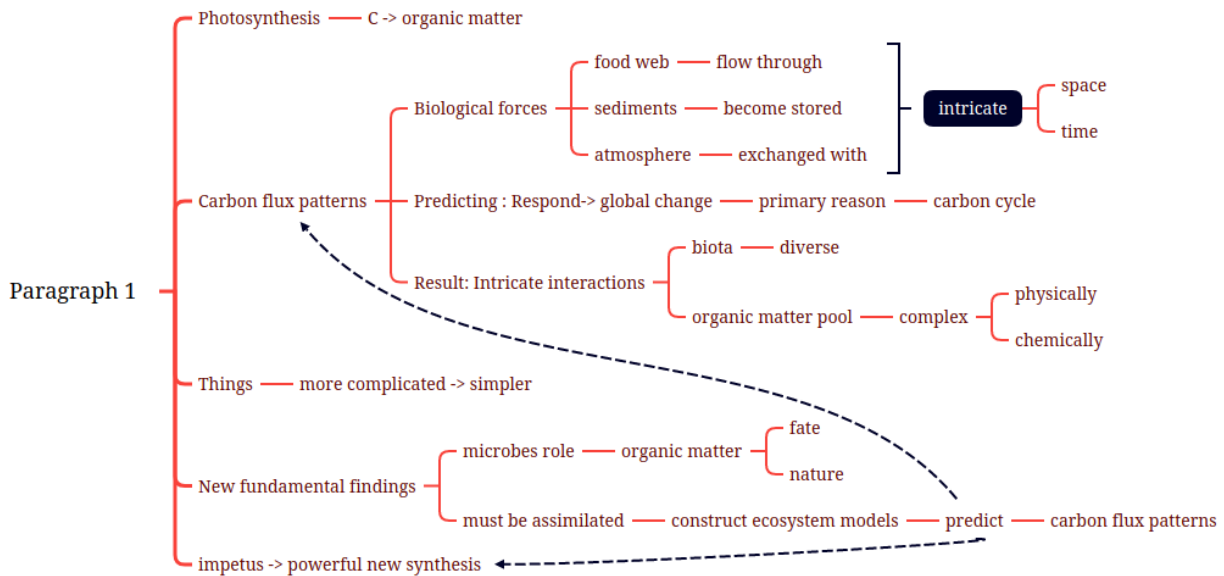


# Microbial Control of Oceanic Carbon Flux: The Plot Thickens

FAROOQ AZAM 1998

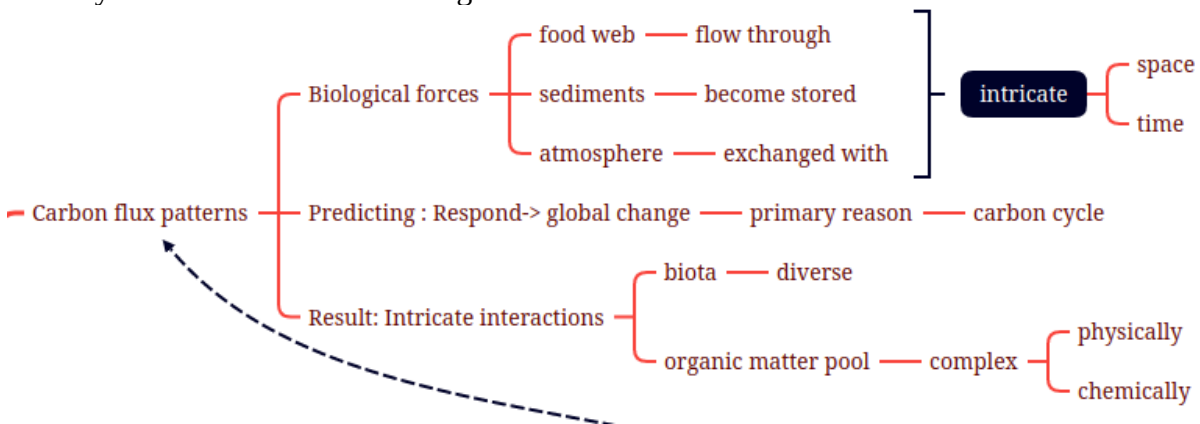


Photosynthesis fixes carbon into organic matter in the ocean. Biological forces then paint intricate flux patterns for carbon in ocean space and in time, as it flows through the food web, becomes stored in the sediments and exchanged with the atmosphere. Predicting how these carbon flux patterns might respond to global change (or to human manipulation) is a primary reason for learning more about the workings of the ocean's carbon cycle. The flux patterns are a result of intricate interactions of a diverse biota with a physically and chemically complex pool of organic matter. It now seems that things will get even more complicated before they get simpler. New fundamental findings on the roles of microbes in the fate of organic matter and, recently, on the nature of the organic matter itself (1-4) must be properly assimilated before we can hope to construct ecosystem models to predict the patterns of carbon flux. This impetus could lead to a powerful new synthesis.

## Photosynthesis — C → organic matter

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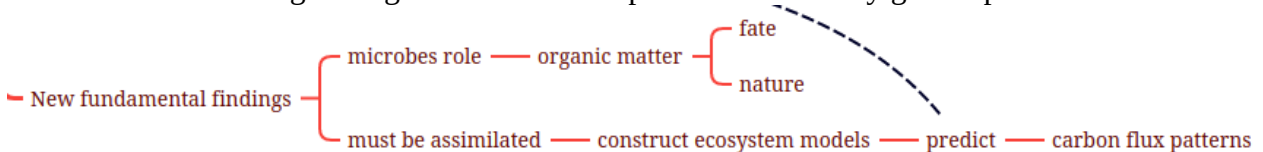
The flux patterns are a result of ~~the~~ intricate interactions of **a** diverse biota with a physically and chemically complex **pool of** organic matter.

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## Things — more complicated → simpler

It **now** seems that things will get **even** more complicated before they ~~can~~ get simpler.

It now seems that things will get even more complicated before they get simpler.



New fundamental findings on the roles of microbes **in the fate and nature of organic matter** must be assimilated before constructing ecosystem models to predict carbon flux patterns.

New fundamental findings on the roles of microbes in the fate of organic matter **and, recently, on the nature of the organic matter itself (1-4)** must be **properly** assimilated before we **can hope to** construct ecosystem models to predict the patterns of carbon flux.

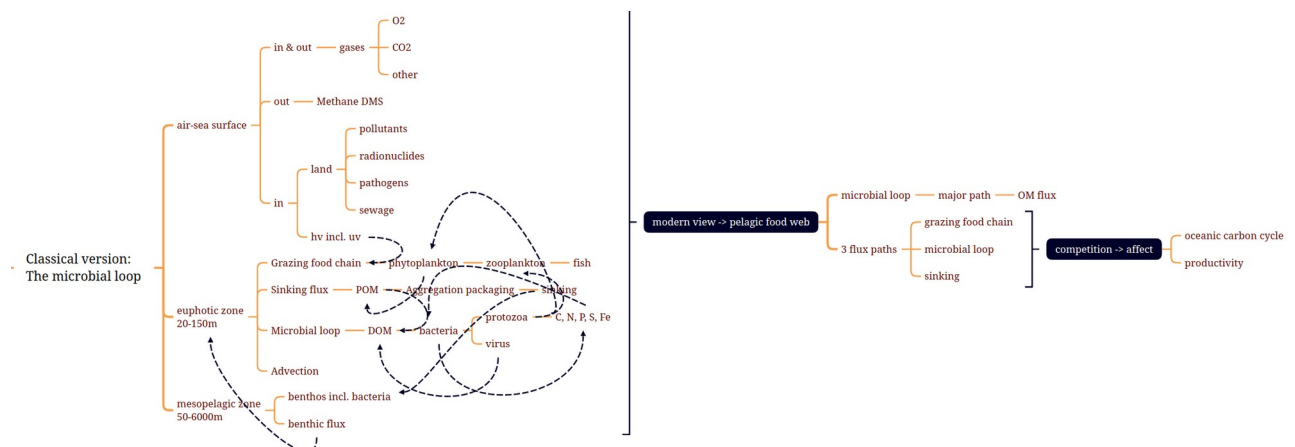
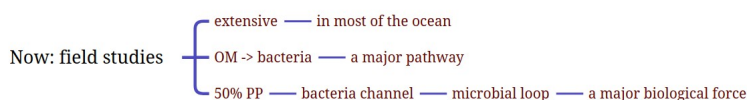
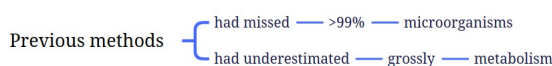
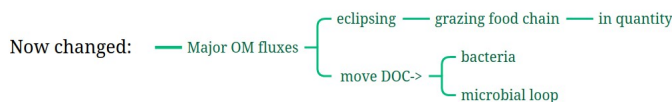
## impetus → powerful new synthesis

This **can be an impetus for** a powerful new synthesis.

This **impetus could lead to** a powerful new synthesis

What biological forces act on photosynthetically produced organic matter in the ocean? Historically, the paradigm has been that essentially all primary production stays within the particle phase (5), it is eaten by herbivores, and the fate of carbon is determined by the “grazing food chain” (see the diagram in the figure below). Little dissolved organic matter is spilled for bacteria to use. It had, therefore, been implicitly assumed to be safe to ignore bacteria, protozoa, and viruses in studying the fate of organic matter—they were too sparse and not active enough (5). This is now changed (5-8): Major fluxes of organic matter, often eclipsing the grazing food chain in quantity, move via dissolved organic matter into bacteria and the “microbial loop” (7, 8) (figure below). Previous methods had missed >99% of microorganisms and had grossly underestimated their metabolism. Now we know from extensive field studies that in most of the ocean, organic matter flux into bacteria is a major pathway; one-half of oceanic primary production on average is channeled via bacteria into the microbial loop (7, 8)—a major biological force in the ocean.

What biological forces -> organic matter — photosynthetically produced in the ocean



The microbial loop: classical version.

Modern view of the pelagic food web, emphasizing the microbial loop as a major path for organic matter flux. Competition between the three main flux paths—grazing food chain, microbial loop, and sinking—significantly affects oceanic carbon cycle and productivity. DOM, dissolved organic matter; DMS, dimethylsulfide.

What biological forces -> — organic matter — { photosynthetically produced  
in the ocean

What biological forces act on the photosynthetically produced organic matter in the ocean?

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Historically, a widely accepted paradigm suggests that primary production essentially all stays in the phase of particle and is eaten by herbivores and the fate of carbon is determined by the grazing food chain.

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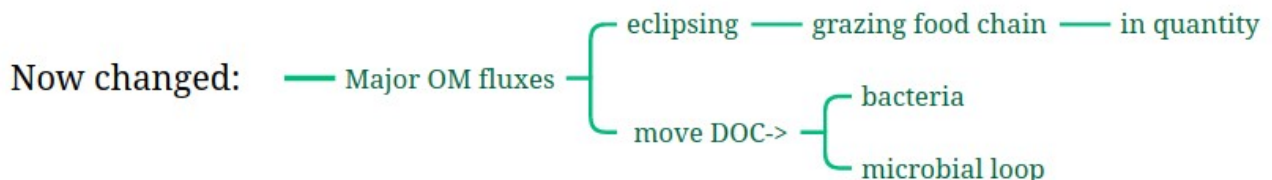
therefore, little dissolved organic carbon is spilled for bacteria to use.

Little dissolved organic matter is spilled for bacteria to use.

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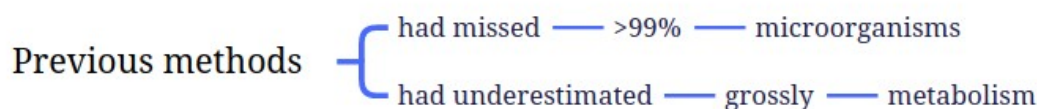
It had, therefore, been implicitly assumed to be safe to ignore bacteria, protozoa and viruses in studying the fate of organic matter -- they were too sparse and not active enough.



Now things are changed: Major fluxes of organic matter, eclipsing the grazing food chain in quantity, move into bacteria and microbial loop via dissolved organic carbon.

This is now changed (5-8): Major fluxes of organic matter, often eclipsing the grazing food chain in quantity, move via dissolved organic matter into bacteria and the “microbial loop” (7, 8) (figure below).

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Now: field studies { extensive — in most of the ocean  
OM -> bacteria — a major pathway  
50% PP — bacteria channel — microbial loop — a major biological force

Now extensive field studies in most of the ocean has found that ~~transport~~ of organic matter via bacteria is a major pathway.

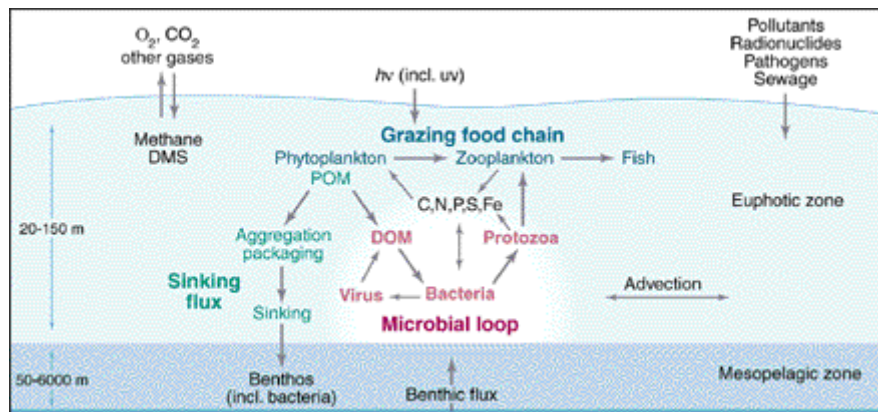
Now **we know from** extensive field studies **that** in most of the ocean, organic matter **flux into** bacteria is a major pathway;

Now we know from extensive field studies that in most of the ocean, organic matter flux into bacteria is a major pathway;

One-half of primary production is channeled via bacteria in the microbial loop, ~~which is~~ a major biological force.

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The microbial loop: classical version.



Modern view of pelagic food web emphasizes that the microbial loop is a major path for organic matter flux.

Modern view of the pelagic food web, **emphasizing** the microbial loop as a major path for organic matter flux.

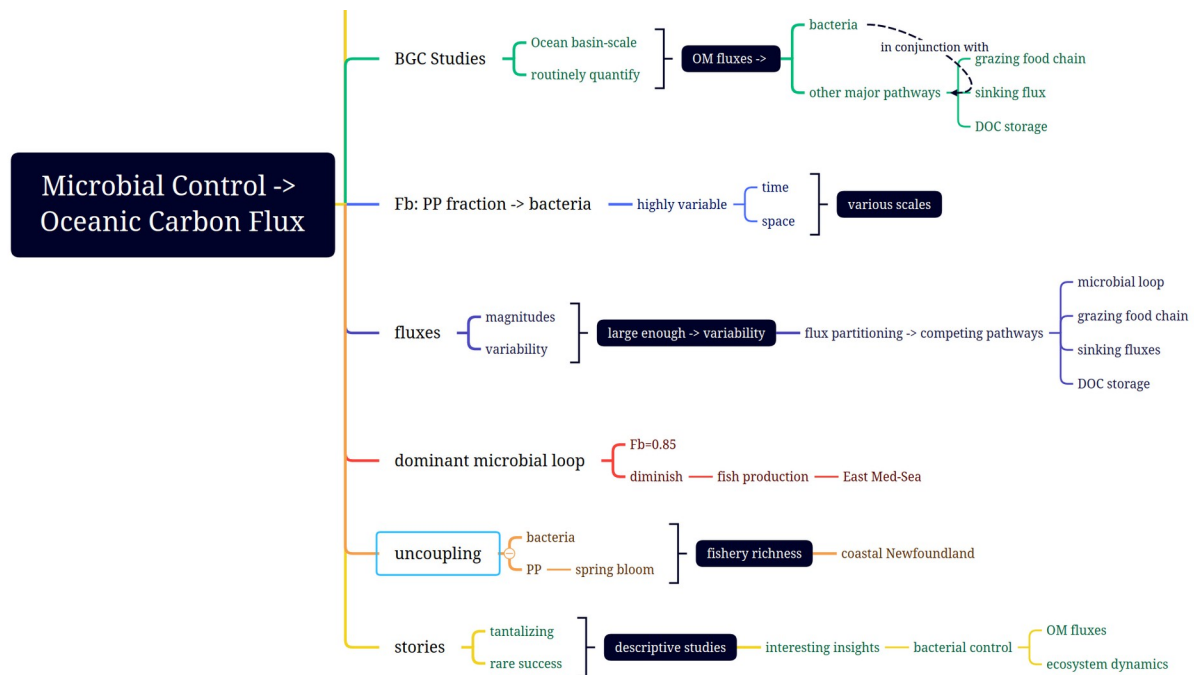
Modern view of the pelagic food web, emphasizing the microbial loop as a major path for organic matter flux.

Competition among three flux paths, grazing food chain, microbial loop and sinking, significantly affect oceanic carbon cycle and productivity.

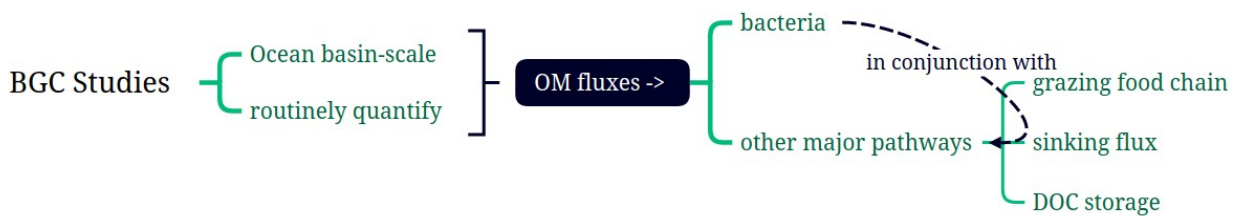
Competition **between the** three **main** flux paths—grazing food chain, microbial loop, and sinking—significantly **affects** oceanic carbon cycle and productivity.

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Ocean basin-scale biogeochemical studies now routinely quantify organic matter fluxes into bacteria in conjunction with other major flux pathways: grazing food chain, sinking flux, and dissolved organic matter “storage.” The fraction of primary production used by bacteria ( $F_b$ ) is highly variable over various time and space scales (7-10). The magnitudes and variability of the fluxes are large enough to cause variability in flux partitioning between competing pathways (see figure below)—the microbial loop, the grazing food chain, sinking fluxes, and storage of dissolved organic matter (8, 9). Fish production in the eastern Mediterranean was diminished by a dominant microbial loop ( $F_b = 0.85$ ) (11). In an earlier study (12), the richness of the fishery in coastal Newfoundland was ascribed to uncoupling of bacteria from primary production during the spring bloom. These are tantalizing but rare success stories where descriptive studies lead to interesting insights into the bacterial control of organic matter fluxes and ecosystem dynamics.



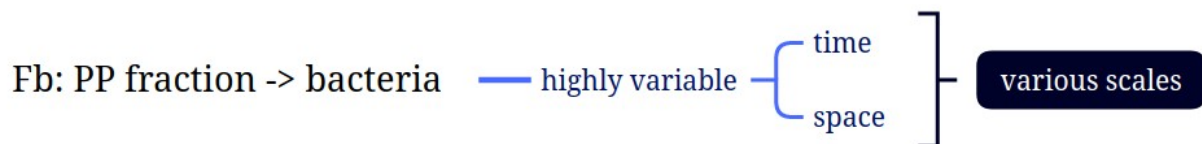




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Ocean basin-scale biogeochemical studies **now** routinely quantify organic matter fluxes into bacteria in conjunction with other major **flux** pathways: grazing food chain, sinking flux, and dissolved organic matter “storage.”

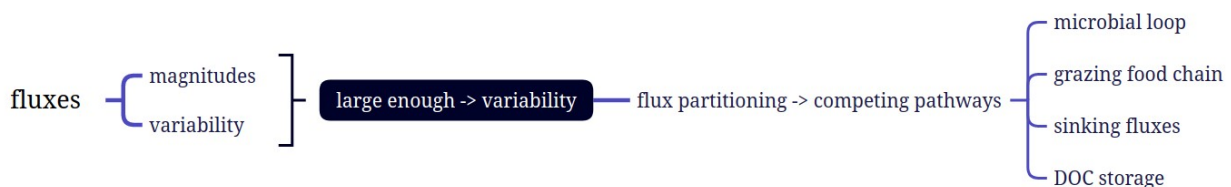
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The fraction of primary production **into** bacteria (Fb) is highly variable over various time and space scales.

The fraction of primary production **used by** bacteria (Fb) is highly variable over various time and space scales (7-10).

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dominant microbial loop —  $F_b=0.85$  — diminish — fish production — East Med-Sea

A study in the East Med-Sea showed that fish production was diminished by the dominant microbial loop ( $F_b=0.85$ ).

Fish production in the eastern Mediterranean was diminished by a dominant microbial loop ( $F_b = 0.85$ ) (11).

Fish production in the eastern Mediterranean was diminished by a dominant microbial loop ( $F_b=0.85$ ).

uncoupling — bacteria — PP — spring bloom — fishery richness — coastal Newfoundland

A few studies found that fishery richness in the coastal Newfoundland was ascribed to the uncoupling between bacteria and primary production during spring bloom.

In an earlier study (12), the richness of the fishery in coastal Newfoundland was ascribed to uncoupling of bacteria from primary production during the spring bloom.

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stories — tantalizing — rare success — descriptive studies — interesting insights — bacterial control — OM fluxes — ecosystem dynamics

These tantalizing and rare success stories show descriptive studies have interesting insights in the bacterial control of organic matter fluxes and ecosystem dynamics.

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However, we lack a conceptual framework to predict variation in organic matter flux into bacteria and how it fits into the overall oceanic flux picture (for example, how the flux partitioning will respond to global change). This requires elucidating the causes and mechanisms of variability of organic matter flux into bacteria. How do bacteria interact with organic matter, and what regulates the flux of organic matter into them?

However, lack — a conceptual framework — predict — { OM flux -> bacteria  
how -> overall flux picture — e.g. how: flux partitioning -> global change

This requires elucidating — { causes  
mechanisms } — variability — OM flux -> bacteria

How: interact with — { bacteria  
OM

What: regulates — OM flux -> them

However, lack — a conceptual framework — predict — { OM flux -> bacteria  
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However, we lack a conceptual framework to predict ~~the flux of organic matter~~ into bacteria and how ~~is the~~ overall oceanic flux picture ~~like~~, for example, how ~~does~~ flux partitioning ~~response~~ to global change?

However, we lack a conceptual framework to predict **variation in organic matter flux** into bacteria and **how it fits into** the overall oceanic flux picture (for example, how **the** flux partitioning **will respond** to global change).

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This requires elucidating causes and mechanisms of variability of organic matter flux into bacteria. This requires elucidating **the** causes and mechanisms of variability of organic matter flux into bacteria.

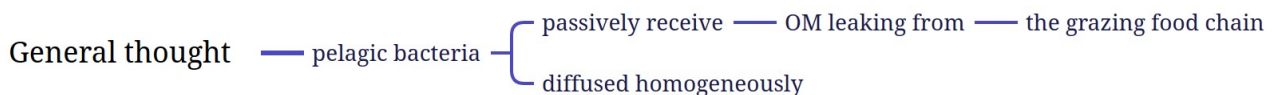
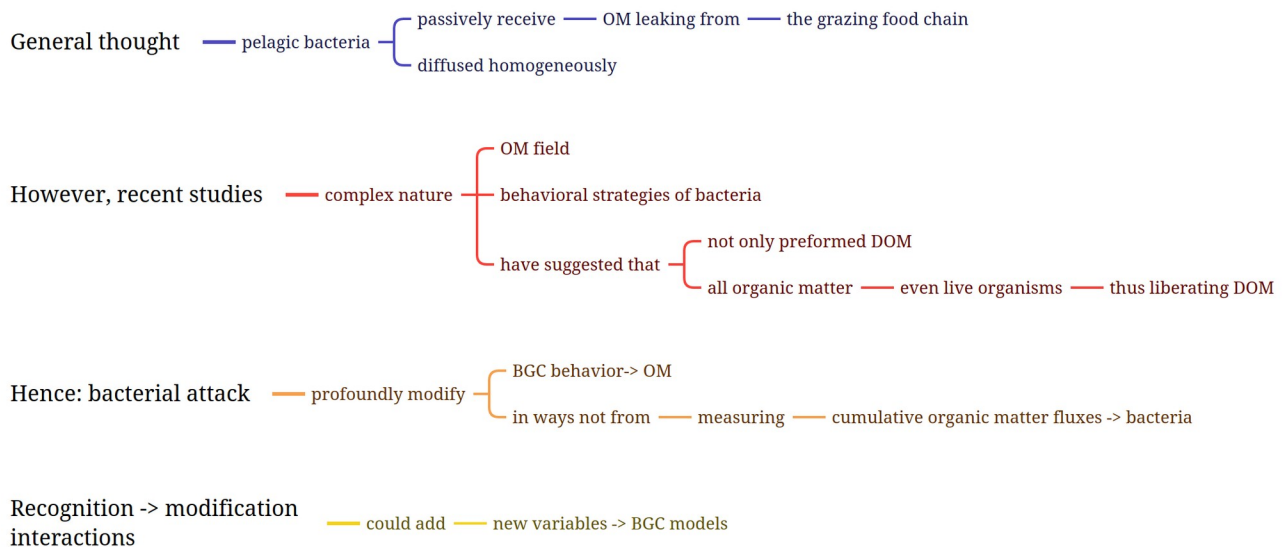
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How bacteria interact with organic matter and what regulates organic matter flux into them.

How **do** bacteria interact with organic matter, and what regulates the flux of organic matter into them?

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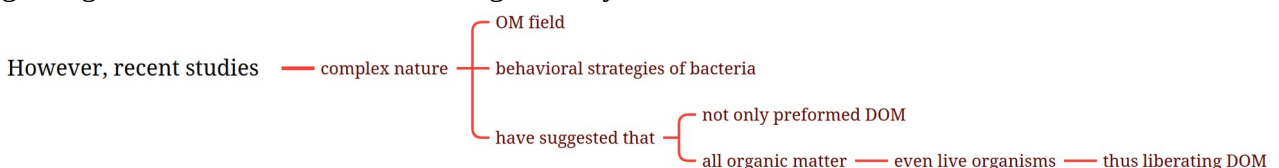
It is generally thought that pelagic bacteria passively receive dissolved organic matter leaking from the grazing food chain and diffused homogeneously. However, recent studies on the complex nature of the organic matter field (1-4, 13) and behavioral strategies of bacteria (14) have suggested (2) that bacteria do not use only preformed dissolved organic matter; they also attack all organic matter, even live organisms, thus liberating dissolved organic matter. Hence, bacterial attack can profoundly modify the biogeochemical behavior of organic matter in ways not inferred from measuring cumulative organic matter fluxes into bacteria. Recognition of such “modification interactions” could add important new variables in biogeochemical models.



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Hence: bacterial attack — profoundly modify — BGC behavior-> OM  
in ways not from — measuring — cumulative organic matter fluxes -> bacteria

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Recognition -> modification interactions — could add — new variables -> BGC models

Recognition of ~~the modification in the interactions~~ could add new variables in ~~the~~ biogeochemical models.

Recognition of such “modification interactions” could add **important** new variables in biogeochemical models.

Recognition of such ‘modification interactions’ could add important new variables in biogeochemical models.

Our view -> OM — changed dramatically

Traditional dichotomy { POM  
DOM } — being replaced by — OM continuum

New classes { abundant colloids  
submicrometer particles  
transparent polymer particles } — have been discovered

Oceanic dark matter — size range — 20nm to hundreds of micrometers

Pelagic bacteria — gel-like polymeric matrix { colloids  
particles } — embedded as — hotspots — suprapolymeric

Interaction -> microscale features { bacteria  
organic matter continuum } — behavioral response -> heterogeneity — activity hotspots — BGC transformations { distinctive natures  
intensities }

Patchiness — may support — bacterial diversity — high

Chin et al { an important recent study  
polymers — indeed form — a gel }

Our view of the organic matter in seawater has changed dramatically. The traditional dichotomy of particulate organic matter versus dissolved organic matter is being replaced by the concept of an organic matter continuum (2). Several new classes of abundant colloids, submicrometer particles, and transparent polymer particles have been discovered (1, 4, 13). This oceanic “dark matter” ranges in size from 20 nm to hundreds of micrometers. It has been proposed (2, 3) that pelagic bacteria experience a gel-like polymeric matrix with colloids and particles embedded as suprapolymeric “hotspots” (8) (see the lower part of the figure). The interaction of bacteria with the organic matter continuum, and their behavioral response to its heterogeneity, creates microscale features—activity hotspots—with distinctive natures and intensities of biogeochemical transformations. Patchiness may also support high bacterial diversity. An important recent study by Chin et al. (1) demonstrated that polymers in seawater indeed form a gel.

## — Our view -> OM — changed dramatically

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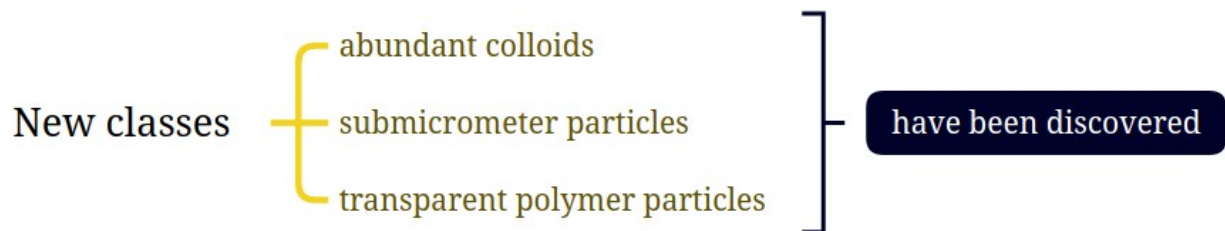
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The traditional dichotomy of particulate organic matter **versus** dissolved organic matter is being replaced by **the concept of an** organic matter continuum (2).

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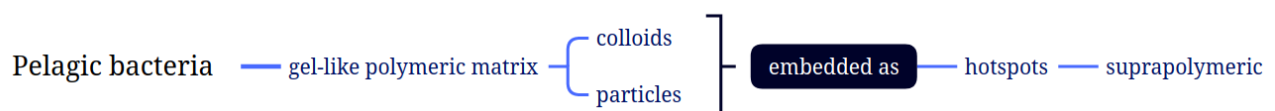
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## Oceanic dark matter — size range — 20nm to hundreds of micrometers

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**This** oceanic “dark matter” **ranges** in size from 20 nm to hundreds of micrometers.

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Pelagic bacteria ~~is~~ a gel-like polymeric matrix ~~of~~ colloids and particles embedded as suprapolymeric hotspots.

**It has been proposed (2, 3) that** pelagic bacteria **experience** a gel-like polymeric matrix **with** colloids and particles embedded as suprapolymeric “hotspots” (8)

It has been proposed that pelagic bacteria experience a gel-like polymeric matrix with colloids and suprapolymeric hotspots.



Interaction between bacteria and organic matter continuum is a behavioral response to the heterogeneity of these activity hotspots with biogeochemical transformations in distinctive natures and intensities which determines the microscale features.

The interaction of bacteria with the organic matter continuum, and their behavioral response to its heterogeneity, creates microscale features—activity hotspots—with distinctive natures and intensities of biogeochemical transformations.

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Patchiness — may support — bacterial diversity — high

The patchiness may support high bacterial diversity.

Patchiness may also support high bacterial diversity.

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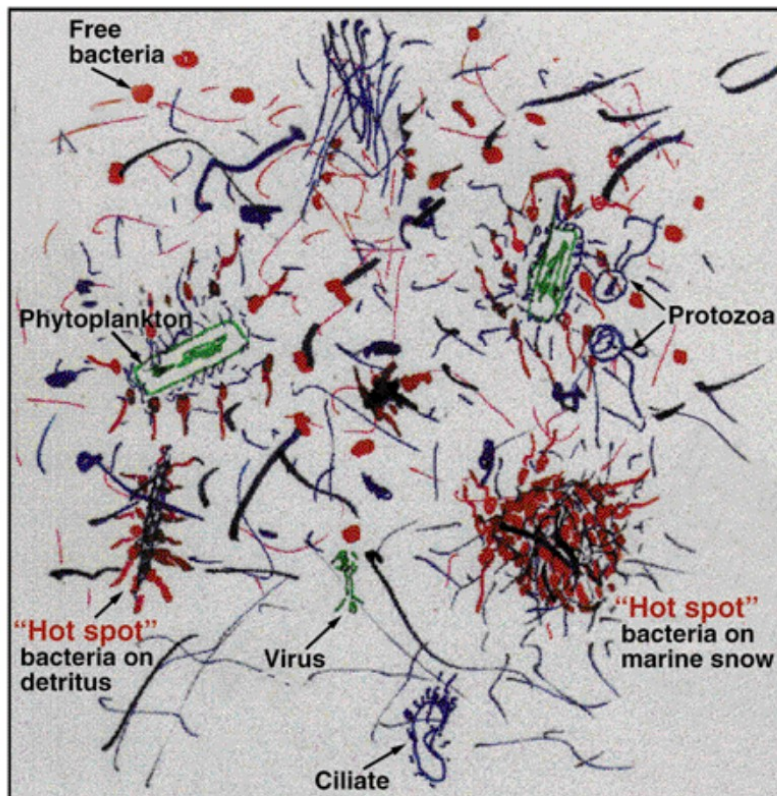
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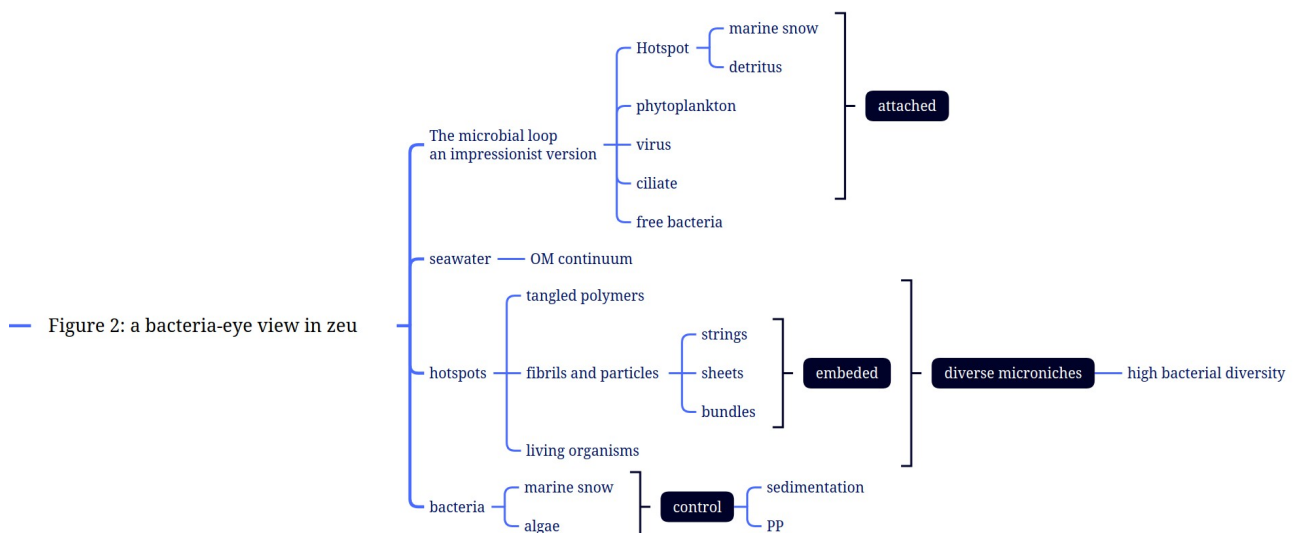
An important recent study by Chin et al demonstrated that polymers in seawater indeed form a gel.





### The microbial loop: impressionist version.

A bacteria-eye view of the ocean's euphotic layer. Seawater is an organic matter continuum, a gel of tangled polymers with embedded strings, sheets, and bundles of fibrils and particles, including living organisms, as "hotspots." Bacteria (red) acting on marine snow (black) or algae (green) can control sedimentation and primary productivity; diverse microniches (hotspots) can support high bacterial diversity.



Do bacteria respond to the structure of the organic matter field? Large bacterial populations can develop on hotspots—for example, marine snow, dead and even living algae—and in association with the “dark matter.” [In one study, 24 to 68% of bacteria were on transparent particles (13)]. Oceanic bacteria (14) exhibit sophisticated behavior—swimming speeds of hundreds of micrometers per second, unusual swimming (run reversals), and chemosensing. The organic matter field is dominantly polymeric and suprapolymeric, so most pelagic bacteria have a diverse repertoire of surface-bound enzymes (proteases, glucosidases, lipases, phosphatases, nucleases) to cause its hydrolysis (15). Small-scale variation of species composition can significantly change the distributions of enzyme activities (16). Pelagic bacteria also have multiphasic permeases for nutrient uptake (17), with nanomolar to millimolar half-saturation constants, suggesting their adaptations to life in a patchy environment. Considering the intimate contact of their “digestive system” with the organic matter gel, motile bacteria are the “ultimate swimming stomachs” (18). They cannot avoid interacting with and changing organic matter.

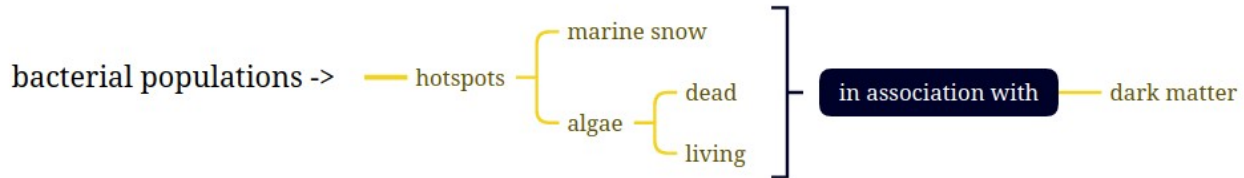


## Bacteria -> OM field structure?

Do bacteria **response** to the structure of organic matter field?

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Large bacterial populations can ~~attach to the~~ hotspots, e.g. marine snow, dead and even living algae in association with the dark matter.

Large bacterial populations can **develop on** hotspots—for example, marine snow, dead and even living algae—and in association with the “dark matter.”

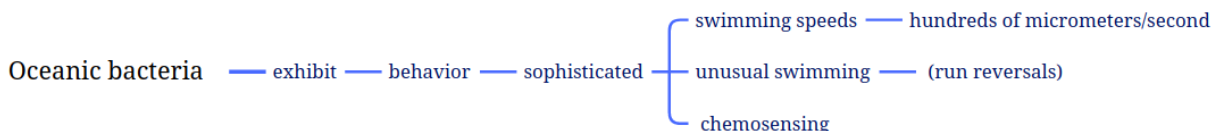
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## In one study — 24 to 68% of bacteria — transparent particles

In one study, 24 to 68% of bacteria ~~are living~~ on transparent particles

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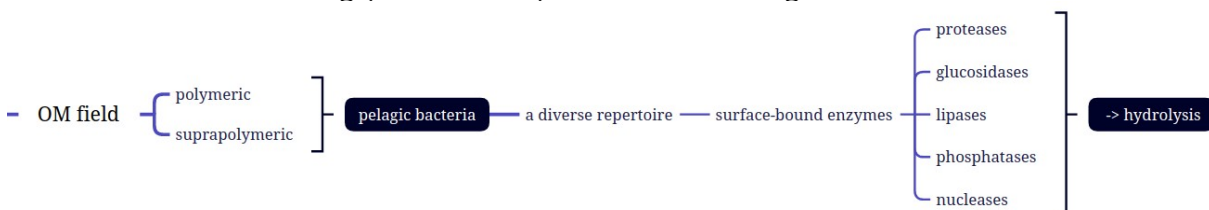
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Oceanic bacteria exhibit sophisticated behavior in swimming speeds of hundreds of micrometers per second, unusual swimming (run reversals) and chemosensing.

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The field of organic matter is polymeric and suprapolymeric ~~which determines~~ pelagic bacteria with a diverse repertoire ~~producing~~ surface-bound enzymes— proteases, glucosidases, lipases, phosphatases, nucleases-- to ~~make~~ hydrolysis.

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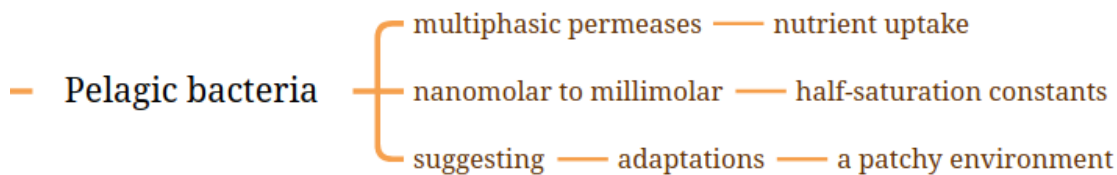
The organic matter field is dominantly polymeric and suprapolymeric, so most pelagic bacteria have a diverse repertoire of surface-bound enzymes (proteases, glucosidases, lipases, phosphatases, nucleases) to cause its hydrolysis.

## Small scale variation — species composition — enzyme activities distributions

Small scale variation of species composition can significantly ~~influence~~ the distributions of enzyme activities.

Small-scale variation of species composition can significantly **change** the distributions of enzyme activities (16).

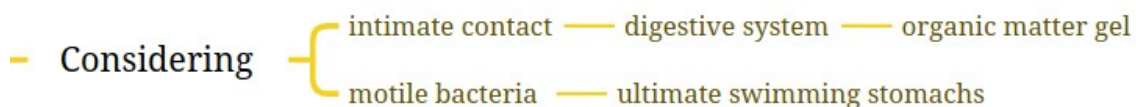
Small scale variation of species composition can significantly change the distributions of enzyme activities.



Pelagic bacteria have multiphasic permeases for nutrient uptake with nanomolar to millimolar half-saturation constants suggesting ~~the~~ adaptations of a patchy environment.

Pelagic bacteria **also** have multiphasic permeases for nutrient uptake (17), with nanomolar to millimolar half-saturation constants, suggesting their adaptations **to life** in a patchy environment.

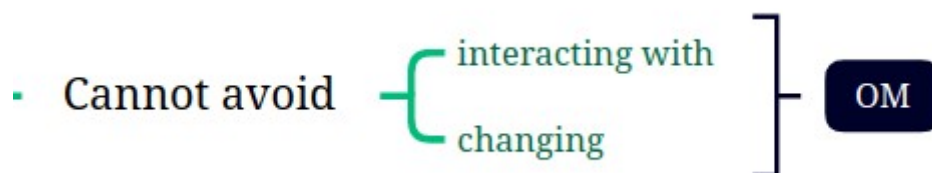
Pelagic bacteria also have multiphasic permeases for nutrient uptake, with nanomolar to millimolar half-saturation constants, suggesting their adaptations to life in a patchy environment.



Considering intimate contact ~~with~~ digestive system **in** the organic matter gel, motile bacteria **exhibit** ultimate swimming stomachs.

Considering **the** intimate contact **of** their “digestive system” **with** the organic matter gel, motile bacteria **are the** “ultimate swimming stomachs” .

Considering intimate contact of their ‘digestive system’ with the organic matter gel, motile bacteria are the ultimate swimming stomachs.

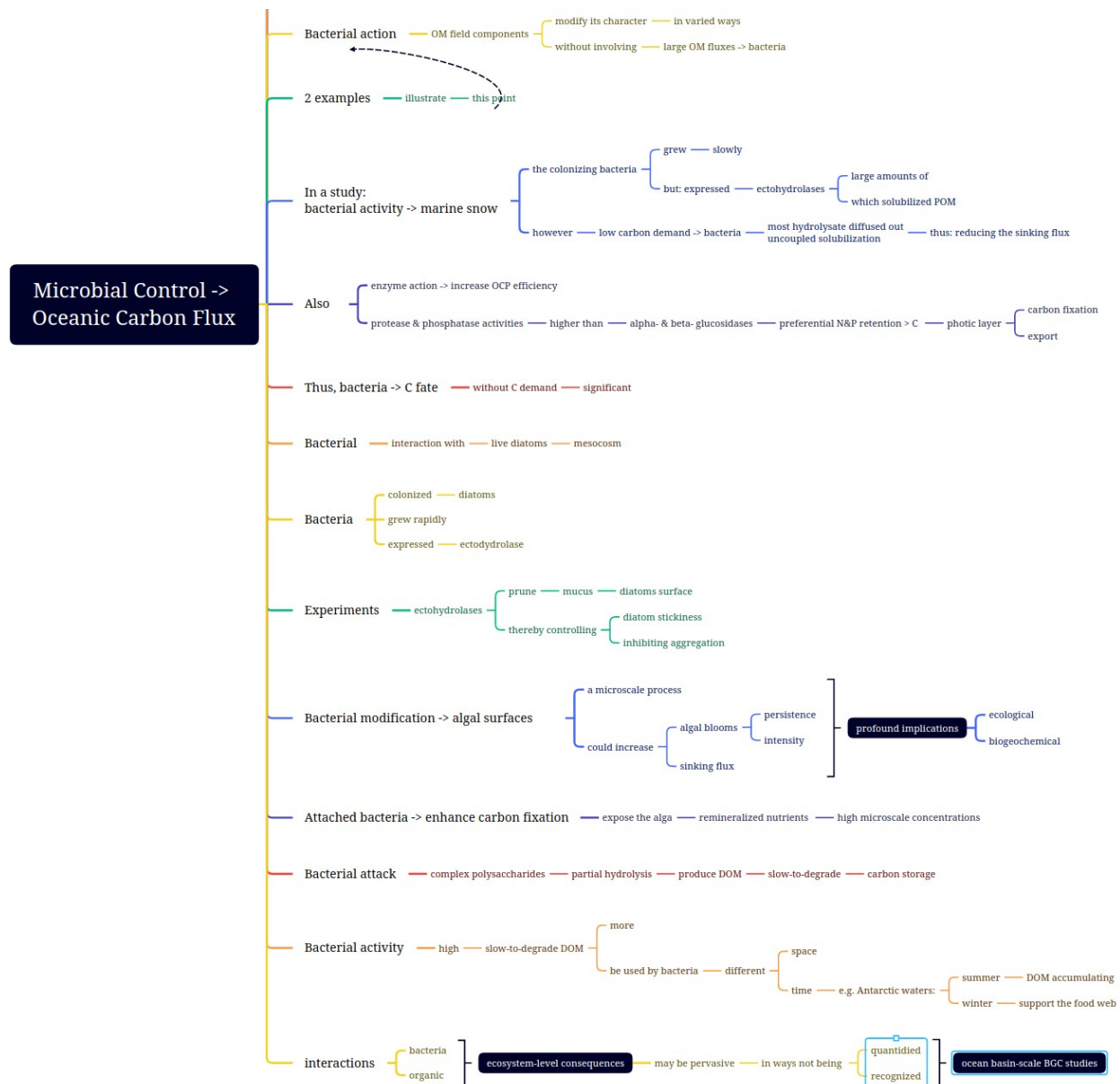


They cannot avoid interacting with and changing **the** organic matter.

They cannot avoid interacting with and changing organic matter.

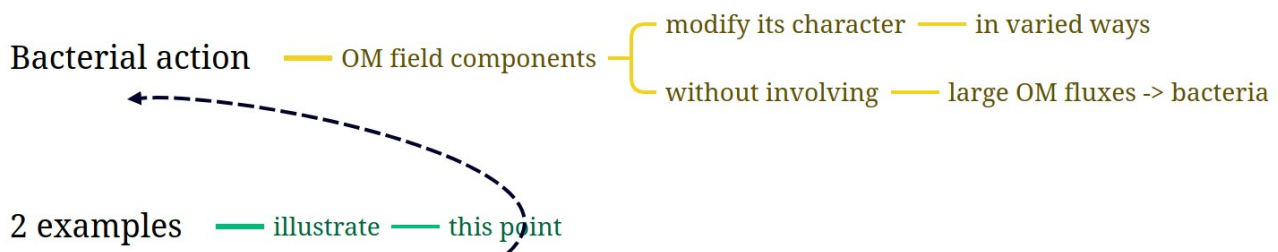
They cannot avoid interacting with and changing organic matter.





Bacterial action on components of the organic matter field can modify its character in varied ways without necessarily involving large organic matter fluxes into bacteria. Two examples illustrate this point. In a study of bacterial activity on marine snow (19), the colonizing bacteria grew slowly but expressed large amounts of ectohydrolases, which solubilized particulate organic matter; however, because of the low carbon demand of these bacteria, most hydrolysate diffused out (“uncoupled solubilization”), thus reducing the sinking flux. Also, enzyme action was thought to increase the efficiency of the oceanic carbon pump; protease and phosphatase activities were much higher than those of  $\alpha$ - and  $\beta$ -glucosidases, and this would cause preferential nitrogen and phosphate retention compared with carbon in the photic layer where it supports more carbon fixation and export. Thus, bacteria influenced the fate of carbon without a significant carbon demand. Bacterial interaction with live diatoms was examined in a mesocosm (20). Bacteria colonized the diatoms, grew rapidly, and expressed large amounts of ectohydrolase. Experiments suggested that ectohydrolases of attached bacteria “prune” mucus from the surface of diatoms, thereby controlling diatom stickiness and inhibiting aggregation. Bacterial modification of algal surfaces, a microscale process, could increase the persistence and intensity of algal blooms, as well as influence the sinking flux, with profound ecological and biogeochemical implications. Attached bacteria could also expose the alga to high microscale concentrations of remineralized nutrients, thus enhancing carbon fixation. Partial hydrolysis of complex polysaccharides by bacterial attack could produce slow-to-degrade dissolved organic matter, resulting in carbon storage (high bacterial activity could actually produce more

slow-to-degrade dissolved organic matter). This could be used by bacteria at a different place and time (for example, dissolved organic matter accumulating in Antarctic waters during summer could support the food web during winter). These and other examples show that the ecosystem-level consequences of bacteria-organic matter interactions may be pervasive in ways not currently being quantified, or even recognized, in ocean basin-scale biogeochemical studies.



Bacterial action ~~can act on the components of organic matter field~~ by modifying its character in varied ways without involving large organic matter fluxes into bacteria.

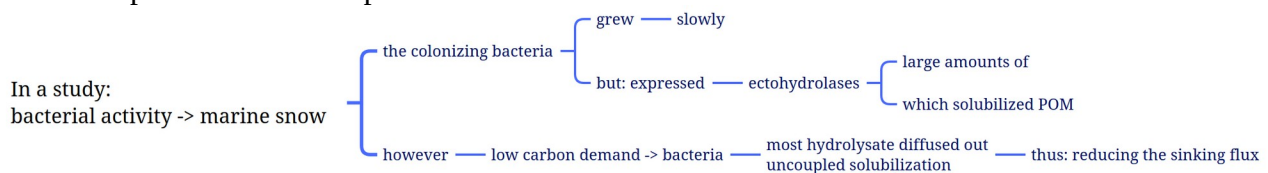
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Bacterial **action on** components of **the** organic matter field **can modify** its character in varied ways without **necessarily** involving large organic matter fluxes into bacteria.

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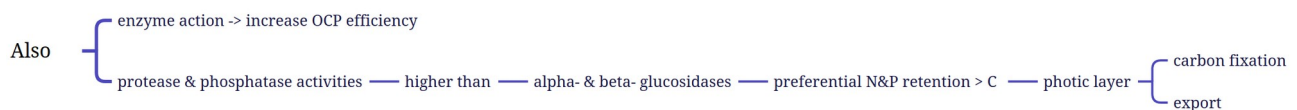
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However, most hydrolysate diffused out because of low carbon demand of bacteria, uncoupled solubilization, thus reducing the sinking flux.

however, because of **the** low carbon demand of **these** bacteria, most hydrolysate diffused out (“uncoupled solubilization”), thus reducing the sinking flux.

However, because of the low carbon demand of these bacteria, most hydrolysate diffused out (‘uncoupled solubilization’), thus reducing the sinking flux.



Also, enzyme action was thought to increase the efficiency of oceanic carbon pump.

Protease and phosphatase activities ~~are~~ higher than alpha- and beta- glucosidases ~~which~~ cause a preferential retention of nitrogen and phosphate ~~than~~ carbon in the photic layer where carbon fixation and export ~~occurs~~.

Also, enzyme action was thought to increase the efficiency of **the** oceanic carbon pump; protease and phosphatase activities **were much** higher than **those of**  $\alpha$ - and  $\beta$ -glucosidases, **and this would** cause **preferential nitrogen and phosphate retention compared with** carbon in the photic layer where **it supports more** carbon fixation and export.

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Protease and phosphatase activities were much higher than those of alpha and beta glucosidases, and this would cause preferential nitrogen and phosphate retention compared with carbon in the photic layer where it supports more carbon fixation and export.

- Thus, bacteria -> C fate — without C demand — significant

Thus, bacteria can influence the carbon fate without significant carbon demand.

Thus, bacteria **influenced the fate of carbon** without a significant carbon demand.

Thus, bacteria influenced the fate of carbon without a significant carbon demand.

Bacterial — interaction with — live diatoms — mesocosm

Bacterial interaction with live diatoms **at a scale of mesocosm.**

Bacterial interaction with live diatoms **was examined in a mesocosm**

Bacterial interaction with live diatoms was examined in a mesocosm.

Bacteria { colonized — diatoms  
grew rapidly  
expressed — ectohydrolase

Bacteria colonized diatoms, grew rapidly and expressed ectohydrolase.

Bacteria colonized **the** diatoms, grew rapidly, and expressed **large amounts** of ectohydrolase.

Bacteria colonized the diatoms, grew rapidly and expressed large amounts of ectohydrolase.

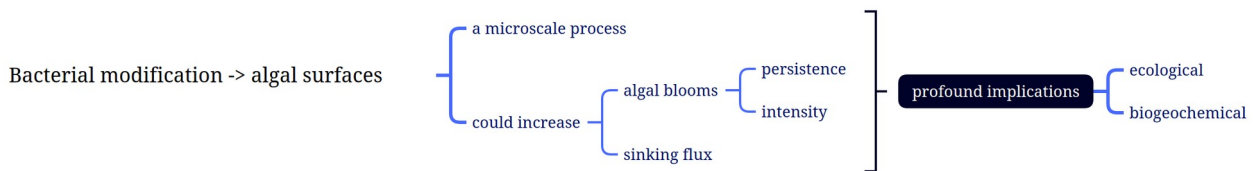
Experiments — ectohydrolases { prune — mucus — diatoms surface  
thereby controlling { diatom stickiness  
inhibiting aggregation

Experiments ~~on ectohydrolases indicated that they can~~ prune mucus from the surface of diatoms, thereby controlling diatom stickiness and inhibiting aggregation.

Experiments **suggested that** ectohydrolases **of attached bacteria** “prune” mucus from the surface of diatoms, thereby controlling diatom stickiness and inhibiting aggregation.

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Bacterial modification of algal surfaces is a microscale process, ~~this~~ could increase persistence and intensity of algal blooms ~~thus increase~~ sinking flux with profound ecological and biogeochemical implications.

Bacterial modification of algal surfaces, a microscale process, could increase **the** persistence and intensity of algal blooms, **as well as influence the** sinking flux, with profound ecological and biogeochemical implications.

Bacterial modification of algal surfaces, a microscale process, could increase persistence and intensity of algal blooms as well as influence the sinking flux with profound ecological and biogeochemical implications.

Attached bacteria -> enhance carbon fixation — expose the alga — remineralized nutrients — high microscale concentrations

Attached bacteria enhance carbon fixation by exposing the alga to high microscale concentrations of remineralized nutrients.

Attached bacteria **could also** expose the alga to high microscale concentrations of remineralized nutrients, **thus enhancing** carbon fixation.

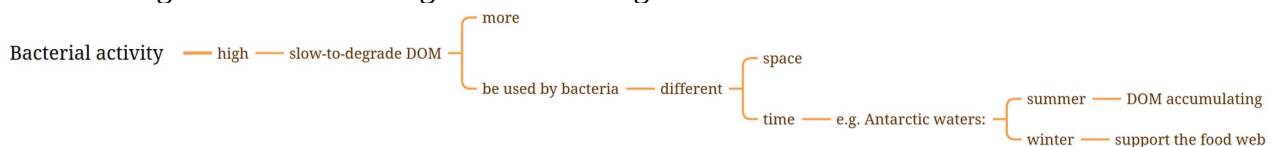
Attached bacteria could also expose the alga to high microscale concentrations of remineralized nutrients thus enhancing carbon fixation.

Bacterial attack — complex polysaccharides — partial hydrolysis — produce DOM — slow-to-degrade — carbon storage

Partial hydrolysis of complex polysaccharides by bacterial attack produce slow-to-degrade dissolved organic matter **and change** the carbon storage.

Partial hydrolysis of complex polysaccharides by bacterial attack **could** produce slow-to-degrade dissolved organic matter, **resulting in** carbon storage

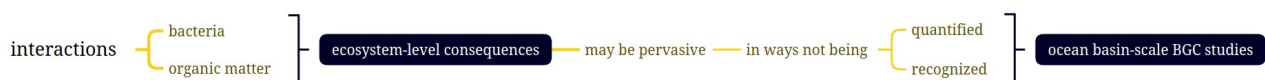
Partial hydrolysis of complex polysaccharides by bacterial attack could produce slow-to-degrade dissolved organic matter resulting in carbon storage.



High bacterial activity produces more slow-to-degrade dissolved organic matter **which** could be used by bacteria **in** different time and space. For example, dissolved organic matter accumulating in Antarctic waters during summer **can** support the food web during winter.

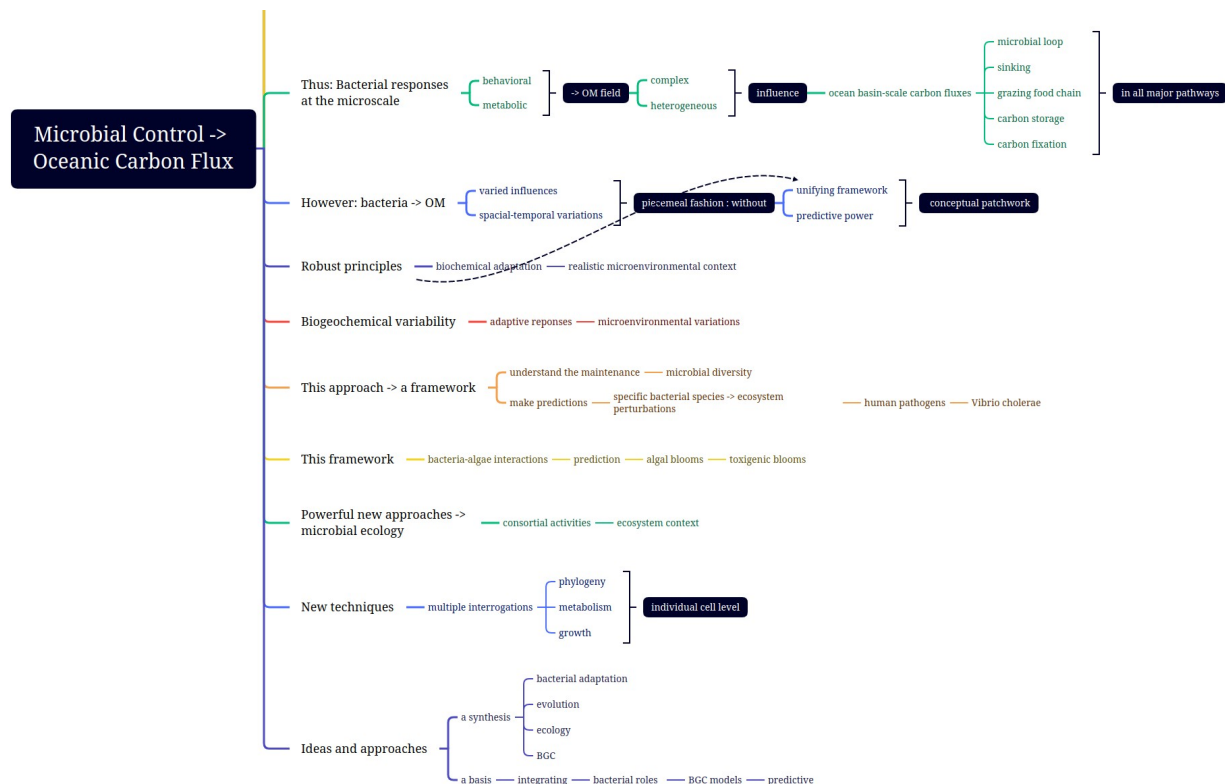
(high bacterial activity **could actually** produce more slow-to-degrade dissolved organic matter). **This** could be used by bacteria **at a** different place and time (for example, dissolved organic matter accumulating in Antarctic waters during summer **could** support the food web during winter).

High bacterial activity could **actually** produce more slow-to-degrade dissolved organic matter, this could be used by bacteria at a different space and time, for example, dissolved organic matter accumulating in Antarctic waters during summer could support the food web during winter.



The ecosystem-level consequences of bacteria-organic matter interactions may be pervasive in ways not being quantified **and even** recognized **by** biogeochemical studies at ocean basin-scale.

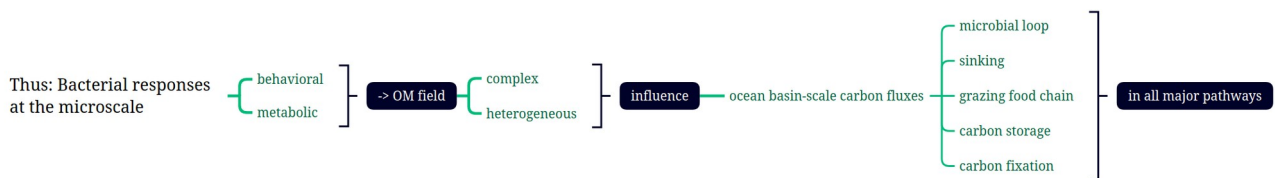
**These and other examples show that** the ecosystem-level consequences of bacteria-organic matter interactions may be pervasive in ways not **currently** being quantified, **or** even recognized, in ocean basin-scale biogeochemical studies



These and other examples show that the ecosystem-level consequences of bacteria-organic matter interactions may be pervasive in ways not currently being quantified or even recognized, in ocean basin-scale biogeochemical studies.

Thus, behavioral and metabolic responses of bacteria to the complex and heterogeneous structure of the organic matter field at the microscale influence ocean basin-scale carbon fluxes in all major pathways: microbial loop, sinking, grazing food chain, carbon storage, and carbon fixation itself.

However, studying such varied influences of bacteria on organic matter, and their spatial-temporal variations, in piecemeal fashion will only result in a conceptual patchwork without a unifying framework or predictive power. A unifying theme should derive from applying robust principles of biochemical adaptation in a realistic microenvironmental context. Biogeochemical variability could then be considered as a consequence of adaptive responses to (micro)environmental variations. This approach should also serve as a framework to understand the maintenance of microbial diversity and to make predictions on the survival of specific bacterial species, including human pathogens such as *Vibrio cholerae*, in response to ecosystem perturbations (21). This framework, which includes bacteria-algae interactions, should also be relevant to the prediction of algal blooms, including toxigenic species. Powerful new approaches are enabling us to study microbial ecology, including consortial activities, in an ecosystem context. New techniques allow multiple interrogations—phylogeny, metabolism, growth—at the individual cell level. These ideas and approaches should lead to a synthesis of bacterial adaptation, evolution, ecology, and biogeochemistry, and should form a basis for integrating the roles of bacteria in predictive biogeochemical models.



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Robust principles — biochemical adaptation — realistic microenvironmental context

This unifying framework requires robust principles of biochemical adaptation to realistic microenvironmental context.

A unifying theme should derive from applying robust principles of biochemical adaptation in a realistic microenvironmental context.

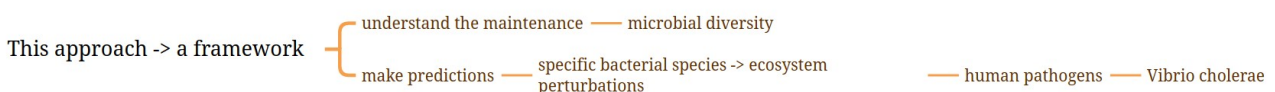
A unifying theme should derive from applying robust principles of biochemical adaptation in a realistic microenvironmental context.

Biogeochemical variability — adaptive responses — microenvironmental variations

Biogeochemical variability has adaptive responses to microenvironmental variations.

Biogeochemical variability could then be considered as a consequence of adaptive responses to (micro)environmental variations.

Biogeochemical variability could then be considered as a consequence of adaptive responses to microenvironmental variations.



This approach can form a framework to understand the maintenance of microbial diversity and make predictions of specific bacterial species in response to ecosystem perturbations ~~for~~ human pathogens such as *Vibrio cholerae*.

This approach ~~should also serve as~~ a framework to understand the maintenance of microbial diversity and ~~to~~ make predictions ~~on the survival of~~ specific bacterial species, ~~including~~ human pathogens such as *Vibrio cholerae*, in response to ecosystem perturbations (21).

This approach could also serve as a framework to understand the maintenance of microbial diversity and to make predictions ~~on the survival of~~ specific bacterial species including human pathogens such as *Vibrio cholerae* to ecosystem perturbations.

This framework — bacteria-algae interactions — prediction — algal blooms — toxigenic blooms

This framework ~~of~~ bacteria-algae interactions ~~can also make~~ prediction of algal blooms including toxigenic blooms.

This framework, ~~which includes~~ bacteria-algae interactions, ~~should also be relevant to the~~ prediction of algal blooms, including toxigenic species.

This framework which includes bacteria-algae interactions should also be relevant to the prediction of algal blooms including toxigenic species.

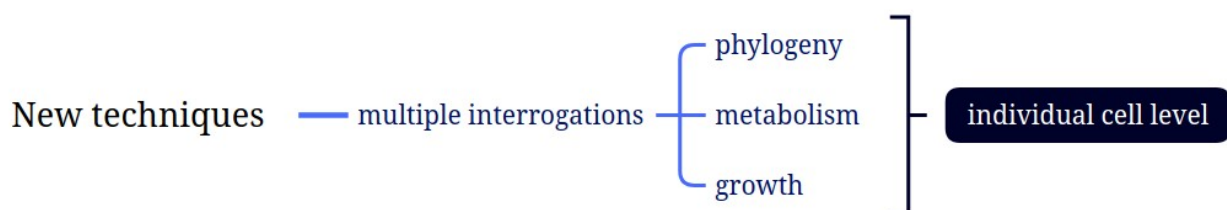
## Powerful new approaches -> microbial ecology

— consortial activities — ecosystem context

~~Powerful new approaches to study consortial activities are required in an ecosystem context of microbial ecology.~~

Powerful new approaches ~~are enabling us to~~ study microbial ecology, including consortial activities, in an ecosystem context.

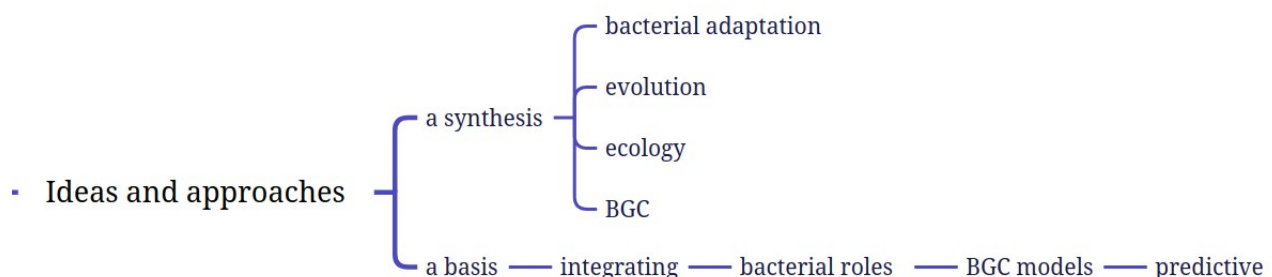
Powerful new approaches are enabling us to study microbial ecology including consortial activities in an ecosystem context.



New techniques ~~support~~ multiple interrogations ~~on~~ phylogeny, metabolism and growth ~~at an~~ individual cell level.

New techniques ~~allow~~ multiple interrogations—phylogeny, metabolism, growth—~~at~~ the individual cell level.

New techniques allow multiple interrogations—phylogeny, metabolism, growth—at the individual cell level.



These ideas and approaches ~~form~~ a synthesis of bacterial adaptation, evolution, ecology and biogeochemistry ~~as well as~~ a basis ~~of~~ integrating the roles of bacteria in ~~the~~ predictive biogeochemical models.

These ideas and approaches **should lead to** a synthesis of bacterial adaptation, evolution, ecology, and biogeochemistry, **and should form** a basis **for** integrating the roles of bacteria in predictive biogeochemical models.

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