and protein (also called primary producer).

Chlorophyll. Pigment which is present in all plants, algae, and cyanobacteria, responsible for the absorption of light to provide energy for photosynthesis.

Biological pump. A biological mechanism that involves the conversion of inorganic carbon and nutrients into organic matter in surface waters, and its transport to the deep ocean, where it is converted back into inorganic carbon and nutrients.

Coastal Zone. National Exclusive Economic Zone (EEZ) (200 nautical miles from the coast) as outlined by the United Nations Convention on the Law of the Sea.

Co-limitation. The limitation of the growth or abundance of a group of organisms by two or more independent nutrients (see also nutrient limitation).

Copepods. Aquatic crustaceans with a body length of 1-10 mm, they are the main component of mesozooplankton and among the most abundant animals on Earth.

Diatoms. Single-celled algae, which have a wall of silica and attain high abundances in nutrientrich waters.

Dinoflagellates. Single-celled algae with flagella, able to swim and migrate vertically in the euphotic layer.

Euphotic layer. The upper, illuminated layer of an aquatic ecosystem, where photosynthesis is possible.

Eutrophication. A process whereby large inputs of nutrients to aquatic ecosystems, mostly from land run-off, causes a dense growth of plant/microbial life.

Fishery. A population of a fish species that is subject to extraction by humans, or the site where that population lives. By extension it includes exploited populations of other species such as crustaceans and mollusks.

Greenhouse gas. A gas that contributes to the greenhouse effect by absorbing infrared radiation. Carbon dioxide, methane and chlorofluorocarbons are examples of greenhouse gasses.

Krill. Shrimp-like, crustacean plankton that are abundant in high-latitude seas, where they constitute the main food for large animals such as whales

Mesozooplankton. Planktonic animals with a body length between 0.2 and 20 mm, such as the copepods.

Nutrient limitation. An ecological state whereby the activity and/or abundance of a group of organisms is lower than could be if an additional supply of nutrients is provided.

Nutrient bioassay. An experimental set-up aimed at determining the limiting nutrient of a given community at a given moment.

Oligotrophic. An environment where nutrients are persistently scarce.

Open ocean. Marine regions located far from the coasts and continental shelves, with seafloor depths > 200 m

Phytoplankton. Microscopic, unicellular organisms (including both eukaryotic and prokaryotic taxa) that drift with the currents and are able to photosynthesize.

Phytoplankton bloom. Massive growth and accumulation of phytoplankton biomass which may cause discoloration of the water bodies.

Photosynthesis. Synthesis of organic matter, such as sugars, using $CO₂$ and the energy provided by light.

Plankton. Organisms or groups of small organisms that live in the water column and tend to drift with the currents.

Pycnocline. The transition layer between less dense water at the ocean's surface and denser water below.

Response ratio. The mean response in an experimental group divided by that in the control group. It is commonly used to quantify the effect of nutrient enrichment in bioassays.

Stratification. The division of the water column into layers with different densities caused by differences in temperature or salinity or both.

Trophic efficiency. The percentage of biomass produced in a trophic level that is passed on to the next

Trophic level. The position an organism occupies in the food chain.

Trophic chain (also food chain). An ensemble of organisms in which some (primary producers) synthesize new organic material, while others consume it (herbivores) and are in turn eaten by predators. A typical marine food chain is formed by algae, zooplankton and fish.

Upper mixed layer. Layer where the mixing driven by the wind and exchanges of heat and salt homogenizes vertical gradients of properties.

Upwelling. Wind-driven motion of dense, cooler, and nutrient-rich water towards the ocean surface, replacing the warmer, usually nutrient-depleted surface water.