

Appendix 2-E. Phytoplankton production: regenerated and new

All production of phytoplankton at the base of food webs for tuna and other large pelagic fish occurs in the photic zone, where there is sufficient light for photosynthesis (Figure 1). This primary production uses nutrients regenerated within the photic zone and ‘new’ nutrients transferred there from deeper water.¹ Regenerated nutrients, consisting mainly of ammonium (NH_4) and soluble reactive phosphorus (SRP), lead to ‘regenerated production’, whereas the nutrients involved in ‘new production’ are nitrates (NO_3) and di-nitrogen (N_2), SRP and silicates. The availability of nitrogen, in the form of either ammonium or nitrate, is the main factor limiting the primary productivity in most oceanic ecosystems, although the supply of SRP or micronutrients such as iron (Fe) can also limit production.²

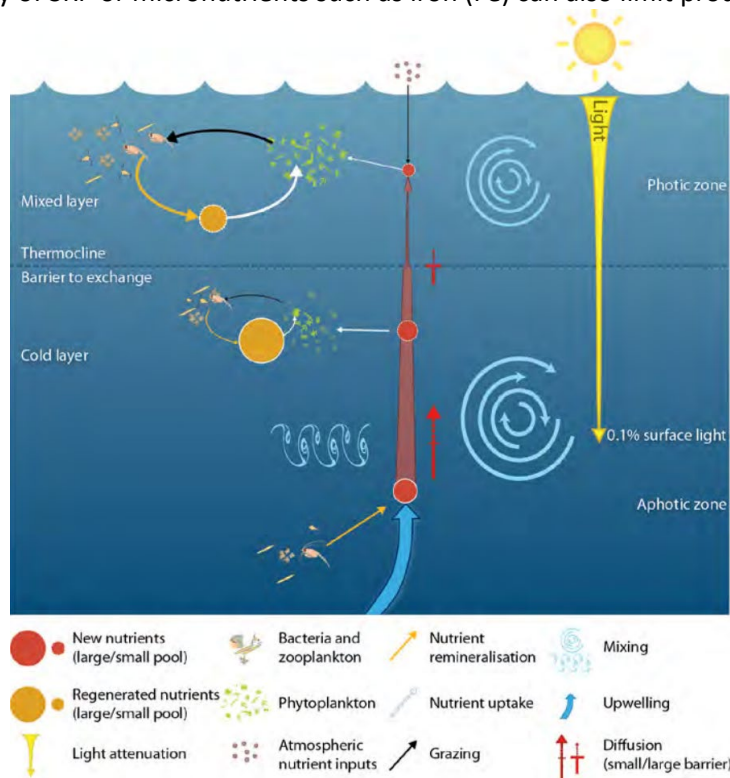


Figure 1. Key features of the surface layer of the ocean that determine primary production. The photic zone, where photosynthesis occurs, typically extends to the depth that receives 0.1% of the surface light intensity in tropical areas. Below this is the aphotic zone, where there is insufficient light for photosynthesis. The warmer mixed surface layer is separated from the deeper cold layer at the thermocline, where water temperature decreases abruptly. The thermocline is a barrier to mixing and the transfer of nutrients from cold, deep water to the surface mixed layer. The cold layer is supplied with nutrients brought up from the aphotic zone by mixing, diffusion and vertical advection (upwelling), depending on the location.³

¹ Ganachaud, A.S., Sen Gupta, A., Orr, J.C., Wijffels, S.E., Ridgway, K.R., Hemer, M.A., Maes, C., Steinberg, C.R., Tribollet, A.D., Qiu, B. and Kruger, J.C. 2011. Observed and expected changes to the tropical Pacific Ocean. In: Bell J.D., Johnson, J.E. and Hobday, A.J. 2011. *Vulnerability of tropical Pacific fisheries and aquaculture to climate change*. Chapter 3. pp. 101–188. Secretariat of the Pacific Community, Noumea, New Caledonia. 941 pages.

² Le Borgne, R., Allain, V., Griffiths, S.P., Matear, R.J., McKinnon, A.D., Richardson, A.J. and Young, J.W. 2011. Vulnerability of open ocean food webs in the tropical Pacific to climate change. In: Bell J.D., Johnson, J.E. and Hobday, A.J. 2011. *Vulnerability of tropical Pacific fisheries and aquaculture to climate change*. Chapter 4. pp. 189–250. Secretariat of the Pacific Community, Noumea, New Caledonia. 941 pages.

³ Le Borgne, R., Allain, V., Griffiths, S.P., Matear, R.J., McKinnon, A.D., Richardson, A.J. and Young, J.W. 2011. Vulnerability of open ocean food webs in the tropical Pacific to climate change. In: Bell J.D., Johnson, J.E. and

Regenerated nutrients alone are not sufficient to support primary production – a minimum level of new nutrients is needed to compensate for losses that occur within the photic zone, and to maintain production of phytoplankton. The vertical structure of the water column determines the availability of new nutrients in the photic zone and four different situations occur in the Pacific (Figure 2).⁴

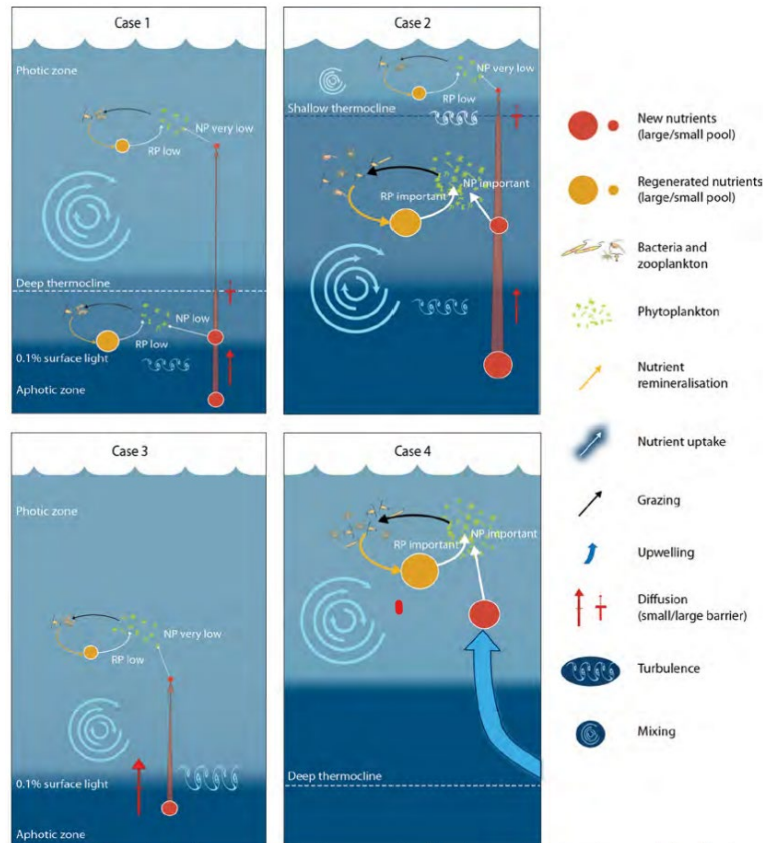


Figure 2. Four typical cases of variation in vertical hydrographic structure and its effect on production of phytoplankton in the tropical Pacific Ocean. In Case 1, the thermocline is deep but still in the photic zone; primary production based on regenerated nutrients dominates in the mixed layer but is supplemented by some new production (NP) below the thermocline. In Case 2, the mixed layer remains nutrient-poor (oligotrophic) but a shoaling of the thermocline allows cold, nutrient-rich water to increase both regenerated production (RP) and NP substantially within the photic zone below the thermocline. In Case 3, the thermocline is weak and deep, allowing some inputs of ‘new’ nutrients from the deep oligotrophic waters to enter the photic zone. However, the biomass of phytoplankton is low and driven mainly by RP. In Case 4, new nutrients delivered by upwelling supply the entire photic zone, even though the thermocline is deep, permitting significant NP and high RP. Note that the photic zone is shallower in Cases 2 and 4 because the higher concentrations of plankton there reduce light penetration.⁵

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⁴ Le Borgne, R., Allain, V., Griffiths, S.P., Matear, R.J., McKinnon, A.D., Richardson, A.J. and Young, J.W. 2011. Vulnerability of open ocean food webs in the tropical Pacific to climate change. In: Bell J.D., Johnson, J.E. and Hobday, A.J. 2011. Vulnerability of tropical Pacific fisheries and aquaculture to climate change. Chapter 4. pp. 189–250. Secretariat of the Pacific Community, Noumea, New Caledonia. 941 pages.

⁵ Le Borgne, R., Allain, V., Griffiths, S.P., Matear, R.J., McKinnon, A.D., Richardson, A.J. and Young, J.W. 2011. Vulnerability of open ocean food webs in the tropical Pacific to climate change. In: Bell J.D., Johnson, J.E. and

In regions where there is a pronounced thermocline (Cases 1 and 2), transfer of nutrients to the mixed layer is inhibited because the thermocline acts as a barrier to exchanges between nutrient-rich deep layers and the superficial mixed layer. In such situations, when the thermocline is deep (Case 1), new production is low because it occurs only in the lower part of the photic zone with low light intensity. In Case 1, net primary production (NPP), which is the sum of new and regenerated production, is low.

In situations where the thermocline is shallower (Case 2), NPP is higher due to more new production occurring in the nutrient-rich water of the photic zone, below the thermocline. The deeper the thermocline, the lower the new production and NPP.⁶ In regions where the thermocline is weak, exchanges between the deep nutrient-rich layers and the photic zone are easier than in Cases 1 and 2. These exchanges occur through processes such as turbulence, mixing, and diffusion, which then drive new production.

In the gyres in the northern and southern tropical Pacific region, however, the anticyclonic circulation, with prevailing downwelling conditions, leads to a very deep thermocline. In these situations, physical nutrient supply is inefficient at transporting nutrients into the photic zone (Case 3), except via temporary eddies linked to wind bursts. Consequently, production in the photic zone of these gyres is very low. Finally, where there is strong upwelling (vertical transport of deeper water masses to the surface), new nutrients are brought into the whole photic zone, leading to high new production (Case 4).⁷

The source of nutrients also influences the composition of the phytoplankton. New primary production is usually dominated by diatoms because they out-grow other phytoplankton.⁸ However, diatoms are replaced by other phytoplankton where the supply of silicon limits growth because diatoms cannot construct their shells without it.⁹ In turn, the size composition of the phytoplankton determines the type and size of zooplankton that graze them. Relatively large zooplankton grazers (mesozooplankton), like copepods (Table 1), dominate areas of new primary production, feeding on the diatoms and large phytoplankton common there. On the other hand, regenerated primary production is dominated by tiny phytoplankton (Table 1), which are grazed by very small zooplankton (nanozooplankton), such as heterotrophic flagellates and ciliates (Table 1).¹⁰

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⁶ Herbland, A. and Voituriez, B. 1979. Hydrological structure analysis for estimating the primary production in the tropical Atlantic ocean. *Journal of Marine Research* 37, 87–101.

⁷ Le Borgne, R., Allain, V., Griffiths, S.P., Matear, R.J., McKinnon, A.D., Richardson, A.J. and Young, J.W. 2011. Vulnerability of open ocean food webs in the tropical Pacific to climate change. In: Bell J.D., Johnson, J.E. and Hobday, A.J. 2011. Vulnerability of tropical Pacific fisheries and aquaculture to climate change. Chapter 4. pp. 189–250. Secretariat of the Pacific Community, Noumea, New Caledonia. 941 pages.

⁸ Mackey, D.J., Blanchot, J., Higgins, H.W. and Neveux, J. 2002. Phytoplankton abundances and community structure in the equatorial Pacific. *Deep-Sea Research II* 49, 2561–2582.

⁹ Dugdale, R.C., Wischmeyer, A.G., Wilkerson, F.P., Barber, R.T. and others. 2002. Meridional asymmetry of source nutrients to the equatorial Pacific upwelling ecosystem and its potential impact on ocean-atmosphere CO₂ flux; a data and modelling approach. *Deep-Sea Research II* 49, 2513–2531.

¹⁰ Landry, M.R. and Kirchman, D.L. 2002. Microbial community structure and variability in the tropical Pacific. *Deep-Sea Research II* 49, 2669–2693.

Table 1. The sources of food that build the food web for tuna and other large pelagic fish in the tropical Pacific Ocean, together with their size, representative organisms, trophic status and depth of their habitat. The first three sources of food belong to the ‘paraprimary’ level, which is at the base of the food web, like primary production, but is not the direct result of photosynthesis.^{11,12,13}

Food source	Size range	Representative organisms	Trophic status	Depth of habitat
Dissolved organic matter	< 0.2 μm		Paraprimary level	All depths
Detritus	> 0.2 μm		Paraprimary level	All depths
Heterobacteria	> 0.2 μm		Paraprimary level	All depths
Picophytoplankton	0.2–2 μm	Cyanobacteria (<i>Prochlorococcus</i> , <i>Synechococcus</i>), pico-eukaryotes	Primary level	Photic zone
Nanophytoplankton	2–20 μm	Diatoms, dinoflagellates, haptophytes, pelagophytes	Primary level	Photic zone
Microphytoplankton	20–200 μm	Diatoms, dinoflagellates, filamentous cyanobacteria (<i>Trichodesmium</i>)	Primary level	Photic zone
Nanozooplankton	2–20 μm	Heterotrophic flagellates, small ciliates	Secondary level	All depths
Microzooplankton	20–200 μm	Radiolarians, foraminiferans, tintinnids, larval copepods	Secondary level	All depths
Mesozooplankton	200–2000 μm	Copepods, chaetognaths, larvaceans, ostracods, doliolids, larval fish	Secondary/tertiary level	All depths
Macrozooplankton	2–20 mm	Pteropods, heteropods, siphonophores, jellyfish, salps	Secondary level and over	All depths
Epipelagic micronekton	2–10 cm	Small fish, amphipods, cephalopods, and shrimp	Secondary level and over	0–200 m
Mesopelagic micronekton	2–10 cm	Small fish, amphipods, cephalopods, and shrimp	Secondary level and over	200–500 m
Deep micronekton	2–10 cm	Fish, cephalopods, and shrimp	Secondary level and over	> 500 m

In general, therefore, food webs supporting tuna based on significant new production and larger phytoplankton tend to have fewer trophic levels. New production is augmented by the uptake of N_2 , a dissolved gas, in a process called ‘diazotrophy’.

The main organisms supported by N_2 (diazotrophs) are unicellular cyanobacteria¹⁴, endosymbiots and filamentous cyanobacteria, which bloom in summer.¹⁵ Large populations of cyanobacteria can

¹¹ Dussart, B.H. 1965. Les différentes catégories de plancton. *Hydrobiologia* 26, 72–74.

¹² Legand M, Bourret P, Fourmanoir P, Grandperrin R and others. 1972. Relations trophiques et distributions verticales en milieu pélagique dans l’océan Pacifique intertropical. *Cahiers ORSTOM, Série Océanographie* 10, 303–393.

¹³ UNESCO. 1968. Zooplankton sampling. Monographs on oceanographic methodology 2, UNESCO, Paris, France.

¹⁴ Zehr, J.P., Waterbury, J.B., Turner, P.J., Montoya, J.P. and others. 2001. Unicellular cyanobacteria fix N_2 in the subtropical North Pacific Ocean. *Nature* 412, 635–638.

¹⁵ Dore, J.E., Letelier, R.M., Church, M.J., Lukas, R. and Karl, D. 2008. Summer phytoplankton blooms in the oligotrophic North Pacific Subtropical Gyre: Historical perspective and recent observations. *Progress in Oceanography* 76, 2–38.

help alleviate the effects of nitrogen limitation in oligotrophic regions, where they can contribute 30–50% of new production.¹⁶ However, the contribution of blooms of cyanobacteria to the food web appears to be highly variable, and is still not fully understood.

Abundance of zooplankton have also sometimes been linked to blooms of cyanobacteria.¹⁷ However, a high biomass of cyanobacteria does not always result in increased productivity of zooplankton because some cyanobacteria are toxic or unpalatable, except to harpacticoid copepods.¹⁸ In such situations, the decayed organic matter from cyanobacteria needs to be mineralised before contributing to a new production cycle that may support other grazers.¹⁹

¹⁶ Karl, D., Michaels, A., Bergman, B., Capone, D.G. and others. 2002. Dinitrogen fixation in the world's oceans. *Biogeochemistry* 57/58, 47–98.

¹⁷ Landry, M.R., Al-Mutairi, H., Selph, K.E., Christensen, S. and Nunnery, S. 2001. Seasonal patterns of mesozooplankton abundance and biomass at Station ALOHA. *Deep-Sea Research II* 48, 2037–2061.

¹⁸ O'Neil JM and Roman MR (1994) Ingestion of the cyanobacterium *Trichodesmium* spp. by pelagic harpacticoid copepods *Macrosetella*, *Miracia* and *Oculosetella*. *Hydrobiologia* 292/293, 235–240.

¹⁹ Le Borgne, R., Allain, V., Griffiths, S.P., Matear, R.J., McKinnon, A.D., Richardson, A.J. and Young, J.W. 2011. Vulnerability of open ocean food webs in the tropical Pacific to climate change. In: Bell J.D., Johnson, J.E. and Hobday, A.J. 2011. Vulnerability of Tropical Pacific fisheries and aquaculture to climate change. Chapter 4. pp. 189–250. Secretariat of the Pacific Community, Noumea, New Caledonia. 941 pages.