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Climate Change Threats to Earth's Oceanic Biological Pump: A Critical Review of Biogeochemical Variables

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Abstract

Biological and solubility pumps play crucial roles in transporting carbon and organic matter from the ocean surface to deeper oceanic depths. The export of carbon varies depending on location, and the variation with depth is affected by fluctuating planktonic food webs in the upper epipelagic seas. Climate fluctuations can affect sinking and vertical movements. The effect of climate change on this system is unclear, but zooplankton faecal pellets play a significant role in transporting particles and chemicals to deeper layers. However, in some cases, these pellets are recycled and remain in the upper waters owing to coprophagy and microbial decomposition. By exploring the impact of future human-induced climate change on the biological pump of the ocean, this paper reviews all uncertainties associated with the role of key biochemical variables in current climate fluctuations.

Keywords: climate change, oceanographic biological pump, carbon export, solubility pump, food web

1. INTRODUCTION

The mechanism known as the 'biological pump' is responsible for transporting organic matter produced through photosynthesis in the ocean's surface layer to deeper depths [1]. This is achieved through several processes, including sinking of particles, advection, and vertical mixing of dissolved organic matter, as well as transportation by marine creatures. Another key component of this process is the 'solubility pump', which plays a significant role in transferring carbon from the atmosphere to surface layers of the ocean. Carbon is dissolved in seawater, transformed into particulate matter through primary production, consumed by pelagic biota, and transported to the deeper layers or stored in the deep sea. Approximately two-thirds of the vertical carbon gradient in the ocean is attributed to the biological pump, whereas the remaining portion is attributed to the solubility pump [2]. However, biological pumps are ineffective. The carbon fixed by phytoplankton during near-surface photosynthesis is mainly remineralised in the epipelagic and higher mesopelagic zones. The export of carbon varies depending on the area, and the variation in carbon export with depth is partly caused by the fluctuation of planktonic food webs in the upper epipelagic seas. It is important to differentiate between the 'export flux' that exits the bottom of the euphotic zone and the 'sequestration flux' from the bottom of the mesopelagic zone.

It is estimated that carbon sequestered at a depth below this level remains in the deep sea for over a century. Smetacek and Naqvi [3] confirmed that the export of material from the lower part of the euphotic zone is approximately equal to the amount of new photosynthetic production derived from new nitrogen sources, such as nitrate brought into the euphotic zone through convective mixing or upwelling from deeper waters, as well as external sources such as atmospheric deposition, horizontal movement, and nitrogen fixation. Sequestration flow is mainly determined by the reduction in flux and breakdown of organic waste in the mesopelagic zone. The use of the depth of winter mixing, instead of a single depth, for sequestration in various regions across the Atlantic has been suggested. The sequestration depth varied depending on location as a result of the differences in the depth of winter mixing. It was determined that the definition of export depth and sequestration depth is more accurate based on light penetration and mixing rather than a fixed depth, as the depth of the euphotic zone fluctuates depending on the location. It has been verified that inefficient but quick export through a biological pump occurs. Lyon and Mock [2] have illustrated the basic schematics of an oceanic biological pump where particulate organic carbon (POC) is produced by photosynthesis by phytoplankton in the euphotic layer of the epipelagic zone. Microbes, zooplankton, and their consumers break down organic matter produced by surface-dwelling phytoplankton into faecal pellets, organic aggregates known as 'marine snow’, and other forms of particulate organic carbon (POC).

The organic carbon generated through microbial remineralisation can be carried to the mesopelagic and bathypelagic zones by zooplankton and fish through sinking and vertical movement. Microbial decomposition and zooplankton/fish consumption of particulate organic carbon (POC) and dissolved organic carbon (DOC) occurs in the mesopelagic zone (200-1000 m deep). This results in a significant decrease in the export of organic compounds as they are transformed into inorganic nutrients and other substances. The sequestration depth refers to the depth at which carbon has been stored in the ocean for over a century. The depth of sequestration is also considered the lower boundary of the mesopelagic zone. Researchers have used radioactive isotopes from nuclear power plant incidents in deep-sea sediment traps to determine the presence of sediment traps in the northern Pacific Ocean prior to the Fukushima Daiichi nuclear power plant incident. Fukushima radionuclides were found in zooplankton and mesopelagic fish, suggesting transfer through the biological pump, although the amounts were very low. Fukushima-derived radionuclides will serve as tracers for water mass transfer in the northwest Pacific Ocean for many years because of their extended residence durations.

The effectiveness of ocean biological pumps varies with the climate. The operation of the biological pump is thought to have had an impact on the changes in atmospheric carbon dioxide levels that occurred during the historical glacial and interglacial periods. It is also believed that biological pumps are influenced by climatic fluctuations. The influence of future human-induced climate change on biological pumps of the ocean remains unclear. Zooplankton faecal pellets are considered to play a crucial role in marine biological pumps. Moran et al. [6] conducted a thorough examination of the literature on the significance of zooplankton faecal pellets in both marine and freshwater ecosystems. The analysis conducted by Hamilton et al. [7] covered various aspects, including the vertical transport capacity of the particles, nutritional value, breakdown and consumption of faecal pellets, and levels of contaminants present in faecal pellets. Studies have revealed that sinking zooplankton faecal pellets play a significant role in transporting particles and chemicals from the surface to deeper layers of the ocean. However, in certain circumstances, zooplankton faecal pellets are recycled and kept in the upper few hundred meters of the water column through the process of coprophagy and microbial decomposition.

Moreover, it should be noted that in many cases, a substantial portion of the downward movement is not attributable to faecal pellets but rather to marine, snow, and sinking phytoplankton blooms that settle on the ocean floor without significantly influencing the food chain in the open sea. Findings from over 300 studies conducted since 2001 on vertical export flow using various methods, such as sediment traps and large-volume filtration systems across the world's oceans, have revealed several common patterns. The downward movement of sinking particles is often caused by a mixture of faecal pellets, marine, snow, and direct sedimentation of phytoplankton blooms. Particle aggregation increases the downward movement of particles by converting small suspended particles into larger ones that sink quickly. Aggregation plays a crucial role in the settlement of plant materials from blooms of surface-layer algae. Phytoplankton blooms that settle as sediments typically consist of diatoms, coccolithophorids, and gelatinous colonial species of the genus Phaeocystis, dinoflagellates, and other plankton. The proportions of faecal pellets, marine snow, and phytodetritus in the overall particle flow change significantly depending on phytoplankton, zooplankton, and microbial plankton populations in surface waters, and vary over time and location. The retention of faecal pellet components in near-surface waters, instead of their export to abyssal depths, is caused by a combination of microbial degradation and zooplankton-mediated processes, such as the disruption of faecal pellets by zooplankton. Lyon and Mock [2] argued that the surface ocean influences the strength of the biological pump, whereas the subterranean ocean affects its efficiency. Computational simulations [4, 5] have suggested that the phytoplankton community controls the export of phytodetritus, which manages the majority of organic carbon remineralisation into carbon dioxide, and large zooplankton play a critical role in transferring particulate organic carbon to large metazoans, primarily through faecal pellets and vertically migrating animals.

2. LITERATURE REVIEW

Biological pumps have been a significant factor in shaping the global climate in the past, present, and future. It has been present in water for over 500 million years. This process is believed to have occurred exclusively within the Phanerozoic Aeon, which spans the last 540 million years since the Cambrian ‘explosion’ of life documented in the fossil record. During the Neoproterozoic era, which occurred 1 billion to 540 million years ago, there were severe glacial periods where the worldwide ocean may have been entirely covered in sea ice, referred to as ‘snowball Earth’. Changes in carbon cycling and oxidation of organic matter in the ocean may have significantly impacted the biological pump over the past 500 million years. Precambrian water had lower oxygen levels compared to the current ocean; therefore, certain components of DOM that are currently deteriorating rapidly may have become refractory substances at that time. The inorganic carbon stores in both the atmosphere and ocean would have been substantial, but they were possibly overshadowed by the vast magnitude of the ocean dissolved organic matter pool. Ocean oxygenation enabled the evolution of protists and metazoans, leading to the establishment of a biological pump. This pump involves a significant downward movement of organic matter, which decreases exponentially with depth because of aerobic decomposition in oxygen-rich waters.

The emergence of marine eukaryotes during the Late Proterozoic, commencing 800 million years ago, would have enhanced the episodic biological pump by increasing the proportion of organic matter in larger aggregates that sank more efficiently because of their greater size. Worldwide ice ages may have arisen because of the heightened transfer of biological material from the ocean's surface to oxygen-depleted deep waters and sediment layers. This organic material would have been broken down without oxygen at a deep level by sulfate- or iron-reducing bacteria. Upon the oceans becoming more oxygenated, the anoxic remineralisation chemistry in the deep sea shifted, preventing the biogeochemical process that caused the Neoproterozoic 'snowball Earth' glaciation from recurring. The biological pump may have contributed to cooling the Earth, potentially terminating the 'greenhouse climate' from the past. The concentration was approximately 280 parts per million by volume (ppmv). Alteration involves elevated levels of nitrate and phosphate in surface waters at low latitudes, where the present levels are insufficient to support biological production and export to deeper waters. Another approach would entail increasing the biological output and export flow of fully abundant nutrients in high-latitude seas, where a substantial amount of nutrients are not being utilised. Significant fluctuations in nitrogen levels may have occurred as a result of denitrification and/or nitrogen fixation during the glacial and interglacial periods.

Keil [1] argued that during glacial periods, nitrogen fixation was enhanced due to an increase in airborne dust, which introduced iron into the ocean and consequently boosted nitrogen fixation. Moreover, the widespread occurrence of suboxic water resulting from denitrification caused by ocean acidification has been projected in the future. Processes in high-latitude seas, notably the Southern Ocean, are believed to contribute to the improved performance of biological pumps during glacial periods. In Polar Regions, the surface water descends to lower depths, thereby aerating the deep ocean. The abundance of nutrients in upwelled waters stimulates primary production in the upper layer, resulting in an increased transfer of organic matter to deeper waters.

Researchers have determined that a combination of biological and physical factors leads to this decline. The effectiveness of the biological pump may have altered in response to modifications in nutritional and physical systems during the ice ages, which could have impacted the 'Southern Ocean leak'. The efficiency of a biological pump can differ based on latitude, with the highest efficiency occurring in extensive low-latitude surface waters with low nutrient levels. The process of bringing nutrient-rich water from deeper levels into the euphotic zone and the loss of nutrients due to photosynthesis can result in Southern Ocean leaks. During the previous ice age, the efficiency of the biological pump was lower in the Antarctic zone south of the Antarctic Circumpolar Current, but higher in the Subantarctic Zone north of the Antarctic Circumpolar Current, compared to the present. The decreased flow of water between the Antarctic surface waters and deeper layers may have sealed this connection during the previous ice age. The interaction of these and other potential processes or variables may have influenced the changes in carbon levels in the deep sea during the glacial periods. These factors may have varied during the ice eras, including alternating cycles of deep-sea ventilation by waters sinking from the Southern Ocean and the North Atlantic or from the expansion of Antarctic Sea ice, which may have limited carbon exchange between the ocean and the atmosphere.

The continued removal of nutrients from surface waters by the biological pump, without replenishment from deep waters, could result in the depletion of nutrients in the surface layer. This leads to a decrease in the primary productivity of the phytoplankton. The primary route for silicic acid and other nutrients to return to surface waters from deep waters is upwelling in the Southern Ocean. These nutrients are then incorporated into the sinking SubAntarctic Mode Water (SAMW), which descends from the Subantarctic Zone above the Antarctic Polar Front Zone and disperses northward throughout the Southern Hemisphere and North Atlantic. A vertical recycling loop between the surface and deep waters in the Southern Ocean supports heavy diatom growth due to the movement of silica in diatom shells sinking from northward moving surface waters and returning to the surface in southward-moving waters upwelling at the Antarctic divergence. This process forms a global Si trap. The high concentration of silicic acid in the Southern Ocean may have led to the development of thick silica frustules in some Antarctic diatoms, potentially acting as a protective armour against copepod grazers. Thick-shelled diatoms can export more silica than carbon through the biological pump, whereas thinner-shelled diatoms, when exposed to iron fertilisation, can export more carbon than silica. There has been a reduction in opal accumulation rates in glacial sediments of the eastern equatorial Pacific (EEP). Predicting the direction of change is a challenging task. A significant but unspecified fraction (between a quarter and half) of the biological pump's impact on the ocean carbon cycle is still unknown. The effects of human-caused global warming on ocean biological pumps are unclear and may be influenced by the conversion of rising temperatures into carbonic acid. Various disturbances in the biological pump vary in terms of their enhancement or reduction of processes, with variable levels of sensitivity, intensity, and duration of impact.

The heating of the ocean is likely to intensify the stratification of its upper layer, resulting in a decreased nutrient supply from deeper layers. This could lead to reduced primary production and a decline in export flux through the biological pump, especially in the already stratified waters of the tropical and subtropical regions. The reduction in nutrient supply due to increased stratification can cause changes in phytoplankton community structure, transitioning from diatom dominance to coccolithophorids or from large diatoms to small microflagellates and cyanobacteria. This shift could result in longer marine food chains with reduced trophic efficiency. Long-term changes in cyanobacteria have been observed when stratification increases in the subtropical gyres of the North Atlantic and North Pacific. Moran et al. [6] reported an increase in the nitrogen fraction entering the euphotic zone through nitrogen fixation at HOT station in the subtropical gyre over the past 20 years. The power of the biological pump increased more than anticipated because of the influx of nitrogen into the euphotic zone through ocean circulation. Simulations indicate that the anticipated rise in temperature by the end of the 21st century will increase the prevalence and broaden the geographical range of picoplanktonic cyanobacteria, Prochlorococcus, and Synechococus. Enhanced stratification can lead to higher concentrations of phytoplankton in well-lit upper mixed-layer waters, boosting primary production by limiting the downward movement of phytoplankton into deeper, darker layers of the water column, especially in deep mixed waters at high latitudes. The heating of the upper ocean can also lead to more frequent and intense storms, which can improve the sudden release of nutrients into the euphotic zone, resulting in higher primary production.

Stigebrandt and Gustafsson [4] proposed an alternative to the notion that stratification results in diatom displacement by smaller phytoplankton, leading to a decrease in carbon productivity and export. Researchers have observed that certain diatoms possess adaptations that enable them to thrive in stratified waters, including the ability to survive under low-light conditions at deep chlorophyll maxima, vertical movements between deep nutriclines and sunlit surface depths, and symbiotic relationships with nitrogen-fixing cyanobacteria. These adaptations allow diatoms to preserve their seed populations in oligotrophic subtropical marine waters by exploiting mixing events and bloom opportunities. The accumulation of these diatoms can increase the transfer of materials to the deeper ocean layers. Comeau et al. [5] reported recurring summer blooms of diatoms and nitrogen-fixing cyanobacteria, along with increased export flow, in the North Pacific Subtropical Gyre under highly stratified and consistently nutrient-poor conditions. Evidence of diatom blooms in stratified seas has been discovered in laminated sediments from the Mediterranean during the Cretaceous period as well as in other records of ‘palaeo-sediment traps' in laminated strata. Moran et al. [6] suggested that diatom production and export could potentially increase with more stratification, contrary to common expectations of reduction. This could serve as a negative feedback mechanism for global warming by strengthening biological pumps. Ocean warming leads to changes in biological communities that can impact biological pumps.

Increased temperatures can accelerate microbial breakdown of organic matter, which may lead to reduced transfer of this material to deeper ocean layers, as more is absorbed at the surface. Rising temperatures may alter pelagic surface ecosystems, resulting in a shift from a predominance of diatoms and larger zooplankton to one dominated by picoplankton and microzooplankton. This change could result in a decrease in the transfer of particulate detrital food to deeper depths, leading to a reduction in the abundance, species diversity, body size, and taxonomic composition of the abyssal benthic animal communities. Several models have predicted a decline in the primary production and export of organic carbon due to ongoing ocean warming. Increased warming may decrease the biological absorption of dissolved inorganic carbon (DIC) in the surface layer, leading to greater accumulation of dissolved organic carbon (DOC) than particulate organic carbon (POC). This may have resulted in a decrease in POC export through the biological pump. Simulations indicated that warming-induced stratification may cause the depth of remineralisation to move upward, resulting in the redistribution of carbon from deeper waters to the surface. This process can enhance the transfer of carbon from the ocean to the atmosphere, thereby exacerbating greenhouse warming.

Decreases in the extent of polar sea ice may significantly impact biological populations and pumps. The population of Antarctic krill (Euphausia superba) has declined substantially by a factor of ten since 1950 in the southwest Atlantic sector near the Antarctic Peninsula, while salps (Salpa thompsoni) have proliferated in various regions. The abundance of krill was positively associated with recruitment from the previous spawning season, which, in turn, was positively associated with substantial sea ice during the previous year. Consequently, as sea ice increased, krill abundance decreased. Notably, there has been a decrease in the occurrence of winters with widespread sea-ice coverage over the past 50 years. Sea ice algae, primarily diatoms, play a vital role as winter food for krill, aiding adult reproduction during spring and larval survival throughout winter. The increase in krill recruitment is supported by the presence of abundant summer food, mostly diatoms. The decline in chlorophyll levels appeared to be related to a simultaneous decrease in the extent of sea ice. The reduction in krill and phytoplankton populations, together with the increase in salps, appears to be associated with reductions in sea ice. Furthermore, the decline in phytoplankton is linked to a shift in the phytoplankton population from larger cells, such as diatoms, which are a crucial food source for krill, to smaller cells, which are more effectively consumed by salps.

The potential impact of reductions in sea ice and larger phytoplankton due to climate change, as well as the replacement of krill by salps, on biological pumps is a matter of concern. It is worth noting that during salp blooms, a significant amount of primary production is consumed by salps, as they produce large, rapidly sinking faecal pellets that increase export flow. This, in turn, reduces the amount of primary production available to krill, which plays a crucial role in breaking down phytoplankton chains and aggregates, and serves as a food source for higher-level pelagic consumers such as penguins and marine animals. The decline in krill populations and sea-ice coverage has also led to changes in the distribution and number of many Antarctic carnivores, including Adélie penguins, crabeater seals, Gentoo penguins, and fur seals. Additionally, decreases in the export flow to the seafloor have been linked to rising temperatures and a decrease in the extent of sea ice in the northern Bering Sea. The impact of increased temperature on the biological pump also extends to the creation and breakdown of aggregates. Higher temperatures can increase the rate at which aggregates are formed and accelerate sedimentation. These factors, combined with the proliferation of bacteria and an increase in biomass, result in faster breakdown of aggregates. Overall, higher temperatures can significantly impact the effectiveness of the biological pump by increasing the rate of aggregation and accelerating the sedimentation rate.

Reducing the export of calcareous plankton might result in the oxidation of calcareous-ballasted plankton in shallower near-surface waters with lowered dissolved oxygen levels owing to higher temperatures, consequently leading to the expansion of hypoxic environments. The proliferation of hypoxic zones in water can promote denitrification and reduce nitrification in oceans. It is anticipated that ocean acidification will alter the cycles of essential nutrients, particularly nitrogen. The expected modifications include increased nitrogen fixation by cyanobacteria, increased denitrification due to the spread of suboxic water, and diminished nitrification in the ocean, leading to the loss of fixed nitrogen. Altered nutrient levels are expected to benefit certain forms of phytoplankton, such as cyanobacteria and picoplankton, while disadvantaging others, such as diatoms, which play a crucial role in biological pumps. Warming and acidification result in changes in temperature, carbonate levels, stratification, mixing patterns, nutrient availability, and biological communities in various ocean basins. Presently, oceanographers cannot precisely forecast whether a biological pump will intensify or decrease in the coming century.

The outcomes of various research studies have been determined by examining diverse geographic areas, habitats, situations, and organisms. The biological pump is influenced by numerous interaction factors and synergistic effects, which can affect the export and sequestration flux, as well as flux attenuation. Measuring the efficiency of biological pumps, both present and future, is crucial for the development of precise global carbon models. However, considerable uncertainties persist in contemporary models that forecast the consequences of ocean warming and acidification on biological pumps, particularly regarding the response of the epipelagic production system to these changes.

3. GEOCHEMICAL VARIABLES

3.1. Export flux of particulate organic carbon (POC)

The efficiency of the downward transport of particulate organic carbon via a biological pump depends on the quantity and type of near-surface plankton populations, as well as the recycling and degradation of sinking particles at depth. Since 2001, various studies have focused on the concentration and vertical transit of particulate organic pollutants. Sediment traps have been employed for most of these observations; however, differences in design and deployment specifics can lead to highly variable and often incomparable results. Several comprehensive evaluations were conducted to investigate the transit flow of organic particles. The transit flow of POC exhibited significant variations. These variations may occur on a seasonal or inter-annual basis. Export flows vary as a result of climatological fluctuations such as the El Niño-Southern Oscillation, Indian Ocean monsoon, North Atlantic Oscillation, and North Pacific Gyre Oscillation cycles. The export of plankton to depth depends on the quantity and composition of the plankton community.

As such, long-term increases in zooplankton biomass have been observed in the subtropical gyres of the North Atlantic and North Pacific [6-10]. The rise in zooplankton populations has been linked to the movement of carbon through vertical migration and the sinking of zooplankton faecal pellets, together with the migration of phosphorus from surface waters to deeper levels. The ALOHA station, which is part of the Hawaii Ocean Time Series (HOT) study area and is located in the oligotrophic subtropical gyre, has low nutrient levels and warm surface temperatures. This has led to a system dominated by picoplankton with minimal seasonal variation, low primary production, and low flux of particulate organic carbon (POC) to the base of the euphotic zone. The subarctic gyre of the northwest Pacific is characterised by Station K2, where high-nutrient waters are cooler and dominated by diatoms, resulting in increased phytoplankton biomass, productivity, and vertical export. The mesopelagic transfer efficiency measures the attenuation of flux, which is an important factor in understanding the dynamics of oceanic ecosystems.

3.2. Dissolved organic carbon (DOC)

Vertical mixing is a crucial factor in the transportation of dissolved organic carbon (DOC) to deeper depths, thereby enhancing the efficiency of biological pumps. The biological pump is responsible for transferring a substantial amount of carbon, particularly dissolved organic carbon (DOC), to the deep ocean annually. Three billion tons as carbon is used as particulate matter and over 700 billion tons of dissolved organic carbon (DOC). It is important to note that approximately 95% of dissolved organic matter (DOM) in the ocean is refractory dissolved organic matter (RDOM), which is not bioavailable to marine organisms. The biological pump interacts with particulate organic carbon (POC) exported from the ocean surface waters. A substantial amount of dissolved organic carbon (DOC) in the ocean plays a significant role in the efficiency of biological pumps. Recalcitrant dissolved organic matter (RDOM) is generated through a process referred to as the 'microbial carbon pump' (MCP), in which marine microorganisms transform bioavailable dissolved organic carbon (DOC) into RDOM. Marine bacteria cause significant shifts in carbon distribution, which have an impact on the global carbon cycle, particularly in response to climate change. It has been demonstrated that a specific strain of the bacterial species Alteromonas has the ability to consume all labile dissolved organic carbon (DOC) in coastal waters, highlighting the significant impact of this particular bacterium on carbon cycling in the ocean. Determining whether the ocean's primary production generates more carbon than that consumed through respiration is crucial for understanding the global carbon cycle. The question of whether ocean metabolism is mostly autotrophic or heterotrophic has been actively discussed by several researchers for over a decade. Carbon respiration may exceed production in many parts of the ocean, especially in oligotrophic regions, for a vast majority of the time.

Research on biological pumps has predominantly focused on the sinking of particulate organic carbon (POC) into deeper layers, whereas the respiration of heterotrophic planktonic bacteria is primarily fuelled by dissolved organic carbon (DOC). Estimates of respiration that rely mainly on POC fluxes may underestimate the overall flux by neglecting the respiration supplied by DOC. The stoichiometry of carbon, nitrogen, and phosphorus in dissolved organic matter (DOM) significantly exceeds the Redfield ratio, which might lead to surplus respiration observed in the deep ocean. Ancient dissolved organic carbon (DOC) from primary production thousands of years ago could fuel modern-day microbial respiration, sometimes more than what can be sustained by current primary productivity. The debate between net autotrophy and heterotrophy focuses on the advantages and disadvantages of incubation (in vitro) versus incubation-free (in situ) methods for quantifying primary production and net plankton community metabolism are still being developed. Addressing these ongoing challenges is critical for understanding the global carbon budget, particularly in light of anticipated responses to climate change in the near future.

3.3. Zooplankton fecal pellets

Zooplankton excrete fecal pellets, which have a significant impact on the transfer of particulate organic carbon to deeper ocean layers. The zooplankton community consists of various components that produce faecal pellets of different types and sizes. Organic matter is produced by different marine organisms, including minipellets by protistan; microzooplankton, such as heterotrophic dinoflagellates, ciliates, and radiolarians; and small metazoans, such as copepod nauplii and small copepodites. Copepods produce cylindrical or ovoid faecal pellets, while euphausiids produce larger faecal strings, and salps, appendicularians, and other tunicates produce tabular faecal flakes. The sinking rates and densities of different types and sizes of faecal pellets may affect their export or retention in different water column strata. The proportion of total sinking particulate carbon flow from identifiable zooplankton faecal pellets varied considerably.

Differences in the quantities and types of phytoplankton and zooplankton can substantially impact the transfer of particulate organic carbon (POC) to deeper layers through faecal pellets. The contribution of marine snow, phytodetrital aggregates, and other biological aggregates to the biological pump can influence the fraction of the overall POC flow that is attributable to zooplankton faecal pellets. Research has shown that in the California Current Ecosystem, zooplankton faecal pellets constitute a significant portion of passive particulate export, ranging from 1. 9% to 94%, depending on the season. During spring, these pellets were more prevalent, whereas in the fall, marine snow and unidentifiable particles were more dominant in the vertical fluxes. Furthermore, the choice of collection technique can lead to variability in the proportion of export flow assigned to faecal pellets.

Hamilton et al. [7] demonstrated that the presence of polyacrylamide gels in sediment traps reduces the degradation of particles, resulting in a higher concentration of identifiable faecal pellets in the sediment traps. Data on the total particulate organic carbon (POC) flow and the proportion of faecal pellets in the total POC flux were collected from various studies and locations. Their examination revealed no significant relationship between these two parameters at the depths of the epipelagic and mesopelagic layers, as well as in most bathypelagic layers. When POC increased, the proportion of POC in faecal pellets decreased. They suggested that during periods of high total POC flow, the main sources of POC were non-faecal pellet sources such as marine, snow, or phytodetritus. Phytodetrital aggregates were observed at the bottom during periods of elevated total POC export flow in the northeast Atlantic and northeast Pacific, as documented by Comeau et al. [5]. When the overall amount of particulate organic carbon (POC) was diminished, the proportion of POC in faecal pellets increased. This pattern was discerned at their research facility in the northeast Pacific Ocean and other areas, as delineated in the literature. The flow and faecal pellet POC flux with depth could be a typical attribute of deep-sea fluxes.

3.4. Epipelagic retention of zooplankton fecal pellets due to zooplankton activity

Recycling of zooplankton faecal pellets in the upper layer of the ocean appears to be facilitated by the actions of other zooplankton organisms. In examining the export of particulate organic carbon (POC), sediment trap studies often reveal that a considerable proportion of zooplankton faecal pellets produced in the upper epipelagic zone remain within this zone. This suggests that faecal pellets are being reutilised or retained in the upper layer of the ocean. Although microbial breakdown rates are generally slower than recorded faecal pellet sinking velocities (which can reach hundreds of metres per day), the rapid descent of the pellets enables them to fall beyond the epipelagic zone before being broken down by microorganisms. It has been proposed that copepods, a specific group of zooplankton, play a significant role in retaining faecal pellets within the epipelagic zone. The following actions involve consuming whole faecal pellets (coprophagy), breaking them into smaller particles (coprorhexy), or disrupting the protective membrane to release some of their contents into the water (coprochaly). These actions are likely to break down larger sinking particles into smaller suspended particles, which helps to maintain faecal contents in the upper ocean layer and slows down their movement to deeper depths. Hamilton et al. [7] proposed that the cyclopoid copepod Oithona similis consumes faecal pellets of several calanoid copepod species, which is supported by limited experimental data. It is suggested that similar organisms in the ocean could act as a 'coprophagous filters to trap many copepod faecal pellets in the epipelagic zone. However, Oithona similis does not generate a typical feeding current for calanoid copepods; instead, it feeds like an ambush predator.

Remaining stationary in water until reacting to hydromechanical signals from prey movement or sinking faecal matter. This copepod could play a significant role in copepod coprophagous filtration systems for sinking copepod faecal pellets. Mesocosm investigations provide evidence that Oithona sp. could play a crucial role in consuming fecal pellets produced by calanoid copepods, as demonstrated by a notable negative association between the vertical flow of fecal pellet carbon and Oithona sp. biomass. Recent sediment trap research on faecal pellet distributions has supported the theory of copepod coprophagous filtration. Copepods, such as those in the Oncaea genus, and pelagic harpacticoids, such as Microsetella norvegica, have been linked indirectly to the consumption or breakdown of zooplankton faecal pellets and other detrital particles. Recent research has cast doubt on the significance of a coprophagous filter involving copepods of the genus Oithona. Non-Oithona copepods have been seen consuming fecal pellets from other copepods. Accidental consumption of faecal pellets is a possibility. Hamilton et al. [7] revealed that the calanoid copepods Acartia tonsa and Temora longicornis ingested their own faecal pellets. However, the availability of alternative food sources has resulted in the increased consumption of faecal pellets. In the absence of other options for phytoplankton food, copepods do not generate a feeding current, leading to minimal ingestion of faecal pellets. When copepods had access to various phytoplankton as food, they employed suspension feeding via a feeding stream. Faecal pellets were consumed along with phytoplankton, potentially due to accidents.

Seifert et al. [8] discovered that a larger faecal pellet size correlated with a lower clearance rate for copepods feeding on them. Given that the size of the copepod faecal pellet is influenced by the type of food consumed, and diatom diets result in larger faecal pellets, it is anticipated that coprophagy of copepod faecal pellets by other copepods will decrease as the size of the faecal pellets increases. Moran et al. [6] found that copepods Oithona similis, Calanus helgolandicus, and Pseudocalanus elongatus consumed fecal pellets regardless of the availability of alternative phytoplankton food. However, the consumption of faecal pellets increased when alternative foods were available. Elongatus appears to accidentally ingest small particles of faecal pellets while feeding on phytoplankton. Most faecal pellets were rejected by these two copepods, resulting in damage to the pellets during the rejection process. Copepods primarily reduce the vertical flux of faecal pellets through coprorhexy rather than coprophagy [7]. Copepods damage faecal pellets, transforming them into smaller fragments that sink more slowly and are more susceptible to microbial degradation. Planktons other than copepods likely play a crucial role in the breakdown of copepod faecal pellets in the epipelagic zone. Comeau et al. [5] found that the copepod population was primarily composed of Oithona similis, and faecal pellet breakdown occurred through coprophagy. Moran et al. [6] validated the significance of microzooplankton in the breakdown of copepod fecal pellets. Microscopic examination revealed that heterotrophic dinoflagellates such as Gyrodinium dominans, G. spirale, and Protoperidinium spp. may consume faecal pellets. Dinoflagellates have a more significant role in the degradation of faecal pellets than ciliates. The impact of bacterial culture on faecal pellet breakdown was greater than that of bacteria present in natural water. In July, a relationship was observed between high copepod numbers, low protozooplankton numbers, and slow faecal pellet breakdown rates. A study was conducted to investigate the consumption of Acartia tonsa faecal pellets by heterotrophic and mixotrophic dinoflagellate species using feeding and dinoflagellate growth assays, along with video recordings of eating behaviour. Two of the three mixotrophic dinoflagellates and all four heterotrophic dinoflagellates consumed faecal pellets and thrived on diets consisting of faecal pellets.

Dinoflagellates exhibit diverse behaviours when consuming faecal pellets, such as direct ingestion of whole pellets, selective removal of small pieces for consumption, using a feeding tube to attach to the pellet, enveloping the pellet with their cell membrane to form a food vacuole, and feeding outside the dinoflagellate cell using a feeding veil. Research indicates that large dinoflagellates can fully explain the observed rates of faecal pellet degradation in field studies, which underscores the significant role of dinoflagellates in the protozoan filter for sinking faecal pellets. Previous findings on the consumption of copepod faecal pellets by the heterotrophic dinoflagellate Noctiluca scintillans suggest that dinoflagellate coprophagy is more common than previously thought. Studies have investigated the breakdown of copepod faecal pellets by protozooplankton. The substantial deterioration of plankton communities is primarily caused by athecate dinoflagellates and ciliates. It is important to note that not all zooplankton excrement takes the form of faecal pellets.

3.5. Vertical migration and fecal pellet repackaging

Zooplankton can play a role in the vertical export flow by consuming phytoplankton and producing fecal pellets that sink, as well as actively exporting organic material through their vertical movement. The term 'active flux' refers to the process by which zooplankton, while migrating vertically, carry food acquired at the surface downward in their bellies to be egested, or consumed by predators of zooplankton, or digested at deeper levels. Estimations suggest that the active flux can contribute to the downward transfer of carbon. Observations of active flow in subtropical gyres, such as the HOT and BATS gyres, indicate that this process may be equivalent to sinking particle flux when the zooplankton biomass is high. Several copepods exhibit vertical migration behaviour, and estimates suggest that there are sufficient suspension-feeding and detritivorous copepods to meet the metabolic requirements of carnivorous copepods. It is likely that the copepod population plays a significant role in the active export of organic matter to the deeper ocean layers.

The importance of active zooplankton movement appears to vary based on hydrographic and biological factors. On the other hand, Keil [1] argued that faeces recently excreted by deep-sea migrants may be a more nourishing food source for mesopelagic organisms than faeces generated in surface waters that have begun to decay while sinking. Hamilton et al. [7] revealed that carbon flow from vertically migrating zooplankton can sometimes equal or even surpass the amount of carbon from sinking faecal pellets and other particles. Additionally, the estimated carbon flow caused by vertically migrating zooplankton during winter was higher (131-136%) than the flux of sinking faecal pellets at two locations in the subarctic and subtropical northern North Pacific.

Bird et al. [9] played a pivotal role in examining the biological pump in the subarctic Pacific during seasons other than spring, attributable to the heightened activity of diel vertical migration by copepods when the sedimentation flux of phytoplankton and other organic matter was low. The amount of organic particulate carbon lost in the mesopelagic zone due to bacterial and zooplankton metabolism in the subtropical and subarctic Pacific. Estimates revealed that the sinking of particulate organic carbon (POC) failed to meet the metabolic demands of zooplankton and bacteria at both locations. The authors concluded that the increased carbon requirements in the mesopelagic zone were likely satisfied by vertical migration from the epipelagic zone to the mesopelagic zones. Schlunegger et al. [6] observed that lunar cycles influence vertical migratory patterns in the Gulf of Mexico. A model in which migration speeds varied at various depths and organic particles were recycled at varying depths (POC).

Modifications in the physiology, morphology, and pigmentation of zooplankton faecal pellets at varying depths suggest that numerous faecal pellets sank and were broken down by other zooplankton, which subsequently consumed the faecal pellet contents. This implies that there was a process of repackaging faecal pellets in the upper ocean layer, and the active movement of copepod faecal pellets to deeper layers played a significant role in the transfer of carbon to those depths, especially when the phytoplankton consisted mostly of microscopic cells that did not sink quickly. The carbon flow resulting from the death of copepod overwintering in the deep region was at least as high as the sedimentation flux in the subarctic North Pacific. Two methods demonstrated that mesopelagic zooplankton consume particulate particles from the epipelagic zone. The proportions of fatty acid indicators in both the zooplankton and particulate assemblages were comparable, indicating that the zooplankton were feeding on sinking particles. Indicators of carnivorous behaviour in midwater zooplankton increased with depth.

Zooplankton that consume detrital aggregates, including connected picoplankton, facilitate the transfer of surface primary production to deeper waters, as discovered by Moran et al. [6]. Mesopelagic zooplankton in the subtropical north Pacific primarily rely on surface-derived food resources rather than suspended mesopelagic ones, as indicated by the findings. This reliance on surface-derived food resources was achieved by consuming sinking particles, carnivory by vertical migrants, or feeding in the epipelagic zone by vertical migrants during the night. Vertical migration plays a significant role in transporting dissolved organic matter (DOM) to the deeper parts of the ocean. The maximum flux of total dissolved nitrogen from the migrators exceeded the sinking flux of organic nitrogen flux by 1.6-3.5 times at the three depths. Vertical migration of zooplankton is believed to significantly influence the elimination of phosphorus from the surface ocean through active export. The increase in the biomass of migratory zooplankton between 1994 and 2005 has contributed to the heightened significance of this process in the removal of phosphorus from surface waters. This active transportation could potentially play a pivotal role in imposing stricter regulations on phosphorus usage in primary agriculture within the region.

4. BIOGENIC VARIABLES

4.1. Microbial Ecology of fecal pellets

Zooplankton fecal pellets, marine snow, and phytoplankton aggregates are deemed 'microbial hotspots' in the marine environment. These detrital particles contain substantial concentrations of bacteria and other microorganisms, surpassing those present in the surrounding water. Microorganisms thrive, colonise, and proliferate within the particles to which they are attached. Microorganism colonisation enhances the nutritional value of faecal pellets and other organic aggregates in detritivorous organisms. Additionally, sinking aggregates release dissolved solutes into the surrounding water column. Bacteria colonise organic aggregates through a dynamic process in which motile bacteria and other microorganisms adhere to and detach from particles.

A series of trophic interactions occur within the microbial community that attaches to the particles. Bacterial populations are regulated by flagellate predation, whereas flagellates and ciliates experience rapid turnover owing to continuous attachment and detachment. Russell et al. [11] found that the breakdown of particulate organic matter by associated bacteria was significant, leading to a notable decrease in the vertical movement of particles in water as they sank. The bacteria found on particles plunging to depths in Arctic waters likely originated from suspended bacteria at the water's surface. Bacteria were found to adhere to both particles and inside the faecal pellets of copepods and doliolids. Copepods consume organic substrates through food, which are then used by bacteria for rapid development [4-6].

The bacterial population within the digestive systems of the copepods increases as they consume more food. There is a balance between the growth of bacteria, which is encouraged by copepod feeding, and the reduction of bacteria due to copepod faeces. Mock et al. [12] found that the number of bacteria associated with copepods and their faecal pellets was significantly higher than that of free-living bacterioplankton in nearby waters. Decomposing aggregates and faecal pellets release dissolved organic carbon (DOC) as a substrate for the development of free-living bacterioplankton in water. Copepod faecal pellets break down to emit dissolved organic carbon (DOC), but salp faecal pellets do not release detectable amounts of chromophoric dissolved organic matter (DOM).

Hamme et al. [13] revealed that the faecal pellets of the copepod Acartia tonsa comprise ammonium and urea. The researchers uncovered that the disintegration of organic matter from Sargassum epifaunal grazer faecal pellets occurred swiftly, most likely due to the loss of dissolved organic matter. The pace at which microorganisms break down zooplankton faecal pellets and other organic aggregates determines whether these particles are recycled at the surface or sink to deeper depths. There is less information available regarding the rates at which microbes break down faecal pellets or other organic particles in the ocean. Moran et al. [6] discovered that the breakdown rates of copepod faecal pellets varied based on the diet used to create the pellets. Moreover, they validated the presence of methanogenic Archaea in copepod faecal pellets, suggesting the existence of oxygen-deprived microenvironments.

Recently, it has been established that metasome sections of the intestines of calanoid copepods display more acidic properties and lower oxygen levels than seawater. Copepod guts and faecal pellets can serve as microenvironments for obligate anaerobic organisms within an oxygen-rich water column. There have been ongoing investigations into the relative significance of bacteria found 'inside' faecal pellets prior to excretion compared to bacteria from the surrounding water that inhabit faecal pellets after excretion and whether bacterial breakdown of zooplankton faecal pellets occurs predominantly from the 'inside' or outside of the pellets. Bacterial populations found in faecal pellets belong to a variety of copepods in the coastal waters of Hong Kong. The faecal pellets harbour bacteria from different phylogenetic groups compared with those present in natural seawater.

In the field investigations of Russel et al. [11] and Ravaglioli et al. [15], seawater bacterial communities showed a greater variety of species than the bacterial communities found in faecal pellets. There were significant alterations in the composition of the bacterial community in faecal pellets during the initial 48 h of experimental incubation in natural seawater. Bacteria that were initially exclusive to faecal pellets were not present in the nearby seawater. Over time, the bacterial communities in the faecal pellets and seawater became more similar, suggesting that seawater bacteria colonised the faecal pellets during the degradation experiments. It was discovered that free-living bacterioplankton absorbed dissolved organic material from copepod faecal pellets, while internal bacteria inside the pellets or external bacteria on the pellet surfaces destroyed the particle matter. The microorganisms found in faecal pellets and bacterioplankton, both internal and external, exhibited distinct phylotypes, as determined by molecular studies.

Research findings indicate that the breakdown of copepod faecal pellets by internal bacteria is as significant as the breakdown by bacteria attached to faecal pellets from the surrounding water [1-4]. Additionally, studies have found that bacterial populations in the guts of copepods depend on the initial food sources they consume [5-7]. In specific situations, the decomposition of faecal pellets of copepods can lead to a substantial depletion of oxygen levels. Some particles, such as faecal pellets and marine snow, can sink rapidly through the water column without undergoing microbial decomposition owing to the influence of pressure. However, the microbial community in the ocean changes with increasing depth, owing to variations in pressure. The sinking speed of faecal pellets and aggregates can vary greatly and may be influenced by heavy mineral ballast, including phytoplankton thecae or terrigenous particles. Turner analysed data on the rate at which faecal pellets sink from various sources until mid-2001.

Subsequent research has suggested that incorporating dense materials, such as diatom tests and coccoliths, into faecal pellets and aggregates may boost their sinking speed. Investigations into organic carbon export fluxes have revealed a relationship with mineral fluxes, particularly carbonate fluxes, but to a lesser extent with opal and terrigenous materials. These ballast minerals are thought to shield certain organic materials in the particles from microbial degradation in the deep ocean. The diet of zooplankton can significantly influence the sinking speed of their faecal pellets, depending on the type and amount of ballast minerals ingested. Ballast theory was experimentally examined. Moran et al. [6] have studied the rates of faecal pellet production, microbial respiration, and sinking velocity of faecal pellets from the copepod Temora longicornis. The copepods were fed diets comprising three species of phytoplankton: the nanoflagellate Rhodomonas sp. The samples included organic carbon, the diatom Thalassiosira weissflogii with opal, and the coccolithophorid Emiliania huxleyi with calcite.

The results of this study did not reveal any pronounced discrepancies between the three diets. The ballast was found to have a positive impact on the sinking rate of copepod faecal pellets, but it failed to prevent them from undergoing decomposition. Hamilton et al. [7] demonstrated that carbonate-ballasted coccolithophorid aggregates descend at a faster pace than opal-ballasted diatom aggregates. However, they did not record any variation in the carbon-specific respiration rates of the aggregates with different ballasts. The researchers measured the dry mass, sinking velocity, and diffusivity of natural faecal pellets obtained from sediment traps situated off Cape Blanc, Mauritania.

The faecal pellets, which were substantial in size, were found to be composed of opal, calcite, and Saharan dust, serving as a natural ballast that accelerated their descent. In experiment conducted to determine the sinking velocities of faecal pellets from the doliolid Dolioletta gegenbauri, it was discovered that the velocities were notably slower than those reported in other studies for the same species. The differences in sinking speeds were attributed to the diets used to create the faecal pellets, as non-ballasted diets resulted in the production of lighter and more slowly descending faecal pellets. Although some studies have not provided evidence for the "ballast hypothesis", it remains a subject of ongoing investigation and debate in the scientific community.

Lyon and Mock [2] found that the descending velocities of the particles collected by sediment traps in the Arabian Sea and the Equatorial Pacific grew as the depth grew. This increase was not related to the amount of lithogenic minerals present but rather to a decrease in organic carbon as the depth increased. Mock et al. [12] concluded that the rising velocities are not affected by the lithogenic components of the particles. Hamm discovered that incorporating lithogenic mineral particles into diatom aggregates had uncertain effects on the sinking speed of the aggregates. As the quantity of lithogenic material increased, the sinking rate of the aggregate increased until saturation was achieved. However, the addition of lithogenic material did not significantly enhance the sinking speeds of the aggregates, and in some cases, even reduced them. Stigebrandt and Gustafsson [4] discovered that adding minerals to aggregates decreases their size and sinking speeds. Seifert et al. [8] found that adding calcite (coccoliths) and Saharan dust to abandoned appendician dwellings increased the sinking speed of marine snow, whereas adding opal (diatoms) had a minimal impact. Moran et al. [6] suggested that POC fluxes govern the fluxes of mineral ballast materials, rather than vice versa. Marine snow from surface layer biological activities can collect tiny, non-sinking mineral particles and transport them to deeper depths. Pfister et al. [14] found that the sinking speeds of phytodetritus aggregates with varying levels of mineral ballast were not straightforward and that the movement of particulate organic carbon (POC) controlled the movement of minerals to deeper levels, rather than the opposite. Recent studies of zooplankton faecal pellet sinking velocity suggest that water temperature influences pellet sinking velocity. Comparison of the quantity and sinking velocity with existing data indicated that the faecal pellets of Gazellae exhibited one of the fastest sinking rates among the faecal pellets tested. Gazellae had lower values than other chaetognaths, as documented by Stigebrandt and Gustafsson [4]. This variation can be attributed to the water temperature used in the sinking velocity measurements. The investigators discovered that the sinking velocities of faecal pellets from Antarctic euphausiids (Euphausia superba) varied significantly based on diet and food absorption. There is a relationship between pellet density, feeding rate, and meal absorption. Low feeding rates resulted in delayed intestinal transit duration and enhanced meal absorption efficiency, leading to compact, dense pellets with reduced carbon and nitrogen contents that sank swiftly. When favourable feeding circumstances prevailed, the pellets exhibited extended gut transit duration and ineffective food absorption, resulting in pellets with elevated carbon and nitrogen content that sank slowly. The composition of food was critical, as diatom diets produced rapidly sinking pellets that were likely weighed down by silicon. Faecal pellets derived from diets comprising phytoplankton, other than diatoms, displayed reduced sinking rates. Euphausiid food processing determines whether their faecal pellets sink quickly, facilitating the export of organic matter to deeper depths, or sink slowly, but contain high levels of carbon and nitrogen, serving as a food source for detritivores in the water column. Although sinking at a slower pace than salps, euphausiid faecal pellets were more commonly detected in samples collected from sediment traps in the Antarctic. Ravaglioli et al. [15] utilised an upward-facing echo sounder to quantify the sinking speeds of faecal pellets from the euphausiid Meganyctiphanes norvegica in Oslofjord, Norway.

The sinking rate of aggregates, including faecal pellets, is influenced by temperature. Stigebrandt and Gustafsson [4] showed that temperature did not have a direct impact on the sinking velocity of aggregates but did play a significant role in the vertical transport of particulate organic carbon (POC). Cold temperatures were observed to slow the degradation of aggregates by warm-temperature epipelagic microbes, which can be detrimental to suspension-feeding bivalves and shellfish. Phytoplankton cysts, whole cells, and toxins from harmful algae can be transferred to the seafloor through zooplankton faecal pellets, which can contaminate these organisms. Zooplankton fecal pellets have been found to contain cysts or whole cells of dangerous algal species, which can be harmful to suspension-feeding bivalves and shellfish. Toxic dinoflagellate resting cysts capable of germination have been discovered in copepod faecal pellets and some benthic species. Dinoflagellate cells from the toxin-producing genus Dinophysis were undamaged in copepod faecal pellets that were fed on natural Dinophysis blooms in the North Sea and off the coast of Spain.

Coprophagy, or the consumption of faeces, can pose a threat to pelagic organisms by exposing them to poisonous substances in the faecal pellets. Similarly, benthic organisms may be at risk owing to the sedimentation of these pellets. Certain dinoflagellate and diatom species can survive in copepod faecal pellets, which can contain phycotoxins that are harmful to marine life. Cyanobacteria and dinoflagellates have been found in copepod faecal pellets. The presence of dinoflagellate toxins in faecal pellets from zooplankton communities, particularly the marine cladoceran Evadne nordmanni, has been verified during natural blooms of the poisonous dinoflagellate Alexandrium fundyense in the Gulf of Maine. The faeces of several species of benthic ascidians have been found to contain living cells of harmful phytoplankton, which can pose a threat to marine ecosystems. In some cases, toxic phytoplankton sink to depth during dangerous algal blooms. For instance, domoic acid from diatoms was found in sediment traps off California during blooms of this diatom. During a period of fifteen years, there was a sudden increase in the occurrence of Pseudo-nitzschia blooms and hazardous domoic acid occurrences around the year 2000, which may be associated with climatic fluctuations caused by the North Pacific Gyre Oscillation.

4.2. Fecal pellets from various types of zooplankton

Zooplankton fecal pellets are known to play a crucial role in the biological pump. Several studies have been conducted to establish the significance of faecal pellets produced by different zooplankton species. This study examined faecal pellets from various marine organisms such as salps, appendicularians, pteropods, chaetognaths, copepods, euphausiids, and heterotrophic dinoflagellates. Many of these observations involved faecal pellets sinking through settling columns on ships or in the laboratory. Salp faecal pellets, in particular, play a significant role in the vertical flux during salp swarms in the Arabian Sea slope water off the northeastern United States and the Southern Ocean. Both models and sediment trap samples demonstrated that appendicularian faecal pellets play a significant role in the transfer of materials to deeper ocean layers.

Appendicularians are responsible for breaking down tiny phytoplankton cells and transforming them into larger faecal pellets, which subsequently sink to the ocean floor. Faecal pellets produced by appendicularians are the primary constituent of the flow that follow a change in water mass due to the influx of warm Atlantic water into the Fram Strait situated east of Greenland. Appendicularians, particularly Oikopleura dioica and Fritillaria borealis, play a critical role in the upward transport of materials including faecal pellets and homes in a Swedish fjord during the autumn season. This is particularly true when O. borealis is abundant. Pteropods and chaetognath faecal pellets are major contributors to the export flow in Antarctica. The faecal pellets produced by the pteropod Limacina helicina make up 10-30% of the composition in Terra Nova Bay, Ross Sea, and Antarctica.

The Lazarev Sea in the Southern Ocean periodically experiences the presence or absence of ice. The size of the faecal pellets influences their role in transporting material vertically. Research conducted by Hancock et al. [16] has revealed that small copepods play a role in exporting faecal pellets. The study also found that larger copepods, such as late-stage copepodites or adult females of Rhincalanus gigas, Calanoides acutus, Calanus simillimus, Calanus propinquus, Neocalanus tonsus, Pleuromamma robusta, and Metridia spp., are responsible for transferring particulate organic carbon (POC), which is the main contributor to total organic carbon flow. In summer (November to April), POC accounted for 67% of the total organic carbon flow, while in winter (May to October), it accounted for 34%. Salps are most likely to be observed in the winter months. Euphausiid faecal pellets constitute the majority of the export flow from the western Antarctic Peninsula. Abundant phytoplankton in the summer and sea ice in the winter are essential for the recruitment of Antarctic krill. Salps thrive in open seas with few phytoplankton and do not require sea ice to survive. Climate change has resulted in a decline in sea ice habitat chlorophyll levels and a decrease in the number of euphausiids relative to salps, which could affect the transfer of organic particles to deeper levels in the western Antarctic Peninsula.

Stigebrandt and Gustafsson [4] emphasised the importance of euphausiids in export flow during the austral summer in the Southern Ocean. In the mesopelagic zone, with a depth range of 100-1000 metres, heterotrophic dinoflagellates produce faecal pellets containing remnants of consumed diatoms. In Monterey Bay, California, a large teardrop-shaped athecate dinoflagellate from the genus Gyrodinium was found to consume several diatom species. Although their faecal pellets were sometimes observed in the water column, it was suggested that dinoflagellates in Monterey Bay were not common and played a minimal role in consuming diatoms. Nonetheless, radiolarian faecal pellets are significant carriers of organic carbon in the deep ocean. According to the Continuous Plankton Recorder study, radiolarians were abundant in this area during late summer and early fall. Furthermore, the annual fluctuation in radiolarian abundance closely corresponds to the variation in organic matter deposition in the deep sea. Examination of the sediment trap material revealed a substantial correlation between radiolarian faecal pellets and the conveyance of organic carbon. The ingestion of oil droplets by doliolids and the formation of oil-laden faecal pellets could serve as vital mechanisms for the transfer of oil to the seafloor in the event of a spill [17].

4.3. Zooplankton fecal pellets and picoplankton export

Zooplankton fecal pellets play a crucial role in transmitting photosynthetic picoplankton from the ocean's surface layer to deeper waters. Picoplankton cells are central components of biomass and production. These microscopic cells are generally considered too small to sink individually or be effectively consumed by larger mesozooplankton. Picoplankton are often thought to have a minimal effect on export flow, unless they adhere to sinking aggregates, marine snow, or phytodetritus. Recent research indicates that a substantial amount of picoplankton is incorporated into sinking faecal pellets, which alters the perspective of picoplankton in the export flux.

Recent research has discovered both intact and degraded picoplankton cells in the mesopelagic water columns and sediment traps. To achieve this, researchers have employed flow cytometry, microscopy, and molecular or diagnostic pigment methods, which have suggested that picoplankton play a significant role in export flow [8-11]. Furthermore, it has been verified that the picoplanktonic cyanobacterium Synechococcus is transported to the deeper parts of zooplankton faecal pellets in the upwelling dome of Costa Rica. The levels of phycoerythrin in sediment trap samples indicated that intact and unassimilated Synechococcus cells in faecal pellets have eight times greater export contributions than ungrazed sinking cells. Lastly, evidence of mesozooplankton feeding on Synechococcus cells has been established through the presence of phycoerythrin in the digestive system and direct observation of Synechococcus cells in faecal pellets.

The primary route for Synechococcus to enter faecal pellets was by protozoans that consumed Synechococcus, followed by mesozooplankton preying on protozoans. The primary means by which carbon generated by primary production is transferred to depth is through mesozooplankton preying on protozoan grazers of Synechococcus, ultimately resulting in the formation of zooplankton faecal pellets. Biochemical indicators suggest that picoplankton-sized particles are transported to the mesopelagic zone by incorporation into sinking particles. Research has revealed that the lipid profiles, radiocarbon signatures, and stable carbon isotope signatures in submicrometre-sized particulate organic matter (POM) differ from those in larger POM sizes in the subtropical gyre of the surface layers of the North Pacific. The lipid components of particulate organic matter (POM) in the mesopelagic zone have been found to originate from the epipelagic zone and are likely transported by sinking particles via a biological pump.

4.4. Marine snow

Marine snow is a phenomenon that results from the aggregation of various particles, including phytoplankton, faeces, and detrital particles. The presence of bacteria and other microorganisms in the water may facilitate the formation of marine snow. Phytoplankton and phytodetritus are crucial components of marine snow, along with other animal, microbial, and faecal particles that are not phytodetritus. Marine snow is often found in abundant and widely distributed. It was first identified on the continental shelf of North Carolina, USA, by Alldredge. It can be observed in thin layers or fronts, which are the physical characteristics associated with marine snow.

In the San Juan Islands, Washington, USA, marine snow with a high density of diatoms has been found to occur during density changes in a fjord. The settling speed of marine snow decreases at density interfaces with steep slopes, resulting in the formation of thin layers. Marine snow is a habitat for various living or decaying particles and organisms that are collected from the water column. Marine snow comprises a diverse range of organisms and particles, including bacteria, microorganisms, phytoplankton, protozoans, zooplankton, larvacean homes, faecal pellets, macrophyte detritus, and mineral particles. The concentration of particles in the aggregates is much higher than that in the surrounding water. Microbial communities in aggregates exhibit elevated levels of metabolism, metabolic diversity, and carbon compared with those in the surrounding water. Aggregates typically have higher levels of nutrients than surrounding water, making them more valuable to consumers.

4.4.1. Consumption and fragmentation of marine snow by animals

The ingestion of marine snow or connected particles is a common occurrence among various organisms. Zooplankton, such as euphausiids and copepods, are known to consume marine snow. These zooplankters have the ability to break down marine snow into smaller pieces. This fragmentation process results in a decrease in the size of marine snow particles, which in turn causes rapid breakdown and release of solutes and particles into the surrounding water. Consequently, this reduces the vertical flow of marine snow to deeper depths. Additionally, a range of fish and larvae have been observed to consume large aggregates. This collection includes both marine and freshwater species. The process of fish feeding on macroaggregates bridges the gap between the microbial food chain and higher trophic levels, as fish may ingest bacteria attached to aggregates that they cannot consume while swimming. Additionally, benthic suspension-feeding bivalves consume marine snow. These bivalves, including clams, mussels, oysters, and scallops, feed on small artificial beads of picoplankton that are enclosed within marine aggregates. By consuming marine snow, benthic bivalves are able to feed on picoplankton more efficiently than they would be able to through filtration alone.

4.4.2. Pathogens associated with marine snow

Marine snow can function as a repository for microbial infections that affect various marine organisms. Marine snow may serve as a reservoir for several microbial infections. It is possible that clams (Mercenaria mercenaria) in the USA are affected by thraustochytrid protist parasites when consuming infected aggregates of marine snow. Mena et al. [17] discovered that marine snow aggregates collected from different coastal seas in the northeastern United States contained numerous harmful bacterial species such as Vibrio cholerae and Escherichia coli. Research has shown that marine snow and other organic aggregates act as biogeographic islands for microbial and aquatic disease. Consumers may become infected by ingesting tainted aggregates consumed by suspension feeders. Viruses can infiltrate and degrade bacteria that adhere to surfaces inhabited by marine snow, as reported by He et al. [18]. The protozoan pathogen Toxoplasma gondii enters coastal waters off California via terrestrial runoff, where it combines with marine snow. When marine organisms ingest polluted marine debris, they may transmit T. gondii to California sea otters and humans, as per the study.

4.4.3. Phytodetritus Pulsed export of phytodetritus

Transporting phytoplankton from the euphotic zone to deeper depths through aggregation and direct sedimentation is a crucial aspect of the biological pumps. In the early 1980s, the concept of the gradual rain of organic debris reaching ocean depths was broadened to include sudden influxes of rapidly sinking plant debris from sinking phytoplankton blooms. Moran et al. [6] conducted an extensive examination of phytodetritus and identified multiple locations in both shallow and deep seas in all ocean basins where phytodetritus pulses were observed. Often, these pulses account for most of the annual transfer of organic matter from the upper ocean layers to the seafloor. When the amount of phytodetritus reaching the ocean floor exceeds the capacity of the benthic population to break it down, a layer of phytodetrital 'fluff' can accumulate on the seafloor. The deposition of phytodetritus occurs seasonally at various locations and is often associated with surface layer activities such as phytoplankton blooms in spring in temperate regions, summer blooms in the Southern Ocean, or blooms caused by seasonal upwelling. Episodic occurrences of plant material sinking have been linked to surface phenomena, including red tides, dinoflagellate blooms, and toxic algae, as well as physical processes, such as the deepening of the upper mixed layer, mesoscale eddies, oceanographic fronts, and ice edge impacts. Phytodetrital fluff typically contains diatoms, coccolithophorids, Phaeocystis spp., dinoflagellates, and other phytoplankton, as well as faecal pellets, microzooplankton cells, and other animal remnants, which are often found in larger gelatinous clumps. The presence of intact or live phytoplankton cells or phytoplankton colour may indicate rapid sedimentation in certain situations. Several types of phytoplankton are the primary components of the seasonal accumulation of plant debris at lower depths. Diatoms can descend rapidly to the seafloor, especially a few weeks after spring blooms in the upper layers of the ocean. Furthermore, coccolithophorids may create large surface blooms in temperate and polar seas that eventually sink to the ocean floor [19].

Dinoflagellates occasionally contribute to the buildup of organic matter on the seafloor, as evidenced by the 1976 red tide bloom of Ceratium tripos in the New York Bight, where the aggregation and disaggregation of plant debris and other particles occurred. Accumulation of phytoplankton and other particles through aggregation increases the sedimentation of phytodetritus, which significantly influences the biological pump. Phytodetritus aggregation occurs in two forms: biological and physical. Biological aggregation occurs when animals consume particles and include them in faecal pellets. Physical aggregation, on the other hand, is the process by which small individual particles collide and adhere to one another, forming larger, more heterogeneous particles. Physical coagulation is influenced by factors such as the particle concentration, density, size distribution, and form. The diatom aggregation process involves shear stress, differential settling velocities, and particle collisions, resulting in stickiness. Transparent exopolymer particles (TEPS) play a crucial role in enhancing the adhesiveness of phytoplankton cells and other particles that combine to form aggregates. Following cell death, the autolysed cytoplasm acts as a binding agent for the formation of diatom aggregates. Diatom aggregation is a critical factor in the settlement and conclusion of diatom blooms, with diatom phytodetritus reaching the deep-sea floor within 2-3 weeks of surface bloom. The aggregation of diatoms varies based on the species and morphological characteristics, such as chain formation or spines, environmental conditions, concentration, and the presence of extracellular polysaccharides, such as TEPS. Phytoplankton blooms aggregate at the surface, but disaggregation occurs in deeper waters owing to fragmentation, microbial degradation, and repackaging by zooplankton feeding.

Phytoplankton play a crucial role in the removal of organic materials generated during photosynthesis from the surface layers of water, making them available as food for mesopelagic and deep-sea benthic organisms. Aggregation increases the accessibility of organic materials in phytoplankton cells for ingestion by larger organisms while also contributing to the formation of diverse aggregates. These aggregates may contain phytodetritus, faecal pellets, mineral ballast, and other particles and possess fractal dimensions and some porosity, including total extractable phosphorus, interstitial water, and microbes. The relationship between the density and particle size, as well as the sinking speed, varies between the solid and fractal particles. Coagulation processes, which include both physical and biological aggregation, contribute to the formation of aggregates in the water column. Araujo et al. [19] utilized food web and coagulation models to explore the relationships between physical and biological aggregation. These findings suggest that these processes are both non-exclusive and competitive, as faecal pellets may be incorporated into aggregates through physical aggregation. Disaggregation, which involves the redistribution of larger particles into smaller ones, is the opposite of aggregation. Physical activities, such as fluid shear, and biological processes, such as microbial degradation and zooplankton feeding, can cause disaggregation. Furthermore, physical and biological disaggregation can interact as swimming zooplankton can disrupt larger aggregates into smaller ones. Finally, disaggregation may be more significant than aggregation, particularly in the deeper ocean regions.

5. BIOCHEMICAL VARIABLES

5.1. Transparent exopolymer particles (TEPS)

Transparent exopolymer particles (TEPS) are a recently discovered type of organic aggregate found in the ocean that plays a significant role in the aggregation of phytodetritus. These minute, transparent, and discrete particles can only be observed under light microscopy when stained with a dye specific for acidic polysaccharides (Alcian blue). They are formed by exopolymers released by phytoplankton and bacteria. Transparent exopolymer particles (TEPS) function as adhesives in the formation of clusters of phytoplankton and phytodetritus, as well as marine snow. The concentrations of TEPS in the water column closely correspond to those of phytoplankton, peaking during phytoplankton blooms, particularly diatoms. It is important to note that TEPS can be formed by both biological and non-biological processes. Transparent Exopolymer Particles (TEPS) are produced by the shedding of polysaccharide mucus from the cell surfaces of bacteria and phytoplankton. Additionally, TEPS can be abiotically produced from dissolved precursors released by actively growing or dying phytoplankton. Moran et al. [6] demonstrated that both bacteria and phytoplankton can produce TEPS precursors, with phytoplankton being the primary contributor to the generation. Diatoms play a crucial role in the creation of TEPS, which is a significant component of diatom aggregates. They observed that photosynthetically active diatoms and certain diatom-attached bacteria were necessary for the formation of TEPS and diatom aggregation. Furthermore, TEPS can be produced by decaying Phaeocystis spp. colonies and triggering deposition events. Nutritional regime determines whether Phaeocystis spp. blooms and their mucus are exported vertically or retained in the epipelagic zone.

Nutrient scarcity and turbulence can affect the properties of Transparent Exopolymer Particles (TEPS) under bloom conditions. TEPS can sink or rise within the water column. Wang et al. [20] found that laboratory-created TEPS, in the absence of other particles, rose and accumulated at the upper levels of the water columns. However, the TEPS containing mineral particles had the opposite effect and sank. The densities of the epenineural aggregates and their sinking or ascending speeds were calculated by determining the relative quantities of TEPS, mineral particles, and interstitial water. TEPS are densely populated by bacteria and other microorganisms, and their microbial densities are significantly greater than those of the nearby water. When dissolved organic matter is converted to particulate organic matter, which subsequently combines tiny particles in the water into larger particles that sink quickly, TEPS can significantly impact the vertical movement of nutrients and biogeochemical processes.

The number of transparent exopolymer particles (TEPS) is related to the diversity and abundance of bacteria in the mesopelagic zone of the Mediterranean Sea. TEPS often exhibits C: N ratios that surpass those of Redfield ratios. This suggests that TEPS may contribute significantly to carbon export and storage at high depths. TEPS can be inhabited by viruses that infect bacteria colonising the TEPS. Zooplankton, including protozoans, appendicularians, euphausiids, and copepods, consume TEPS. Copepods consume TEPS containing numerous small bacteria and microorganisms that cannot be captured individually. This indicates that TEPS play a critical role in the transfer of organic matter from the microbial loop to the classical food web and to higher trophic levels. Moran et al. [6] discovered that an abundance of colloidal and submicrometre-sized transparent exopolymer particles (TEPS) in seawater alters the movement of dissolved organic carbon (DOC) in the ocean. DOC enters the food chain by being absorbed by phytoplankton, then transforms into particulate matter, and is passed on to higher trophic levels through a series of feeding interactions involving zooplankton and other consumers.

In the microbial loop, bacterioplankton consume dissolved organic carbon (DOC), which is sequentially digested by protozooplankton, mesozooplankton, and higher consumers. According to Laffoley et al. [21], the 'aggregation web' is formed when terrestrial extracellular polymeric substances (TEPS) are utilised as precursors for DOC, leading to the formation of larger particles that can be consumed by mesozooplankton and other larger consumers in the food web. This process enables the quick settling of small particles attached to the TEPS, allowing them to join larger fast-sinking particles that sink deep into the ocean as part of the biological pump. As a significant portion of the biological pump relies on fast-sinking aggregates and TEPS are crucial elements of most aggregates, the impact of ocean acidification on TEPS is potentially significant. However, experiments on ocean acidification across various levels, from preindustrial to projected future, did not affect the equilibrium conditions between the TEPS and its antecedents. Notably, acidification experiments may not accurately replicate future ocean acidity developments, as suggested by González-Gaya et al. [22], who discovered that the aggregation of particulate organic carbon is not influenced by three different degrees of experimental ocean acidification.

5.2. Grazing of Phaeocystis spp. by copepods and other mesozooplankton

Phaeocystis, a type of prymnesiophyte, may create large clusters of cells in gelatinous colonies that have been observed sinking to different depths in various places. Phaeocystis deposition is more common in shallow areas than in the deep sea mainly because sinking Phaeocystis colonies are often recycled in the water column. Phaeocystis spp. Phytodetritus typically makes a minimal contribution to vertical carbon exports. Analysis of data collected from polar, subarctic, and boreal locations showed that Phaeocystis spp. colonies provided significant carbon input to the depth of the ocean. It has been discovered that euphausiid grazing on Phaeocystis pouchetii in Balsfjord, Norway during bloom episodically increased the POC flux to depth by rapidly sinking euphausiid fecal pellets.

5.3. Picoplankton in phytodetritus

The notion that a substantial portion of the carbon transported to deeper layers originates from large phytoplankton, such as diatoms or Phaeocystis colonies, has been reevaluated. According to Richardson and Bendtsen [23], the majority of carbon export in the open sea is contributed by picoplankton, which constitute the most significant portion of primary production. The contribution of picoplankton to exports was directly proportional to its contribution to primary production. Richardson and Bendtsen based their study on data from the equatorial Pacific Ocean and the Arabian Sea. Toner et al.

[24] examined the findings by analysing models and data collected during their voyages in the equatorial Pacific. This helped to discover a direct relationship between the contribution of picoplankton to exports and their contribution to primary production. However, their findings indicated that the average contribution of picoplankton to export was relatively low, at 23%, in contrast to the prior estimate of 73%. This discrepancy was partly attributable to the inherent sensitivity of the models used. Recent data from the North Pacific suggest a regular seasonal pattern of phytodetritus sinking to deeper depths, possibly influenced by changes in the day duration linked to the summer solstice. A 13-year sediment trap time series from the Hawaii Ocean Time-series (HOT) Program at Station ALOHA showed that every summer has a summer export pulse (SEP). The peak midsummer molar ratios of POC:P and PN:P were 257:1 and 22:1, respectively, exceeding the Redfield ratios of 106:1 and 16:1.

These ratios are a consequence of SEP having a higher concentration of carbon and nitrogen than phosphorus. Enrichment occurs as a result of seasonal variations in the microbial community, including the rise of symbiotic nitrogen-fixing cyanobacteria in conjunction with diatoms (Richelia sp.) during midsummer. This solar energetic particle event occurs at regular intervals over time despite fluctuations in oceanographic conditions, including storm-induced mixing, mesoscale eddies, and atmospheric nutrient deposition, which vary from year to year. It has been suggested that alterations in the duration of the day (photoperiodism) may serve as a crucial environmental signal that triggers the gathering and subsequent transfer of biological material to the deep ocean.

Regular variations in day length could potentially bring about changes in diatom populations, leading to the formation of the SEP. Marine phytoplankton, such as cyanobacteria and diatoms, have pigments called phytochromes that absorb light and regulate various biological processes. These organisms can potentially experience molecular changes triggered by celestial events. These findings highlight the limited understanding of the critical ecological aspects of the planet.

5.4. Benthic community responses to phytodetritus

Deep-sea benthic ecosystems exhibit diverse reactions to sporadic or seasonal inflows of phytoplankton detritus. In response to the sudden input of decaying plant material, benthic organisms adjust their reproductive cycles, increase oxygen consumption in sediment communities, enhance microbial activity, and modify recycling patterns in response to augmented organic matter settling in the sediment. Cossa et al. [25] analysed early research on benthic community responses to phytodetritus. Recent studies have revealed a greater number of instances of benthic reactions due to sudden increases in phytodetritus. At a deep-sea location in the Porcupine Abyssal Plain in the northeast Atlantic, benthic creatures display occasional bursts of organic material sinking from the surface. Between 1991 and 1994, significant accumulation of plant debris occurred on the seabed, and large benthic organisms swiftly consumed all available food on the seabed surface within 2. 5 years. However, between 1997 and 2000, no significant accumulation of plant debris was recorded using time-lapse photography. Despite this, there was a substantial increase in the population of large benthic organisms, which rapidly devoured all available food on the seafloor within six weeks.

It has been proposed that the increase in megabenthos populations and their activity led to the rapid removal of phytodetrital flow from the seabed between1997 and 2000 [13-15]. In September 1998, there were notable spikes in POC and particle nitrogen peak levels as well as higher levels of sediment organic carbon, total nitrogen, and phaeopigments, which coincided with increased particulate matter fluxes. The peak period for the presence of a large number of bacteria, foraminiferal fragments, and metazoa in surface sediments occurred during this epoch. Extensive time-series research conducted off the coast of California has shown correlations between surface phytoplankton productivity, as indicated by climatic indicators, and the occurrence of phytodetritus at depths above 4000 m [26]. Miller et al. [27] discovered cyclical changes in deep-sea sediment disturbance by the echinoid Echinocrepis rostrata, which were linked to intermittent increases in particulate organic carbon. Lyon and Mock [2] discovered that, after 24 years of studying deep-sea benthic reactions to export flows in the northeast Pacific, earlier conclusions about food deficiencies in the supply of surface-originating food reaching the benthos were uncertain.

Over the past two years, notable sedimentation events have occurred, resulting in an excess of particulate organic carbon utilised by benthic organisms. These episodes from the seabed have been linked to increased primary production in the epipelagic zone, possibly because of enhanced upwelling caused by stronger winds resulting from climate change. Between 2011 and 2012, the density of mobile organisms on the seafloor, predominantly holothurians, at this location increased significantly, with several species reaching their highest recorded concentrations during the 24-year period. There was a significant increase in the flow of particulate organic carbon to the seabed at the start of spring 2012, and salp debris covered a considerable portion of the seafloor throughout the following summer. The abundance of benthic holothurians and SCOC increased after the deposition of the salp remains. According to Mena et al. [17], sudden increases in food supply, such as the 2012 salp bloom, can sustain deep-sea benthic ecosystems for extended periods ranging from several months to years. Recent studies have shown that the consumption of phytodetritus by microbes and benthic animals can occur rapidly. Thus, bacteria play a critical role in the rapid decomposition of new organic matter in several deep-sea locations in the Mediterranean and northeast. In fact, off the coast of California, United States, deep-sea macrofauna, including cumaceans and polychaetes, have been found to quickly digest phytodetritus [28].

5.5. Fish fecal pellets and fish-mediated export

Fish faecal pellets and the role of fish in transporting particulate organic carbon may have a larger impact on the biological pump than previously thought, especially in regions with a high concentration of small planktivorous fish, such as upwelling zones. There have been few studies on the significance of fish faecal pellets. Moran et al. [6] analysed the quantity, sinking speed, organic carbon and nitrogen levels, and prey makeup in faecal pellets from forage fish, including the northern anchovy Engraulis mordax, in the Santa Barbara Channel, California. The faecal pellets contained remnants of various plankton prey such as dinoflagellates, diatoms, silicoflagellates, ciliates, and copepods. The levels of particulate organic carbon (POC) and nitrogen in the pellets were comparable to those found in copepods and salps. The sinking speeds of the pellets were greater than those of euphausiid faecal pellets, but comparable to those of salps and mesopelagic fish. DeCarlo et al. [28] discovered that the quantity of particulate organic carbon (POC) that sinks from fish faecal pellets surpasses the overall POC flow measured using sediment traps. If the traps fail to capture occasional bursts of fish faecal pellets, the estimated amount of these pellets might exceed the total amount of particulate organic carbon flow captured by the traps. Seifert et al. [8] found that fish faecal pellets transport significant amounts of reprocessed surface material to the deeper parts of the assessment region. Fish-facilitated active transport may play a significant role in the biological pumps. They calculated the 'fish-mediated export' (FME) of carbon from the euphotic zone by examining the vertical movement of mesopelagic fish in the California Current and the North Pacific. FME incorporates calculations for respiration, faecal production, and fish mortality using individual-based metabolic modelling and catch data from mesopelagic trawls.

Mesopelagic fish species reside at depths below where remineralisation of particles from the epipelagic zone typically occurs because of their vertical migratory patterns. Research has revealed that the transportation of carbon by mesopelagic fish and zooplankton is comparable to the distinction in carbon export estimates obtained using various methods, including sediment traps, thorium disequilibrium techniques, and nutrient and oxygen budgets. The importance of fish in biological pumps is contingent on the abundance of fish in the ocean. During a global research voyage, the biomass of fish in the mesopelagic zone (200-1000 m) was calculated using acoustic techniques to be at least ten times greater than previous estimates.

5.6. Sinking carcasses of animals and macrophytes

Decomposing organisms, such as animals and large plants settling on the ocean floor, along with occasional deposits of tiny organisms, such as zooplankton, and the infrequent sinking of large marine species, such as seaweed, contribute to the biological process of carbon sequestration, referred to as the biological pump. Various taxa, including copepods, pyrosomes, larvaceans, salps, pteropods, and jellyfish, have been reported to accumulate masses in zooplankton carcasses. The export efficiency of jelly-POM was assessed for several species by determining sinking and decomposition rates. A unique predator-prey relationship between sapphirinid copepods and gelatinous doliolids could increase the sinking of particulate carbon flow.

Sapphirina nigromaculata copepods have been observed preying on Dolioletta gegenbauri in the Kuroshio Extension. The copepods penetrated the doliolid body cavities, created distinct bite marks, and then consumed the interior doliolid tissues. The decomposition of submerged corpses or large aquatic plants supports the deep-sea food chains. Deceased jellyfish enhanced microbial populations in a Norwegian fjord. Amphipods fed on dead fish in baited camera investigations in the Arctic, whereas fish effectively consumed dead porpoise carcasses in the northeast Atlantic. Various benthic organisms such as nematodes and polychaetes scavenge whale corpses. Deep-sea fish consume spinach, sargassum, or mackerel bait on the seabed in the North Atlantic, as observed by scientists. The decline in the population of large whales as a result of whaling has negatively impacted the ability of the ocean to store carbon through biological pumps [13]. If whale populations were to recover to their levels prior to industrial whaling, it could potentially have a positive impact on the ocean's carbon storage capacity.

5.7. Feces from marine mammals

Marine faeces from animals can substantially influence biological pumps. Sperm whales inhabiting the Southern Ocean may contribute to the biological pump by aiding in the elimination of atmospheric carbon dioxide rather than by adding it through respiration. Sperm whales dive into deep waters beyond the euphotic zone for food and resume non-essential bodily functions when they surface, causing faeces to be released near the water surface. Sperm whales produce a liquid form of faeces that spreads in the euphotic zone, unlike zooplankton and fish, which rapidly produce sinking faecal pellets. These faeces contain a high concentration of iron, which is a limiting factor for phytoplankton photosynthesis in the Southern Ocean.

Sperm whale faeces can stimulate phytoplankton growth in the euphotic zone. The output of phytoplankton is consumed by zooplankton, and the carbon contained within it is transferred to deeper depths by sinking zooplankton faecal pellets. The faeces of other marine animals can also play a significant role in providing nutrients to phytoplankton. Mena et al. [17] found that dense faecal plumes from whales and seals may potentially contribute more nitrogen to the euphotic zone of the Gulf of Maine than the total nitrogen intake from all nearby rivers.

6. DISCUSSION

Biological pumps refer to the process through which organic matter generated by photosynthesis in marine ecosystems is transported from the surface to deeper layers, facilitated by sinking particles, advection, vertical mixing of dissolved organic matter, and the movement of marine creatures. Sinking particles in the euphotic zone, including zooplankton and fish faecal pellets, organic aggregates known as marine snow, and phytodetritus from sinking phytoplankton, play a crucial role in the biological pump. Several studies have been conducted on biological pumps, up until late 2001. Since then, research on biological pumps has continued, resulting in over 300 articles on vertical export flows using sediment traps, large-volume filtration systems, and other methods worldwide.

This review covers several significant topics, including an overview of the biological pump and its productivity and variability, as well as the role of dissolved organic carbon. Another topic is the contribution of zooplankton faecal pellets to export flux and their retention in the water column due to zooplankton activities, as well as their vertical migration, repackaging, microbial ecology, sinking velocities, ballasting by mineral contents, and the presence of phytoplankton cysts, intact cells, and harmful algal toxins. This review also discusses the importance of faecal pellets from different types of zooplankton and their role in picoplankton export. Additionally, it covers marine snow, including its origins, abundance, and distribution, as well as the associated particles and organisms, consumption and fragmentation by animals, and associated pathogens. The review also includes a discussion on phytodetritus, including its pulsed export, the role of Phaeocystis spp. and picoplankton in phytodetritus, and the summer export pulse (SEP) of phytodetritus in the subtropical North Pacific, as well as benthic community responses to phytodetritus. Other topics covered in the review are fish faecal pellets and fish-mediated export, sinking carcasses of animals and macrophytes, faeces from marine mammals, and transparent exopolymer particles (TEPS). Finally, this review addresses the relationship between biological pumps and climate, including their origins, biological pumps and glacial/interglacial cycles, biological pumps and contemporary climate variations, and biological pumps and anthropogenic climate change.

The conclusion of this study delves into the potential alterations in the biological pump that may arise due to climate change. Presently, climatic fluctuations have a substantial impact on biological pumps and the deep seas. Various indicators of current climatic variability are connected to the export flow of particulate organic carbon (POC) and modifications in deep-sea benthic populations. These connections suggest that fluctuations in the biological pump resulting from climatic changes affect the abundance and composition of benthic communities. Mena et al. [17] revealed a significant decrease in the abundance of two key taxa of holothuroids by 2-3 orders of magnitude, while six other species of holothuroids, echinoids, and ophiuroids showed an increase in numbers by 1-2 orders of magnitude. These changes in abundance were related to three distinct indices linked to El Niño/La Niña events: the Northern Oscillation Index (NOI), Southern Oscillation Index (SOI), and Multivariate El Niño-Southern Oscillation Index (MEI).

The cross-correlation coefficients between climate and the abundance of all five holothuroid species were highest when the abundance of the species lagged behind the climate by 11-22 months. The NOI, SOI, and MEI climate indices showed significantly delayed associations with POC flow to the seafloor. These connections indicate that the deep-sea benthic population reacted to climate-driven pulses of organic matter supplied by a biological pump. Moran et al. [6] discovered that the percentage of total particulate organic carbon (POC) in recognisable faecal pellets that sink to deeper depths was inversely related to the overall POC flux, as well as to climate variability indicators such as the North Pacific Gyre Oscillation (NPGO) and NOI, using samples from the same time-series assessment. The study also proposed that the negative relationships between these climate indicators and the amounts of particulate organic carbon (POC) from faecal pellets were due to changes in the composition of the zooplankton population responsible for making the pellets, specifically the ratios of larvae to copepods. Cossa et al. [25] documented a comparable change in the abundance of epibenthic megafauna due to climatic variability and POC flow on the Porcupine Abyssal Plain (PAP) in the northeast Atlantic. Miller et al. [27] found substantial connections between particulate organic carbon (POC) flow and the North Atlantic Oscillation (NAO). They proposed that climate variability, such as El Niño/La Niña in the North Pacific or NAO in the northeast Atlantic, could significantly influence the delivery of detrital food to deep ocean levels through the biological pump. This variability in food supply may be evident in the patterns observed in the deep-sea megafauna. The NAO appears to be connected to the biological pump in the Sargasso Sea. There was a significant change in the North Atlantic Oscillation (NAO) from a positive to negative phase in the winter of 1996.

Following 1996, the NAO exhibited a shift towards more negative values as a result of an increase in westerly wind activity, which led to increased vertical mixing of the ocean's upper mixed layer. The export flow increased when there was a transition from larger to smaller phytoplankton, as diatoms decreased in number and picoplanktonic Synechococcus increased. The increase in particulate organic carbon (POC) flux when picoplankton dominate suggests that particle aggregation may have played a role in the higher POC export flux. This relationship became stronger with increased vertical mixing caused by changes in the North Atlantic Oscillation (NAO). Climate influences have also been observed to have biological effects on the subtropical North Pacific region. The data collected at Station ALOHA from 1990 to 2004 demonstrated substantial advancements in primary production, including an upward shift of nitrate into the well-lit area and downward movement of nitrogen particles to deeper levels. Simultaneously, there was an increase in the biomass of eukaryotic phytoplankton, zooplankton, and epipelagic cyanobacteria. These biological changes were attributed to the effects of climate, which corresponded to fluctuations in the El Niño/Southern Oscillation (ENSO) and Pacific Decadal Oscillation (PDO) indices. This led to mixing of the upper ocean layers due to enhanced wind activity and the distribution of nutrients in the euphotic zone.

7. CONCLUSION

A biological pump is a vital process on Earth's surface. A significant portion of the world's oceans lack the essential nutrients necessary for surface-level photosynthesis due to temperature stratification. As the temperature rises, the stratification of the oceans increases, leading to a decrease in the supply of nutrients to the surface ocean, which reduces primary production and the transfer of organic matter to deeper layers. Zooplankton, fecal pellets, marine snow, and phytodetritus all play crucial and fluctuating roles in the export of carbon in different ocean regions. Predicting the impact of global warming on these contributions is a complex task. Hence, understanding the effectiveness and behaviour of current biological pumps is essential for forecasting the potential consequences of global warming on the ocean.

Further detailed studies on biogeochemical pumps will provide foundational knowledge; however, accurate quantification is yet to be achieved. Dissimilarities in the estimates of organic carbon export and consumption in deep ocean regions persist, indicating unresolved issues in understanding ocean ecosystems. The collection of long-term ocean time-series data on board ships is crucial for examining the relationship between climate variability, ocean ecology, and biogeochemistry. Although time-series data collection is costly and labour-intensive, it offers irreplaceable insights into the complexities of Earth's largest ecosystem. To enhance our understanding of this critical ecosystem, it is essential to sustain and expand these time-series initiatives. Without further research, our knowledge of the current state of Earth's largest ecosystem will remain inadequate, impeding our ability to predict future changes.

8. DECLARATION OF COMPETING INTEREST

The author declares that there are no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper. The author hereby reiterates that this research is solely the work of the author, and does not belong to any institution, collaboration, agency, sponsorship, or project.

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