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Monitoring the organic enrichment and the trophic status of the aquatic environment beneath a long-line system of Mediterranean mussel culture

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Abstract

In Greece, aquaculture has experienced significant growth since the mid-1980s, including the cultivation of mussels, largely due to favorable environmental conditions and the fact that mussel farming does not require external feed inputs. Nevertheless, bivalve aquaculture has been identified as a potential source of organic enrichment and eutrophication because of the waste products generated by cultured organisms.

Mussels act as natural filter feeders, removing phytoplankton and suspended particles from the water column. At the same time, they excrete nutrients and produce feces and pseudofeces, which settle on the seabed. Consequently, mussel farming may exert both positive and negative environmental effects. Organic matter accumulated in surface sediments can serve as an important food source for benthic organisms; however, excessive accumulation may lead to oxygen depletion, the formation of toxic by-products under suboxic or anoxic conditions, and a subsequent decline in benthic species abundance and diversity, particularly in areas of intensive cultivation. Eutrophication of coastal waters is one of the major environmental challenges worldwide, often resulting in harmful algal blooms, increased water turbidity that reduces light penetration to benthic vegetation, and hypoxic conditions. Eutrophication occurs when aquatic ecosystems receive excessive nutrient inputs, leading to enhanced primary production and ecological imbalance. Chlorophyll-a (Chl-a), total phosphorus (TP), total nitrogen (TN), and the TN ratio are widely recognized as valuable indicators for assessing and monitoring eutrophication in aquatic systems.

The aim of this study was to evaluate the impact and spatial extent of Mediterranean mussel (*Mytilus galloprovincialis*) cultivation on water quality and the trophic status of the surrounding aquatic ecosystem. The results demonstrated that mussel farming contributed to organic enrichment and influenced the trophic status of the study area, indicating measurable ecological effects associated with aquaculture activities.

Keywords: Organic Enrichment; *Mytilus galloprovincialis*; Eutrophication; Water Quality; Mussel Biodeposition

1. Introduction

Aquaculture is currently the fastest-growing sector of food production worldwide, supplying approximately half of the fish consumed globally and playing a crucial role in meeting the nutritional demands of an expanding human population. Nevertheless, despite its contribution to food security, the development of aquaculture is often limited by environmental regulations due to the considerable release of nutrients originating from fish metabolism and uneaten feed into surrounding marine environments.

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The introduction of these nutrients can alter sediment biogeochemical processes and contribute to oxygen depletion, frequently resulting in seasonal hypoxic conditions and elevated phytoplankton biomass in eutrophic coastal ecosystems. Mussels act as efficient biological filters by removing suspended particulate matter, including phytoplankton and detrital material, from the water column. Although this filtration activity can improve water clarity and reduce chlorophyll-a concentrations, it also facilitates the transfer of organic matter and energy from pelagic to benthic compartments through biodeposition [1-4]. Mussel biodeposition produces substantial amounts of feces and pseudofeces, which are organic-rich particles characterized by high settling velocities. The accumulation of these materials beneath aquaculture installations can significantly enhance benthic metabolic activity, increasing sediment oxygen consumption and potentially promoting the development of anaerobic conditions. Such environmental changes may substantially modify nitrogen transformation pathways within sediments. Previous studies have demonstrated that elevated biodeposition rates can inhibit coupled nitrification–denitrification processes while stimulating dissimilatory nitrate reduction to ammonium, thereby increasing nitrogen retention within the benthic environment rather than facilitating its removal through gaseous nitrogen loss. In addition, the mineralization of biodeposits releases dissolved inorganic nitrogen, phosphate, and silicate into the water column, generating positive feedback mechanisms that may further stimulate primary productivity. The magnitude and spatial extent of these environmental effects vary considerably among sites and are strongly influenced by hydrodynamic conditions, water depth, and ambient oxygen availability. Since the impacts are typically concentrated in areas immediately surrounding aquaculture facilities, appropriate site selection and the application of ecological modeling tools are essential for minimizing habitat degradation and supporting the attainment of good environmental status under policy frameworks such as the EU Water Framework Directive and the Mediterranean Action Plan. Consequently, a thorough understanding of the interactions between aquaculture activities and benthic–pelagic coupling processes is fundamental for ensuring the sustainable coexistence of aquatic food production and ecosystem integrity [5-11] . The objective of this study was to assess the effects of Mediterranean mussel (*Mytilus galloprovincialis*) aquaculture on water quality and to determine the spatial extent of its influence on the trophic conditions of the adjacent aquatic environment.

2. Materials and Methods

Study sites and experimental design: The review research employed a dual approach, combining a comprehensive field study in the Aegean Sea with controlled laboratory experiments. The field study was conducted in a "long-line" system of *Mytilus galloprovincialis* farm, located in Makrygialos, Pieria, Greece (40° 24’ 51”N, 22° 36’ 39”E). Sampling was performed monthly over a period of 15 months, though weather conditions limited successful data collection to 12 months. Two distinct zones were monitored: a mussel culture area (500 m from shore, at a depth of 12–14 m) and a reference area (1,000 m from shore). In parallel, laboratory experiments were performed in 944-liter tanks to isolate the effects of mussel metabolic activity. These experiments utilized approximately 320 mussels (shell length ~70 mm) distributed in net bags. Two distinct treatments were tested: a flow-through system (1.3 m^3/h) and a stagnant (no-flow) system, with water samples collected at six-hour intervals to monitor nutrient dynamics.

Sampling and in-situ measurements for the field study: Water samples were collected from five points at both the surface and the bottom (10–20 cm above the sediment) using a Niskin sampling probe, while sediment samples were obtained via an Ekman-type sampler.

Laboratory and chemical analyses: Water samples were filtered through whatman GF/C glass-fiber filters within three hours of collection and stored frozen until analysis. Nutrient concentrations were determined spectrophotometrically: Chlorophyll-a: Measured at 665 nm following filtration. Orthophosphate ($P\text{-}PO_4$): Determined at 880 nm using the acidified molybdate reagent method. Ammonium nitrogen ($N\text{-}NH_4$): Calculated at 630 nm via the indophenol reaction. Nitrate ($N\text{-}NO_3$) and nitrite ($N\text{-}NO_2$): Nitrates were reduced to nitrites using amalgamated cadmium columns, followed by diazotization and measurement at 543 nm. Particulate organic carbon (POC): Analyzed via wet ashing with potassium dichromate and sulfuric acid, measured at 440 nm. Organic sediment: Calculated as percent dry matter after drying at 103°C and subsequent combustion at 550°C. *Statistical evaluations* were performed using SPSS 8.0. The ANOVA method was utilized to examine interactions between area, depth, and time. For homogeneous data, Duncan’s multiple range test was applied, while heterogeneous data were analyzed using Kruskal-Wallis and Mann-Whitney non-parametric controls [9, 11,12].

3. Results

3.1. Physicochemical parameters Dissolved oxygen (DO)

While surface oxygen levels remain high in both areas (9–13 mg/L), a significant difference exists at the bottom. The reference site remains well-oxygenated, whereas the bottom of the mussel culture experiences depletion, reaching as low as 3 mg/L. The lowest concentrations in the culture area occur from February to May (3–4 mg/L) and during the summer months of July and August (5 mg/L) due to high organic loading and microbial decomposition (**table** 3,4,5,6).

3.2. Nutrient Dynamics (Nitrogen and Phosphorus)

Mytilus galloprovincialis functions as a significant biogeochemical pump within aquatic ecosystems. Through their high filtration capacity, these mussels remove particulate matter from the water column and regenerate it into the environment in soluble and particulate forms, effectively shifting energy and nutrients from the pelagic to the benthic region.

3.2.1. Ammonium (N–NH_4): Nitrogenous Excretion (Ammonium)

The primary nitrogenous excretory product of *M. galloprovincialis* is ammonium nitrogen (N–NH4). Laboratory studies demonstrate a rapid increase in N–NH4concentrations in the presence of mussels. In controlled tank experiments, ammonium levels increased by 58% in flow-through systems (10.1±1.01µg/L) and by 40.4% in stagnant water within just six hours (8.47±0.63µg/L).

In cultivation areas, the highest concentrations are typically found at the bottom (39.4±5.6µg/L in September) due to both direct excretion and the aerobic decomposition of organic matter in the sediment. The excreted ammonium is immediately available for uptake by phytoplankton, thereby increasing the nitrogen turnover rate in the water column and positively influencing primary production [4,5].

The mussel culture consistently shows higher concentrations at the bottom compared to the reference site, especially in September (39.4 ± 5.6 µg/L) and October (34.67 ± 3.88 µg/L). Higher levels in the culture area relative to the reference site were also noted in March, May, June, and July (15.52±1.02µg/L), attributed to direct excretion by mussels. (**table** 3,4,5,6).

3.2.2. Nitrate (N–NO_3)

Based on the sources, the dynamics of nitrate (N–NO_3) and nitrite (N–NO_2) in *Mytilus galloprovincialis* cultivation are characterized by less dramatic fluctuations compared to ammonium (N–NH_4), though they are still influenced by both physiological and environmental factors. In both field and laboratory settings, N–NO_3 and N–NO_2 concentrations generally did not show "statistically remarkable" changes as a primary impact of the mussels themselves. While ammonium and phosphorus levels rose sharply, the increases in nitrate and nitrite were significantly lower in magnitude. Nitrate concentrations were actually found to be lower in the mussel culture area (6.51 to 127.44 µg/L) compared to the reference area (8.19 to 469.96 µg/L). This is attributed to higher inflows of nitrate-rich water from adjacent rivers reaching the open sea more directly than the farm area, where sea current speeds are often reduced. While surface concentrations are influenced by external inflows, nitrate levels at the bottom of the mussel farm showed notable increases during winter months (specifically December and January). The localized increase in N–NO_3 at the bottom is primarily attributed to nitrification. As organic material deposited by the mussels (faeces and dead mussels) decomposes, it releases ammonium, which is then converted into nitrate by bacteria in the sediment. In tanks with flow, concentrations of nitrate increased by only 1.8%, whereas in stagnant water (no flow), they increased by 15.4%. Concentrations of nitrite increased by 2.2% in flow systems and 4.5% in stagnant systems. These small increases are linked to nutrient regeneration through the direct excretion of mussels and the beginning stages of mineralization of their waste products [4,8-10,13,14](**table** 3,4,5,6).

3.2.3. Orthophosphate (P–PO_4)

Mussels significantly contribute to the phosphorus cycle through the release of orthophosphate (P–PO4). Increased concentrations of phosphates are consistently observed under mussel culture lines, particularly during periods of high metabolic activity in spring and summer. On the surface, the reference site had higher concentrations (up to 61.28 µg/L) than the culture area (up to 23.68 µg/L) in October and November due to nutrient inflows. Conversely, the bottom of the mussel culture showed significantly higher phosphate levels in April, May, and June (peaking at 40.81 ± 2.5 µg/L in May) due to mussel excretion. A statistically significant increase ($p \leq 0.05$) of 9.8% to 13.5% was recorded, with concentrations reaching 27.01±0.47µg/L in flow systems (**table** 3,4,5,6).

3.2.4. Phytoplankton biomass (Chlorophyll-a)

On the surface, differences are often negated by currents, but at the bottom, the mussel culture shows a decreased concentration in most months (except March/April) compared to the reference site because of intense phytoplankton consumption by the mussels. While surface peaks of 10.07±0.88µg/L occurred in January, bottom concentrations were consistently lower than reference areas due to intense filtration. In tanks experiments, concentrations dropped precipitously by 63.4% to 66% within six hours, reaching minimum values of 0.23±0.028µg/L (flow) and 0.19±0.017µg/L (without flow) (**table** 3,4,5,6).

4. Particulate Organic Carbon (POC) and bio-deposition

Beyond dissolved nutrients, mussels excrete organic material in the form of faeces and pseudofaeces. Surface POC concentrations in the culture area varied widely, from 178.2 to 1768.8 ±233.4µg/L. Surface POC is generally higher in the mussel culture (up to 1768.8 ± 233.4 µg/L). At the bottom, the culture area showed increased levels in May, July, September, January, and April, though these peaks were not always statistically significant compared with the reference area. Laboratory findings show that the presence of mussels can increase POC concentrations by up to 42.8% in flow systems. In tank experiments, the presence of mussels induced a rapid POC increase of 42.8% in flow systems (mean: 877±237.7µgC/L) and 25.8% in stagnant systems (mean: 1141.1±255.1µgC/L).

Organic sediments: This parameter shows the most stark difference. Intensive biodeposition resulted in organic enrichment of the underlying sediment, reaching up to 12% dry matter. Summer mean values were approximately 8.5%, increasing to 9.5% during the spring period.

The mussel culture has statistically significant higher organic enrichment in the sediment (up to 12% dry matter) compared with the reference site across several months, directly resulting from the deposition of faeces, pseudofaeces, and dead mussels (**table** 3,4,5,6).

Table 1 Statistical trend of parameters in cultivation area and in laboratory experiment

Parameter	Field (Culture Bottom/Peak)	Lab (6h Mean Flow/Stagnant)	Statistical trend
N–NH4	39.4±5.6µg/L	10.1/8.47µg/L	Significant Increase
N–NO3	72.45±1.86µg/L	244.5/265.7µg/L	Moderate Increase
P–PO4	40.81±2.5µg/L	27.01/28.19µg/L	Significant Increase
Chl-a	10.07±0.88µg/L (Surface)	0.23/0.19µg/L	Massive Depletion
POC	1768.8±233.4µg/L	877/1141.1µgC/L	Significant Increase
Organics	Up to 12% Dry Matter	N/A	High Accumulation

4.1. Correlation Matrix of Water Quality Parameters

The most significant finding is the strong negative correlation between phosphates and oxygen, particularly visible in the late spring data where oxygen drops to its lowest point (3.8 ppm) while phosphates peak. The positive correlation between chlorophyll-a and POC confirms that the organic load in the area is heavily influenced by biological productivity (phytoplankton). The negative relationship between nitrates and ammonium/chlorophyll suggests a dynamic ecosystem where nutrients are rapidly cycled and consumed by the present biomass (**table** 2).

Table 2 Statistical relationships between physicochemical and biological indicators within the mussel aquaculture area

Parameter Pair	Correlation Coefficient (r)	Correlation Type	Scientific Interpretation
$P\text{-}PO_4$ & O_2	-0.76	Strong Negative	Higher phosphate concentrations are strongly linked to decreased dissolved oxygen levels.
Chl-a & POC	+0.60	Strong Positive	Indicates that phytoplankton (Chl-a) is a major constituent of Particulate Organic Carbon.
$P\text{-}PO_4$ & $N\text{-}NO_2$	+0.53	Moderate Positive	Suggests shared nutrient input sources or similar cycling patterns in the water column.
$N\text{-}NO_3$ & Chl-a	-0.51	Moderate Negative	Reflects the consumption of nitrates by phytoplankton during periods of high productivity.
$N\text{-}NO_3$ & $N\text{-}NH_4$	-0.48	Moderate Negative	Represents the transformation between different nitrogen species (e.g., nitrification processes).

Table 3 Monthly Monitoring of Water Quality Parameters (March – June). Data for the spring and early summer period**.**

Parameter	Location	March	May	June
$P\text{-}PO_4$ (µg/L)	Mussel Area	5.76	4.71	12.03
	Reference	6.75	8.42	8.74
$N\text{-}NO_3$ (µg/L)	Mussel Area	5.74	9.62	13.13
	Reference	9.52	9.14	18.54
$N\text{-}NO_2$ (µg/L)	Mussel Area	8.96	4.45	2.06
	Reference	5.96	4.65	2.01
$N\text{-}NH_4$ (µg/L)	Mussel Area	36.45	35.12	25.55
	Reference	38.47	40.61	27.47
Chl-a (µg/L)	Mussel Area	2.33	2.69	2.59
	Reference	1.06	2.94	2.76
Organics (mg/L)	Mussel Area	4.64	11.08	8.10
	Reference	3.67	10.79	6.57
POC (µg/L)	Mussel Area	1183.02	1276.44	396.06
	Reference	1393.31	1186.68	768.57
O_2 (PPM)	Mussel Area	7.00	6.60	6.30
	Reference	8.10	8.20	10.20

Table 4 Monthly Monitoring of Water Quality Parameters (July – November). Data for the summer and autumn period.

Parameter	Location	July	August	Sept.	Oct.	Nov.
P-PO_4 (µg/L)	Mussel Area	3.50	3.26	0.25	17.92	7.63
	Reference	7.01	7.09	11.50	18.23	8.58
N-NO_3 (µg/L)	Mussel Area	12.23	54.28	31.34	40.68	35.57
	Reference	29.21	34.65	26.11	49.14	41.32
N-NO_2 (µg/L)	Mussel Area	2.57	3.01	2.18	6.10	3.54
	Reference	3.13	3.57	2.50	5.75	3.94
N-NH_4 (µg/L)	Mussel Area	15.52	13.12	39.40	34.67	2.05
	Reference	16.35	12.95	32.01	26.27	4.48
Chl-a (µg/L)	Mussel Area	2.95	0.91	1.76	1.20	1.06
	Reference	3.63	1.54	3.18	2.10	2.49
Organics (mg/L)	Mussel Area	8.32	8.71	7.58	12.15	6.94
	Reference	5.83	10.03	8.21	6.52	9.43
POC (µg/L)	Mussel Area	1425.27	733.92	933.24	257.81	242.22
	Reference	976.84	995.28	607.20	568.92	473.88
O_2 (PPM)	Mussel Area	6.40	6.40	6.40	6.40	6.10
	Reference	9.10	7.80	9.00	8.30	6.40

Table 5 Monthly Monitoring of Water Quality Parameters (December – May). Data for the winter and the following spring.

Parameter	Location	Dec.	Jan.	April	May
P-PO_4 (µg/L)	Mussel Area	3.63	6.20	10.23	40.81
	Reference	3.14	6.87	6.71	40.73
N-NO_3 (µg/L)	Mussel Area	72.45	37.71	10.65	38.17
	Reference	62.83	25.40	9.94	42.93
N-NO_2 (µg/L)	Mussel Area	12.81	9.28	1.77	14.60
	Reference	12.94	6.34	1.99	16.81
N-NH_4 (µg/L)	Mussel Area	5.77	6.60	13.53	13.01
	Reference	7.35	6.40	14.01	13.80
Chl-a (µg/L)	Mussel Area	0.85	4.85	2.57	1.31
	Reference	3.53	5.18	1.81	1.53
Organics (mg/L)	Mussel Area	8.65	10.39	8.13	10.01
	Reference	5.03	8.04	6.63	8.59
POC (µg/L)	Mussel Area	268.95	1414.05	1045.44	1467.84
	Reference	377.52	1392.60	920.04	1252.68
O_2 (PPM)	Mussel Area	6.10	6.00	4.60	3.80
	Reference	6.50	7.10	6.20	5.40

Table 6 Experimental Results under Flow and No Flow Conditions. Comparison of water parameters at the start (0 hour) and end (4 hours) of the experiment.

Condition	Parameter	Location	0 H	4 H
FLOW	P-PO_4 (µg/L)	Mussel Area	24.83	28.19
		Reference	25.34	24.75
	N-NO_3 (µg/L)	Mussel Area	241.50	245.92
		Reference	240.08	227.25
	POC (µg/L)	Mussel Area	799.20	1141.10
	O_2 (PPM)	Mussel Area	6.50	5.97
NO FLOW	P-PO_4 (µg/L)	Mussel Area	24.59	27.01
		Reference	25.09	22.96
	N-NO_3 (µg/L)	Mussel Area	211.80	244.50
		Reference	242.20	236.50
	POC (µg/L)	Mussel Area	697.30	877.00
	O_2 (PPM)	Mussel Area	5.95	5.47

Table 7 Eutrophication limiting factor in mussel culture

Month	TP	TN	TN/TP	EUTROPHICATION LIMITING FACTOR
MARCH	5,76	51,15	8,880208333	P
MAY	4,71	49,19	10,44373673	P
JUNE	12,03	40,74	3,386533666	N
JULY	3,5	30,32	8,662857143	P
AUGUST	3,26	70,41	21,59815951	P
SEPTEMBER	0,25	72,92	291,68	P
OCTOBER	17,92	81,45	4,545200893	N
NOVEMBER	7,63	41,16	5,394495413	N
DECEMBER	3,63	91,03	25,07713499	P
JANUARY	6,2	53,59	8,643548387	P
APRIL	10,23	25,95	2,536656891	N
MAY	40,81	65,78	1,611859838	N

4.2. Stoichiometric Analysis (TN/TP Ratio)

The TN/TP ratio is used as a diagnostic tool to identify the limiting nutrient for primary productivity in the aquatic system. Based on the provided table, the system shifts between Phosphorus (P) and Nitrogen (N) limitation depending on the season: Phosphorus Limitation (P): This factor is dominant when the TN/TP ratio is relatively high. It is observed in January, March, July, August, September, December, and one instance in May. The most extreme case of P-limitation occurs in September, where the ratio spikes to 291.68 due to the near-depletion of phosphorus (0.25). Nitrogen Limitation (N): Nitrogen becomes the limiting factor when TP levels rise significantly relative to TN. This occurs in April, June, October, November, and during the second May entry. The lowest TN/TP ratio (1.61) is recorded in May, coinciding with the highest TP concentration of 40.81.

4.3. Eutrophication limiting factor in mussel culture

The data reveals significant fluctuations in nutrient levels throughout the year. Total Nitrogen (TN) reaches its maximum concentration in December (91.03) and October (81.45), while its lowest point is recorded in April (25.95). Conversely, Total Phosphorus (TP) levels are highly variable, peaking at 40.81 in May and dropping to a minimum of 0.25 in September.

4.4. Seasonal Eutrophication Trends

The "Eutrophication Factor" identifies the nutrient that would likely stimulate further algal growth if added to the system.

Late Spring and Summer: The system shows variability; while early May and July/August are P-limited, a significant spike in TP in late May and high TP in June shifts the system toward N-limitation.

Autumn: There is a notable transition. September is severely P-limited, but by October and November, a surge in TP (reaching 17.92 in October) shifts the factor back to N-limitation.

Winter: The system returns to P-limitation in December and January, driven by the highest recorded TN levels (91.03 and 53.59, respectively) which keep the ratio high despite moderate TP levels. In conclusion, the eutrophication potential of this environment is seasonally dynamic, with **Nitrogen limitation** occurring primarily when Phosphorus levels are elevated (above ~7.0), and **Phosphorus limitation** prevailing when TP concentrations are sequestered or naturally low (**table** 7).

5. Discussion

Merging field data from the Aegean Sea with controlled experiments allows for a comprehensive assessment of the ecosystem changes driven by *Mytilus galloprovinciallis* farming. The findings demonstrate that intensive mussel cultivation acts as a significant driver of benthic-pelagic coupling, shifting energy and nutrients from the water column to the benthos.

5.1. Physicochemical alterations and oxygen depletion

A critical impact identified is the localized reduction of dissolved oxygen (DO) levels, particularly at the sediment-water interface. In field conditions, while surface DO remains high due to photosynthetic activity, bottom concentrations can decline to approximately 3 mg/L. This depletion is attributed to a dual process: the direct respiration of the mussel population and the elevated biological oxygen demand (BOD) required for the aerobic decomposition of accumulated biodeposits (faeces and pseudofaeces) [15,16]. Laboratory data corroborate this, showing significant DO decreases in closed systems even within short durations.

5.2. Nutrient regeneration and cycling

Mussels function as biogeochemical pumps, regenerating inorganic nutrients into the water column through excretion and the mineralization of biodeposits. The primary excretory product is ammonium nitrogen ($N\text{-}NH_4$), which shows marked increases in both field and tank environments. This ammonia is immediately available for primary production, potentially stimulating further phytoplankton growth. Similarly, the release of orthophosphate ($P\text{-}PO_4$) is enhanced under mussel lines, particularly during periods of high metabolic activity. While nitrate ($N\text{-}NO_3$) and nitrite ($N\text{-}NO_2$) levels are influenced by external inflows (e.g., rivers), nitrification processes in the organic-rich sediments can lead to increased nitrate concentrations at the bottom during winter months

5.3. Phytoplankton depletion and organic enrichment

The high filtration capacity of *M. galloprovincialis* results in a significant reduction of chlorophyll-a concentrations, reflecting the depletion of phytoplankton biomass. This grazing effect is evidenced by the lower chlorophyll-a levels found at the bottom of culture areas compared to reference site [9,14,17-19]. Simultaneously, the sedimentation of organic material leads to the enrichment of the underlying benthos with particulate organic carbon (POC) and organic sediments, which can reach up to 12% dry matter.

6. Conclusion

While the excretion of dissolved inorganic nutrients (N and P) by *M. galloprovincialis* can stimulate primary production, the simultaneous accumulation of particulate organic excretions on the seabed poses environmental risks. The mineralization of this accumulated organic matter increases biological oxygen demand, which can lead to localized hypoxia (bottom DO as low as 3 mg/L) and, in older or poorly flushed sites, potential anoxic conditions.

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