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Review Article

Standardising research on marine biological carbon pathways required to estimate sequestration at Polar and sub-Polar latitudes

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ABSTRACT

Marine biological ('blue') carbon pathways are crucial components of the global carbon budget due to the ecosystem services they provide through the fixation of CO_2 from the atmosphere. CO_2 is removed from biosphere through long-term sequestration into seafloor sediments, removing it from the carbon cycle. Coincident with marine ice loss, little studied negative (mitigating) feedbacks to climate change are emerging in polar waters, which is important to quantify and comprehend. Understanding the mechanisms driving these pathways, that could lead to change, is a massive task and to ensure studies are comparable requires standardisation and prioritisation of future research. The expertise of scientists within the EU grant, Coastal ecosystem carbon balance in times of rapid glacier melt (CoastCarb), identified the 23 most important high latitude pathways through a modified Delphi scoring system. Metrics were selected as priorities for future research and for syntheses across broader geographic regions. The metrics with the highest importance scores also scored as the metrics that could be most readily standardised in the next five years. This review provides a definition and description of how each metric is measured, including its central role to blue carbon pathways. It also provides recommendations for standardisation, emphasising the requirement for modelling studies to scale from geographically limited regions where high-resolution data is available. Where methods cannot be standardised, cross calibration between methods is required to ensure reproducibility. An increasing use of remote sensing and innovative technologies will be necessary to scale measurements across this vast and remote region.

Contents

1. Introduction

1.1. Concept

Blue carbon ecosystems (BCE) can be defined as those that store and ultimately sequester biologically fixed carbon providing a key component of Nature's Contributions to People (Díaz et al., 2018) and ecosystem services. Such carbon may pass through a few, or many, links of a food web or directly to the seafloor, where between 1 and 10 % can leave the carbon cycle by burial beyond oxygenated layers in the sediment (Bax et al., 2021). Understanding the importance of blue carbon pathways to carbon removal from the biosphere, and the variability in sequestration, is key to predictions of how much carbon will be removed from the carbon cycle. This understanding relies on clear definitions, particularly of sequestration.

1.2. Defining sequestration

Sequestration is defined as **carbon that is removed from the carbon cycle for hundreds or thousands of years**. Sequestration results in "the removal of carbon from the carbon cycle", which distinguishes it from carbon storage (Nellermann et al., 2025). BCE are, therefore, carbon removal pathways through which carbon is sequestered, i.e. buried deep in anoxic sediment, and removed from the biosphere. "Sequestration" has other definitions, but we define these as long-term storage of carbon in natural ocean and coastal systems, because, even if carbon is removed from the atmosphere, it is still part of the carbon cycle, and therefore not sequestered (Nowicki et al., 2022). This includes storage of carbon below the permanent thermocline (Cavan et al., 2024), where the carbon flux is assumed to be one way and that carbon stored below this depth is retained for decades or centuries. For example, Cavan et al. (2024) compare the amount of carbon exported to the deep sea from krill faecal pellets with that buried in sediment from mangrove, sea grass and salt marsh ecosystems. The assumption is that the deep sea holds carbon as efficiently as the coastal systems. The deep sea is an incredible carbon store (DeVries, 2014) but carbon remains in the carbon cycle and is in flux with shallower waters, facilitating outgassing of CO_2 from the deep sea back into the

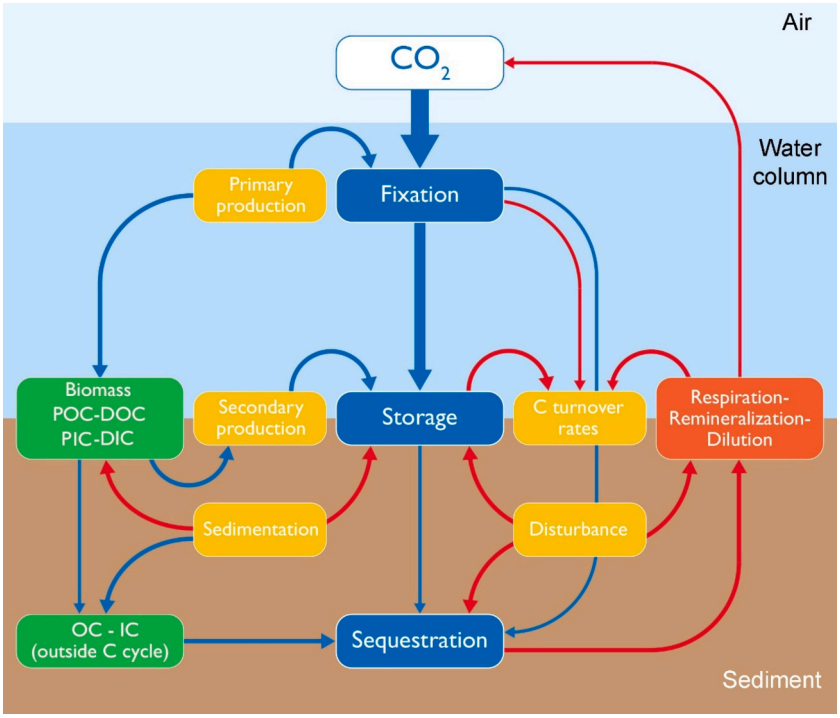

Fig. 1. Carbon pathway conceptual diagram. Blue boxes indicate main blue carbon stages to sequestration. The orange box indicates the main pathway of CO_2 release into the atmosphere. Green boxes indicate structural metrics. Yellow boxes indicate functional metrics. Blue arrows indicate pathways towards sequestration. Red arrows indicate pathways releasing CO_2 to atmosphere. Boxes that straddle the bentho-pelagic interface show processes in both the benthic and pelagic realms, with the exception of sedimentation, which settles from the water column to the seafloor. The carbon metrics selected and prioritised in this manuscript are used to parametrise blue carbon pathway models that create an understanding of these stages. POC = particulate organic carbon, DOC = dissolved organic carbon, OC = organic carbon, IC = Inorganic carbon. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Description of structural and functional metrics.

Category	Examples
Structural metrics: those measured as carbon, grams, or calories per area or volume unit.	Biomass, carbon content, particulate organic carbon (POC) content.
Functional metrics: processes (rates) determining the structure per unit of time.	Primary production, secondary production, net and gross production (measured as units of biomass per unit of time), turnover rate (as net production of the system/biomass), turnover time (the inverse of the previous).

atmosphere (Chen et al., 2022; Nicholson et al., 2022; Nowicki et al., 2022). However, the coastal vegetative systems remove carbon from the carbon cycle (unless disturbed, primarily by anthropogenic mechanisms) and the direct comparison between the two systems is therefore misleading.

Blue carbon pathways are important, even without sequestration, as Nellermann et al., 2025 define them as pathways involving the capture and long-term storage of carbon. However, sequestration improves the efficiency of the system and is key to geopolitical strategies, Nationally Determined Contributions and future carbon trading credits (Pörtner et al., 2021). The deep ocean has the potential to store more anthropogenic carbon (Lord et al., 2016), but at the cost of rising ocean acidification and an increasing inefficiency of CO_2 drawdown. Where carbon is removed from the carbon cycle ocean alkalinity is promoted (Fakhraee et al., 2023), the efficiency of CO_2 drawdown is maintained and the potential of the blue carbon system is more likely to be reached (Bax et al., 2021).

1.3. *The importance of Blue carbon ecosystems*

The oceans absorb up to 30 % of anthropogenic carbon (Gruber et al., 2019) and so blue carbon pathways are a crucial mechanism with a mitigating role against increasing anthropogenic CO_2 concentrations in the atmosphere. Relatively pristine BCE, often associated with high biodiversity, are some of the most efficient pathways to carbon sequestration (Pörtner et al., 2017), particularly in coastal high latitudes where fjords act as efficient sediment traps for blue carbon (Barnes et al., 2020; Deregibus et al., 2023; Smith et al., 2015; Zwerschke et al., 2022), owing to their typically deep and steep morphologies, protecting thick bottom sediments, and the proximity to coastal sources of organic and inorganic matter. Assemblages with higher functional diversity can often store more carbon, emphasising the importance of protecting intact BCEs, which unlike elsewhere, are common and extensive at polar latitudes (Barnes and Sands, 2017; Morley et al., 2022b).

Globally, loss of intact blue carbon habitats is a major issue for both biodiversity loss and climate change exacerbation as it disrupts blue carbon pathways to sequestration (Dinerstein et al., 2020; Hyndes et al., 2014). Whilst the polar regions are the least affected by direct human disturbance, they are among the most impacted by indirect stressors such as those caused by climate change, with the largest impact on Subantarctic and Antarctic Peninsula regions being the cryosphere loss (seasonal sea ice, ice shelves and glaciers; Cook and Vaughan, 2010; Morley et al., 2020). This reduction in ice is opening up new habitats for colonization by marine animals and algae, increasing opportunities for the biosphere to capture carbon (Lagger et al., 2018; Lagger et al., 2017; Quartino et al., 2013). This creates one of the few global opportunities for increasing carbon drawdown, generating negative feedback against climate change (Barnes et al., 2018). To date, in much of the polar regions, for example the Barents Sea, any changes in marine biological carbon and its storage or burial in response to seasonal sea ice loss remains unclear (Souster et al., 2024).

Direct measurements are often difficult because of the complexity of oceanographic campaigns and the challenges in obtaining values of carbon flux under natural conditions. The key components of the blue carbon cycle are represented in Fig. 1. Each of these components has a complex series of inputs and outputs, which each have multiple interactions, so in order to gain sufficient measurements of blue carbon pathways we must rely on modelling (Fig. 1), underpinned by reliable, validated and reproducible, ground-truthing data at appropriate spatial and temporal scales (e.g. www.thebluecarboninitiative.org/manual; Henry et al., 2024; Selden et al., 2024). It is therefore essential to identify key processes within (often complex) blue carbon pathways (Henley et al., 2020) and suggest routes through which measurement can be standardised across regions, allowing us to scale between locations where in-depth studies are possible, to estimate values for data poor regions. How the metrics prioritised here provide the data for these key components forms the basis of this review.

The Marie Curie Action RISE grant "CoastCarb", is funded through the Horizon 2020 Framework Program of the European Union. CoastCarb has brought together over 100 experts, from Europe, South America and North America who conduct multidisciplinary and international research across Southern South America and the Antarctic Peninsula related to marine ecosystems and blue carbon. CoastCarb aims to integrate across high latitude blue carbon research programs, data collation, modelling and social sciences.

This manuscript aims to use the expertise in this group to identify and describe the key metrics for understanding carbon pathways that lead to sequestration, that could realistically be standardised across latitudes within a reasonable (5–10 year) time-frame. These priority metrics were defined, detailed requirements outlined, and challenges discussed during a workshop at the CoastCarb General Assembly, held from 17 to 21 October 2022 in Punta Arenas, Chile. This manuscript is therefore not a review of all blue carbon metrics but a prioritisation of

Table 2
Rank order of median scores for the importance of each metric. Metrics either came from the CoastCarb General Assembly in Punta Arenas or were added during the individual scoring process. Carbon sequestration is the first metric discussed as it is the essential metric being considered in this review.

Rank Importance	Metric	Category	Median score
1	Biomass	Structural	350
1	Export and migration	Functional	350
1	Functional groups	Functional	350
1	Habitat type	Structural	350
1	Particulate organic carbon (POC)	Structural	350
1	Primary production	Functional	350
7	Respiration rates	Structural	325
8	Sediment accumulation rates	Structural	320
9	Burial Rate (discussed within sediment accumulation rate)	Structural	300
9	Carbon turnover rates	Functional	300
9	Disturbance impacts	Structural	300
9	Secondary production	Functional	300
13	CO_2 air-sea fluxes	Structural	250
13	Dissolved Organic Carbon (DOC)	Functional	250
13	Growth Rates	Functional	250
13	Sediment characteristics (discussed within - Habitat type)	Structural	250
13	Downward particle flux	Functional	250
13	Species composition	Structural	250
19	Depth distribution (discussed within - Habitat type)	Structural	200
19	Faecal production rate	Functional	200
19	Ingestion rates	Functional	200
19	Inorganic carbon stocks	Structural	200
19	Life history	Structural	200
	Included within other metrics:		
24	Life Span		187.5
25	Sediment ventilation rates		180
26	Physiological tolerance		175
27	Irrigation rate		150
28	Depth of feeding		100
28	Habitat age		100

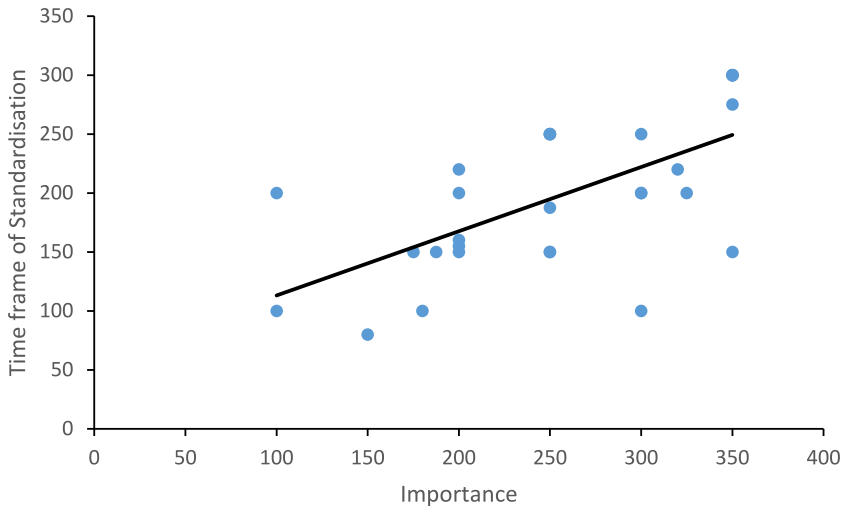

Fig. 2. The correlation between the expert-considered importance score for each metric and the score for whether standardisation is perceived as achievable within a realistic time frame. A score of 0 denotes a metric categorized as un-important or impossible to standardise. A score of 350 meant the metric was highly important or easy to standardise. Time frame = 58.7 + 0.55 x Importance ($F_{1,28} = 18.3$, $P < 0.01$).

the key metrics, their measurement and a set of recommendations for future standardised research.

2. Methods

Workshop participants came from across the CoastCarb work packages (data and information systems, ecosystem modelling, metrics and multiple stressors, ecosystem change and carbon storage, and ocean health and human wellbeing). Participants were separated into groups, independently of their expertise, to conduct horizon scanning on a list of metrics that are required to advance our understanding of carbon pathways. This was completed by four groups in person and one group online (53 participants).

Metrics were categorized, depending on the information they provide, as either structural or functional attributes (Table 1).

These metrics were collated and an anonymous survey form was created that allowed individuals to score the metrics acknowledging potential bias due to individual expertise, within 3 categories, using a modified Delphi scoring system (Mukherjee et al., 2015).

- A metric scored 0 if it was considered a low priority to a maximum of 350 if it was the highest priority.
- A metric scored 0 if it would be impossible to standardise across geographical areas and 350 if considered easy to standardise.
- A metric scored 0 if it could not be standardised over a 5–10 year time frame and 350 if considered easy to standardise over that time frame.

The median importance, ease of standardisation and realistic time frame of standardisation were calculated for each metric.

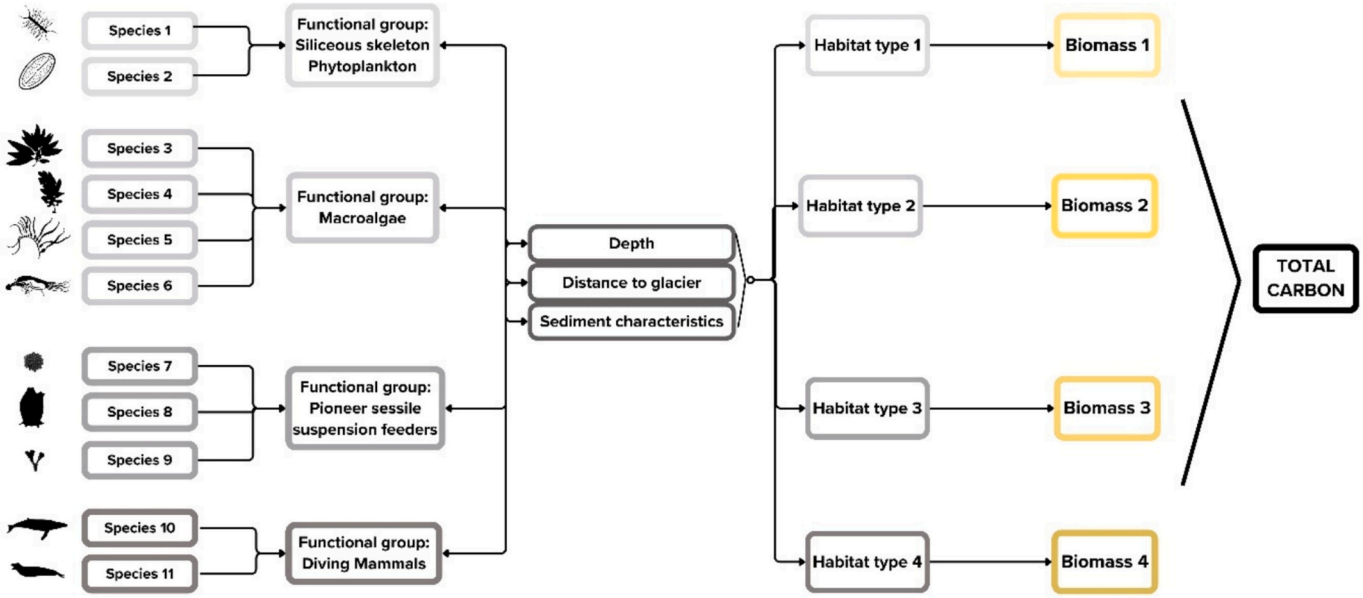

Fig. 3. Diagram showing how example functional groups (Phytoplankton with siliceous skeletons, Macroalgae, Pioneers sessile suspension feeders and diving mammals) and habitat types (Depth, Distance to glacier and Sediment characteristics) can be used to simplify, and scale up, species conversions into carbon. Metrics of carbon storage (yellow) and those that describe properties of assemblages that influence carbon pathways (gray). Icons are for representative taxa and not to scale (www.phylopic.org). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3. Results

A total of 35 forms were returned, from which 23 Metrics received a median score of more than 200 and were therefore, included as key metrics (Table 2).

There was no significant correlation between the importance score and the ease of standardisation ($F_{1,28} = 3.89$, $P > 0.05$). For example, one of the key metrics for carbon storage, biomass, was considered easy to convert into units of carbon and therefore easy to standardise (see Biomass; Supplementary Table 1). On the other hand burial rate, which is key to understand rates of sequestration, was considered a difficult metric to standardise as the methods are complex and time consuming (See Burial Rate) There was, however, a significant correlation between the importance score and the time scale of standardisation, indicating that important metrics are more likely to have an achievable time-frame for standardisation (Fig. 2; Time frame = 58.7 + 0.55 x Importance; $F_{1,28} = 18.3$, $P < 0.01$). Therefore, it was considered that some key metrics, which are currently difficult to standardise (e.g. Burial rate) could become standardised within 5–10 years, whereas the complexity of measuring carbon turnover rates means it was still considered difficult to standardise within the next decade.

4. Metrics

As was agreed at the workshop, and reinforced through the survey, the section on each metric included a definition, prioritisation of key taxa, prioritisation of key processes, standardisation of units and rationalising measurements. These were sufficiently detailed to describe each metrics importance to blue carbon pathways and the biosphere.

4.1. Biomass

4.1.1. Definition

Biomass is the living matter within an ecosystem at a given time. It represents the "standing stock" of carbon and can be used to calculate the quantity of carbon stored in the biomass of an ecosystem (Fig. 3):

4.1.2. Measurement

There are several common methods for measuring biomass in ecological studies (Table 3).

Wet mass: measures the fresh mass of organisms including their water content. While practically straightforward, wet mass is highly variable due to differences in moisture levels and measurement protocol. It is also possible to measure preserved specimens using ethanol or formaldehyde using a correction factor to convert the preserved wet mass to an in vivo wet mass.

Dry mass: provides a more reliable measurement by first drying organisms (at approx. 65 °C) to a constant mass. Freeze drying using a lyophilizer is an alternative that maintains sample integrity for subsequent biochemical analysis by evaporating water directly from its solid phase.

Ash free dry mass (AFDM) combusts dried samples in a muffle furnace at 450–500 °C for several hours to determine the organic fraction (termed loss on ignition). Heating the ash to 900+ °C provides the inorganic carbon content.

Chlorophyll-a: its estimation is widely used to assess bulk biomass of microalgal assemblages such as phytoplankton and microphytobenthos, whereas automated and microscopic counts can provide density values. The latter allows for a better estimation of the organic carbon content of the assemblage by means of biovolume calculation since the relationship between chlorophyll and carbon content per cell is highly variable (see Inorganic carbon stocks).

Carbon mass: a carbon analyser is needed for direct measurements of carbon mass. These instruments precisely determine total carbon as well as organic and inorganic fractions using different analytical techniques. Alternatively, conversion factors can be applied to estimate carbon content from organic matter measurements, though accuracy varies by taxon. Generally, 50 % of organic matter is used for most animal taxa while macroalgae have 20 to 30 % carbon dry mass, but more accurate order- and class-specific factors have also been developed. Carbon mass is ultimately the measure required to assess blue carbon standing stock and measurements should, therefore standardise to carbon.

Biomass is commonly related to spatial dimensions when quantifying ecological communities. Volume is typically used for planktonic biomass measurements, while surface area relates to benthic biomass.

4.1.3. Direct measurements

Direct biomass estimates of species and assemblages are most commonly calculated from three main categories of samples; water column samples collected in nets and bottles, clearance of epifauna from substrata, and either sediment grabs or cores for infauna. This "destructive" sampling involves the direct collection of organisms from

Table 3
Methods for measuring biomass, highlighting their strengths and weaknesses.

Metric	Technique	Strengths	Weaknesses	Citation
Wet mass	Measure mass of organism, blotted dry to remove surface water	Technically simple and quick	Can be subject to high variability. Water content can vary, either within tissues, or within body spaces	(USGS, 2005)
Dry mass	Measure mass of organism after drying, either in oven or freeze drier	Most reliable measurement of biological content	Includes both organic and inorganic fractions of tissues	(Kreeger, 1995)
Ash free dry mass (AFDM)	Measure of either organic component or inorganic carbon content of tissues through loss of mass	Most reliable measurements of organic tissue carbon	Time-consuming for large samples.	(Kreeger, 1995)
Chlorophyll-a	Measure of Chlorophyll in the water or sediment. Typically, by extraction from water, or sediment samples, and measurements using fluorometers	Routine, reliable technique.	Extraction measurements require access to a laboratory	(Sandu et al., 2003)
			Automated measurements require calibration of fluorometers	
			Highly variable relationship between carbon and chlorophyll-a content	(Schagerl et al., 2022)
Carbon mass	Directly through a carbon analyser	Accurate measurements of carbon in tissues and hard structures	Time-consuming and expensive	(Mikaelyan and Belyaeva, 1995) (Nelson and Sommers, 1996)
	Estimated through literature values	Simple	Errors due to natural temporal and spatial variability in carbon content	(Morley et al., 2022b)

the seafloor or water column, can obtain precise biomass or density measurements. Typically quantified in grams per unit area (g m^{-2}), this approach provides data on the density and distribution within a given habitat. These samples allow estimates of the biomass of constituent organisms per unit volume (plankton and infauna) or surface area (benthos), respectively (Wiebe and Benfield, 2003). Macroalgae biomass, in particular, can be achieved through a variety of sampling methods, each offering unique insights into the composition and distribution of algal populations (Krause-Jensen et al., 2018; Quartino et al., 2020). Direct methods for the benthic system are often restricted to SCUBA diving depths ranges (Duffy et al., 2019).

Sampling methods like plankton nets or benthic dredges, which can be deployed below SCUBA depths, increase sampled areas but introduce uncertainties. The sampled volume or area is only approximately known, and replicates for establishing population parameters are typically absent. Although these methods offer greater spatial coverage than quantitative sampling, they also introduce higher uncertainty and lack replication (Wiebe and Benfield, 2003).

Upscaling, from samples within the area of interest, is almost always required. Quantitative samples facilitate determining standard error, mean, median, and other population parameters from replicates. Accuracy of estimated means depends partly on sample size. However, collecting enough samples to be representative of the total study area is challenging, requiring extrapolation (Sparrow et al., 2020). Unless consistent units are used, conversion factors may be needed to compare between studies. Despite practical limitations, quantitative sampling offers robust biomass estimates and uncertainty analyses.

4.2. Indirect measurements

4.2.1. Imagery

Imagery techniques facilitate biomass estimation in a non-destructive manner by quantifying organisms' densities and/or percent cover (Wiebe and Benfield, 2003). This offers advantages particularly in polar regions as it can provide higher spatial coverage and replication than direct sampling. First, the sampled area within images must be estimated accurately. This is straight forwards for orthogonal images captured at a fixed distance, while other image orientations complicate area calculations.

Reliable biomass estimates from images typically require direct biomass measurement on voucher specimens. These serve as a dataset for calibration and validation of specific methods that indirectly estimate biomass from manual or automated image analysis (Schulz et al., 2010). Density/coverage and biomass are then multiplied to derive biomass estimates per image area, which can be upscaled to broader study regions (Degen et al., 2015).

Regardless of the image source or scale, biomass estimated by these methods becomes a derived rather than direct measurement, with errors propagating from constituent variables. It is thus necessary to estimate and report uncertainty in biomass estimates considering variances in both voucher taxa biomass data and density/coverage estimation.

Imagery facilitates quantitative sampling across large spatial scales but poses challenges for modular taxa and macroalgae where percent cover inadequately captures 3D structure. Extensive taxa-specific biomass databases can help reduce dimensionality issues especially for these more difficult taxa. However, there are still taxa that imagery poorly resolve the three-dimensionality issue. For such species e.g. the brown algae *Himantothallus* sp. and *Desmarestia* spp., rank-order biomass descriptors may better capture variability than means (Lamarche et al., 2016; Quartino et al., 2020).

Photogrammetry yields true 3D reconstructions to directly quantify volumes and reduce biomass estimation errors. Advances in computer imagery, machine learning and artificial intelligence show promise to automate analyses and process vast image datasets. However, populating biomass databases with Antarctic taxa will strengthen population inferences from imagery-derived biomass estimates. Overall, imagery approaches advance remote assessments if uncertainties are properly modelled (Wiebe and Benfield, 2003).

It is also important to remark that imagery methods are only valid for epibenthic groups (macro and megafauna, macroalgae and microphytobenthos) within the benthos and zooplankton within the plankton.

4.2.2. Acoustics

Hydroacoustic methods also provide reliable information on abundance especially for zooplankton and nekton assemblages that can be used as an indirect technique for biomass estimation (Jaffe, 2005). It can also be used for the benthic realm to classify benthic habitats and allow scaling across large geographic areas (see Habitat Type; Todd et al., 2020). Uncertainties are, however, higher than with imagery methods.

4.2.3. Remote sensing

Optical remote sensing serves as an effective tool for assessing biodiversity and quantifying the abundance of phytoplankton and algae, as well as monitoring changes in water constituent composition and transparency (Sathyendranath, 2000). It enables regular synoptic evaluations of ecosystem health by capturing spatial and temporal variations (Kutser et al., 2020; Zielinski et al., 2009). Furthermore, satellite imagery can contribute to the quantification of biomass, providing valuable insights into productivity by fluorescence analysis and dynamics of aquatic ecosystems at broader scales (Lavender and Moufaddal, 2013). The method is limited to the shallow, or upper water column depending on water transparency and uncertainties can be high (Mélin and Vantrepotte, 2015), especially in Antarctic waters or later in the season where higher phytoplankton biomass is usually deeper (Holm-Hansen and Hewes, 2004). These can be reduced when images are combined and validated with in situ measurements (including robotic platforms like BGC-Argo-Floats) and/or biogeochemical models (Gregg and Rousseaux, 2014). Specifically for optically shallow waters, where the seafloor is visible from above, lidar remote sensing from airborne platforms is a commonly used tool, that provides three-dimensional assessments and biomass quantification (Chen et al., 2023).

4.2.4. Standardisation

Direct sampling remains necessary for infaunal taxa (from meio- to mega-faunal groups) that imagery approaches cannot adequately resolve. Direct approaches may also provide higher estimation precision, at finer spatial scales, than imagery-derived metrics.

Imagery approaches for biomass estimation demands comprehensive organismal trait databases for Antarctic species. An ideal database would contain measurements of size, volume, and various biomass metrics (e.g. wet, dry, ash-free dry mass, carbon content) for a taxonomically and size-diverse array of specimens, spanning multiple collection localities. Intraspecific variability among populations underscores the need for geographic sampling breadth. When applied in tandem with robust statistical modelling of error propagation, imagery techniques show potential for remotely assessing epibenthic and zooplankton carbon stocks across broad spatial extents and diverse Antarctic ecosystems.

To validate emerging remote sensing methods, ground-truthed data from traditional sampling fulfils two critical roles. First, organismal trait databases underpin conversions between multidimensional attributes like cover, volume, and biomass. Second, in-situ samples offer a benchmark for comparison and accuracy assessment of imagery-based results, especially at smaller scales where direct approaches currently surpass indirect techniques in estimation precision.

4.3. Export and migration

4.3.1. Definition

For blue carbon, export refers to the lateral and depth related advection of biogenic material. Export into the deep sea by advection from the surface to deeper waters or sediments is a process that involves

Table 4
Modelling methods for carbon export and migration.

Model	Scale	Input variables	Carbon Pathway Outputs	Reference
Migration carbon fluxes	Individuals, populations, communities	Metabolic, migration processes	Particle transformation (degradation, flux attenuation) Circulation models Total export rates	(Countryman et al., 2022)
Richard's mathematical model	Diel migration	Light intensity	Export rates	(Richards et al., 1996)
Game-theory food web model	Diel migration	Functional group migrations	Carbon sequestration potential Carbon injection Carbon export	(Pinti et al., 2023)

the descent or transport of biogenic dissolved and particulate carbon, which is ultimately stored in sediments or dissolved into the deep ocean (Legendre and Le Fèvre, 1995). Vertical transfer occurs through gravitational or biological carbon pumps. Lateral transfer of carbon transports carbon, potentially across ecosystem boundaries, through eddies and currents, but also through biological pumps, including the migration pump, as nekton change location within the ocean (Nowicki et al., 2022). In order to assess the levels of carbon sequestration in coastal ecosystems it is essential to understand the export processes of biogenic carbon (Macreadie et al., 2019). Phytoplankton and macroalgae play a key role in blue carbon capture in coastal waters and they are important vectors for carbon export into the deep ocean where it can be sequestered (Ortega et al., 2019). Export is a key uncertainty in our understanding of where carbon, produced in coastal water, is ultimately sequestered.

4.3.2. *Biological carbon pumps*

The migration of animals in the ocean involves their active movement, vertically or horizontally through the water column at different time scales (typically on a diel or seasonal basis). Marine migrant animals are mostly metazoans, including zooplankton (e.g., copepods and krill), fish, and marine mammals (e.g., whales). The migration of animals, when it contributes to the transport of carbon and thus to the carbon cycle, is known as the "migrant pump". Migrant animals contribute to carbon transport by incorporating carbon (e.g., by ingestion) in some places (areas or depths), and releasing carbon (e.g., by respiration, exudation, defecation, excretion, and molt release) in others (see Barnes and Tarling, 2017; Henley et al., 2020). The most studied migrant pump is the Diel Vertical Migration, (DVM) where organisms move carbon upwards or downwards through the water column daily. Vertical movements are influenced by many factors, including endogenous ones like sex, age, size, and internal rhythms, as well as exogenous ones such as light conditions, predator and prey abundance, currents, and the distribution of water temperature, salinity, and dissolved oxygen (Liszka et al., 2021). However, despite this range of factors, optimal light intensity is a fundamental driver of DVM, with animals naturally drawn to light of a preferred intensity. Nekton that respond to variations in light levels through vertical migration can be categorized as their own functional group (Richards et al., 1996).

When moving carbon downwards, the DVM contributes directly to the transfer of carbon to the deep ocean. Vertical migrant pumps, together with gravitational pumps, are considered the most important biological pump pathways for carbon storage, and the highest contribution of migrant pumps to the total export of carbon is at high latitudes (Nowicki et al., 2022). The seasonal migration pump is much less studied than the diel migration pump, but is particularly relevant in high latitudes, as it includes hibernation depths that contribute directly to the storage of carbon (Bradford-Grieve et al., 2001; Kobari et al., 2008). Also, it considers the so-called "seasonal lipid pump", the vertical transport of carbon rich lipids by overwintering zooplankton, which transfers an amount of carbon equivalent to the sinking flux of detrital material (Jónasdóttir et al., 2015).

Table 5
Functional Groups for pelagic organisms.

Functional group	Example taxa	Reference
Diving mammals	Seals and whales	(Halsey et al., 2006)
Vertical migrators	Zooplankton, fish and squid	(Richards et al., 1996)
Heterotrophic bacteria	Archaea, bacteria	(Legendre and Le Fèvre, 1995)
Phytoplankton. Morphologically based functional groups (MBFG).	Correlated with growth rates and sinking rates. Categories such as dimensions (e.g. volume), mucilage, flagella, gas vesicles, heterocysts.	(Kruk et al., 2010, Table 3)
I. Small organisms with high S/V	I. Chlorococcales, Chroococcales, Oscillatoriales, Xanthophyceae, Ulothricales	
II. Small flagellated organisms with siliceous exoskeletal structures	II Chrysophyceae III Nostocales, Oscillatoriales IV Chlorococcales, Oscillatoriales, Xanthophyceae, Zygnematophyceae	
III. Large filaments with aerotopes	V Cryptophyceae, Dinophyceae, Euglenophyceae, Volvocales, Chlorococcales	
IV. Organisms of medium size lacking specialized traits	VI Bacillariophyceae	
V Unicellular flagellates of medium to large size	VII Chlorococcales, Chroococcales, Oscillatoriales	
VI Non-flagellated organisms with siliceous exoskeletons		
VII Large mucilaginous colonies		
Carbonate or Si *exo*-structures	Coccolithophores and diatoms	(Müller, 2019; Rixen et al., 2019)
Sinking rate	Plankton	(Du Clos and Gemmell, 2024)

The migrant pump also forms part of the "particle injection pumps" (PIPs) proposed by Boyd et al. (2019), which include all biological and physical mechanisms that inject suspended and sinking particles to depth. This can transport as much carbon as the gravitational pump (**Downward Particle Flux**).

Although the migration of animals is considered to be an active pump, it overlaps in part with passive pumps, such as the gravitational settling of organic particles and the downslope movement of skeletal fragments. For example, migrant copepods at certain depths release faecal pellets, which are incorporated into the gravitational (and thus passive) vertical transport of carbon towards the deep ocean (Cavan

Table 6
Functional groups for simplification of Polar benthic marine assemblages (Barnes and Sands, 2017).

Functional traits	Example taxa
Pioneer sessile suspension feeders	Encrusting bryozoans, ascidians, some polychaetes
Mature assemblage sessile suspension feeders	Demosponges, glass sponges, brachiopods
Sedentary suspension feeders	Basket stars, valviferan isopods, some polychaetes
Mobile suspension feeders	Some brittle stars, crinoids, krill
Epifaunal deposit feeders	Sea cucumbers, some polychaetes
Infaunal soft bodied deposit feeders	Some polychaetes, echiurans, sipunculans
Infaunal shelled deposit feeders	Bivalves, irregular sea urchins
Grazers	Regular sea urchins, limpets
Soft bodied, sessile scavenger/ predators	Sea pens, soft corals, anemones, hydroids
Hard bodied, sessile scavenger/ predators	Cup corals, whip corals, hydrocorals
Soft bodied, mobile scavenger/ predators	Some polychaetes, nemerteans, octopus
Hard bodied, mobile scavenger/ predators	Sea stars, fish, gastropods, some brittlestars
Jointed legged, mobile scavenger/ predators	Sea spiders, shrimps, amphipods

et al., 2024). Therefore, the transport of carbon by migrant animals described here is directly related to the measurement of **Sediment Accumulation Rate** and **Faecal Production Rates**, both metrics considered in this review.

4.3.3. Vertical advection and dispersion

In addition to biological mechanisms like the migrant pump, carbon in the ocean is also transported through physical processes such as advection by ocean currents (Lévy et al., 2013). These currents have the potential to move dissolved and particulate organic carbon (POC) horizontally and vertically across vast distances (Ito et al., 2010), but also to disperse it over a much wider area. Organic matter, originating from surface waters through processes like phytoplankton photosynthesis or river runoff, are either consumed by marine organisms or sink as detritus through the gravitational pump (Ducklow et al., 2001). As this detritus sinks, ocean currents transport these carbon-rich substances to different regions, where they can be utilized by animals or contribute to passive carbon transport mechanisms (Bauer and Druffel, 1998). For example, the biogenic products of phytoplankton blooms that are advected by currents into waters of low biological productivity may serve as food for zooplankton and larger animals, facilitating the incorporation of carbon into marine food webs and its effective sequestration (Behrenfeld et al., 2006). Macroalgae, which generally grow attached to hard substratum in coastal waters, are also an important component of global carbon fluxes. They support a global net primary production of about 1.5 Pg C yr^{-1}, and export 2.4 Pg organic C yr^{-1} to the open ocean(Krause-Jensen et al., 2018). About 11 % of macroalgal net carbon production is transported offshore and potentially sequestered in sediments and deep-sea waters, estimated at 0.17 Pg C yr^{-1} (Krause-Jensen et al., 2018, and citations in source). Coastal sequestration is estimated at 0.014 Pg C yr-1 and deep-sea sequestration at 0.15 Pg C yr^{-1} (Ortega et al., 2019).

Similarly, dissolved organic carbon (DOC) can be transported to deeper layers by the three-dimensional thermohaline circulation, and sequestered by physical mixing or biological uptake (Hansell et al., 2009). Marine currents also play a critical role in redistributing carbon between coastal zones, offshore areas, and deep ocean regions, interacting with both the biological pumps (e.g., migrant and gravitational pumps) and the physical carbon sequestration (i.e. solubility pump) processes that altogether regulate the global carbon cycle (Passow and Carlson, 2012).

Vertical transport plays a fundamental role in regulating the movement of carbon through the ocean, affecting both horizontal and vertical pathways (Ito et al., 2010; Lévy et al., 2013). As organic matter, such as DOC and POC, is mainly produced at the surface through biological processes like photosynthesis, it is dispersed by ocean currents across multiple spatial scales (Hunt Jr et al., 2016; Isla et al., 2009). This dispersion spreads carbon-rich materials throughout different regions of the ocean, influencing where and how carbon is incorporated into food webs or exported to the deep ocean. Horizontal dispersion is key to distributing carbon across nutrient-poor regions, where it can be consumed by organisms, or across oceanic gyres and coastal areas, influencing the biological carbon cycle (Yamamoto et al., 2018). Vertically, dispersion moves carbon particles from surface waters into deeper layers, facilitating the effective sequestering of carbon for climate-relevant periods of time. In this way, dispersion contributes to both short-term carbon cycling within marine ecosystems and long-term carbon sequestration by spreading organic matter across various regions and depths (Le Moigne, 2019).

Submesoscale fronts, which are characterized by sharp gradients in temperature, salinity, and density over small spatial scales, significantly enhance vertical carbon transport in the ocean, through strong vertical fluxes of particles and organic matter. These fronts can rapidly inject POC from surface blooms or sinking detritus into deeper layers, accelerating the biological pump's efficiency in exporting carbon (Mahadevan, 2016). Unlike slower, large-scale oceanic processes, submesoscale fronts create narrow zones of intense vertical movement that can transport carbon-rich material into the deep ocean more efficiently (Lévy et al., 2024; Lévy et al., 2018). Additionally, these fronts trap and concentrate carbon in convergence zones, where downwelling currents can quickly subduct this carbon to greater depths (Omand et al., 2015). This direct export of carbon to the deep ocean bypasses the more gradual remineralization processes that occur in surface waters, contributing significantly to carbon sequestration and influencing global carbon storage (Kessouri et al., 2020).

4.4. Standardisation

4.4.1. Biological Carbon Pumps

To quantify the contribution of the migrant pump to carbon sequestration is possible by combining direct measurements and modelling (e.g., (Davison et al., 2013)). Direct measurements include invasive and non-invasive methods. Echosounders and other acoustic methods are considered non-invasive tools (except perhaps to marine mammals) that allow the determination of assemblage density and spatial distribution with depth. Invasive methods include fishing of plankton and nekton with special nets and trawls. Measurements relevant to understanding carbon fluxes generally include animal abundance and biomass, as well as their carbon capture through feeding and carbon release by different mechanisms such as respiration, egestion rates, and molt rates. Additionally, marine migrant animals have patchy distributions, which makes the measurement and extrapolation of direct measurements very challenging. The range of these migrations, across international boundaries, requires multi-national co-ordination of tagging and observation programs. These allow hotspots of usage to be identified (e.g. (Requena et al., 2020) that can prioritise areas for research through the designation of marine protection, for example important bird (IBA; (Donald et al., 2019)) and marine mammal areas (IMMA; (Hoyt and di Sciara, 2021)). Sharing of information, samples and the genetic and biochemical analysis, through established global programs, such as GOOS (Global Ocean Observing Systems) and the Antarctic Treaty systems, are key. Measuring the role of the biological pumps for all species is impossible, demanding a focus on key carbon pathways. In much of the Southern Ocean this focus has been on one of the key pathways from phytoplankton to krill to marine mammals (Johnston et al., 2022).

Modelling overcomes direct measurement limitations and allows extrapolation at different temporal and spatial scales (Table 4). The models used to study carbon fluxes by migrant animals can focus on

individuals, populations, or communities, and include both metabolic and migration processes (Countryman et al., 2022). In addition, the values of carbon released during migration can be linked to models of particle transformations (to observe the degradation of the particles over space and time and thus flux attenuation) and circulation models (to predict the fate of the particles). Models can also contribute to defining relevant facets of particle flux that govern carbon sequestration, such as the total export rate and fluxes (including the depth of peak flux and depth scale of flux attenuation).

Richards et al. (1996) mathematical model for studying diel vertical migration examines the light-mediated mechanisms and is applicable in shallow waters, including fjord ecosystems, at depths of approximately 20 m, encompassing a diverse range of zooplankton species. In 2023, Pinti and co-authors introduced a sophisticated model that employs a game-theory food web framework and Nash equilibrium to assess the equilibrium distribution and daily migration patterns of various functional groups simultaneously, including mesozooplankton, macrozooplankton, mesopelagic fish, forage fish, large pelagic fish, and jellyfish. The model includes carbon sequestration potential, carbon injection, and carbon export. However, it does not take seasonality into account, which at polar latitudes is non-trivial. The code can be accessed at https://gitlab.gbar.dtu.dk/jppi/.

4.4.2. *Vertical advection and dispersion*

To quantify the various pathways of carbon transport in the ocean, including those affected by dispersion and submesoscale fronts, requires a combination of biological, chemical, and physical measurements. Sediment traps and optical sensors are commonly deployed to capture and measure the flux of POC sinking through the water column, providing insights into vertical carbon transport (Downward Particle Flux). To measure DOC concentrations and fluxes, water samples are collected at different depths and analyzed through chemical methods such as high-temperature combustion or ultraviolet oxidation (Hansell et al., 2009). Acoustic Doppler current profilers (ADCPs) and oceanographic moorings equipped with biogeochemical sensors can track the movement of carbon-rich particles, both horizontally and vertically, offering real-time data on carbon dispersion and its interaction with biological processes (Bourne et al., 2021).

Lagrangian drifters are particularly useful for observing carbon pathways, especially when examining processes driven by submesoscale fronts and dispersion. By deploying Lagrangian drifters in regions of interest, researchers can track water mass horizontal advection and dispersion (Martín et al., 2023; Meyerjürgens et al., 2020). Additionally, when deployed near submesoscale fronts, they provide crucial information on how these physical structures influence vertical mass transport (Tarry et al., 2022) and dispersal properties of the surface layer (Meyerjürgens et al., 2020; Ricker et al., 2021). Drifters can thus reveal the pathways by which carbon is transported from surface waters to deeper layers, as they allow to observe the trajectory and fate of carbon-rich particles in response to vertical motions associated with fronts (Omand et al., 2015). By integrating Lagrangian observations with remote sensing and in-situ measurements, researchers can gain a more comprehensive understanding of the dynamics governing both vertical and horizontal carbon transport in the ocean. This combination allows for real-time tracking of water parcel movements, enhanced by satellite data and direct sampling, providing a clearer picture of how carbon is dispersed, transported, and sequestered throughout different oceanic layers. This understanding is crucial as markets emerge to value blue carbon ecosystem services, valuations that rely on knowing where most fixed carbon is ultimately sequestered.

Table 7
The main environmental factors that can be used to classify habitat type.

Predictors of habitat	Reference
Suspended particulate matter	(Neder et al., 2022)
Light intensity	(Deregibus et al., 2023)
Turbidity	(Sahade et al., 2015)
Distance to the glacier (a proxy for glacial influence)	(Sahade et al., 2015)
Seasonal sea ice cover	(Frinault and Barnes, 2024)
Depth	(Nasir et al., 2024)
Meltwater input	(Jerosch et al., 2018)
Ice impacts	(Barnes, 2017)
Sediment grain size	(Nasir et al., 2024)
Salinity	(Jerosch et al., 2018)
Temperature (water)	(Bates and Morley, 2020)
Nutrients (macro-nutrients)	(Frinault and Barnes, 2024)
Distance to the coast	(Barnes et al., 2016)
Duration since permanently ice covered	(Barnes et al., 2016)
Current velocity	(Souster et al., 2020)
Sediment organic content	(Morley et al., 2022b)
Terrestrial Vegetation	(Convey et al., 2024)
Geology	(Anderson, 1999)
Topography	(Frinault and Barnes, 2024)
Meteorology (Atm. T, wind, precipitation)	(Smith et al., 2014)
Mixed layer depth	(Venables et al., 2023)
pH	(Morrison et al., 2015)
Pressure	(Somero, 1992)
Sediment mineralogy	(Edwards and Goodell, 1969)
Wave exposure	(Barnes and Conlan, 2007)

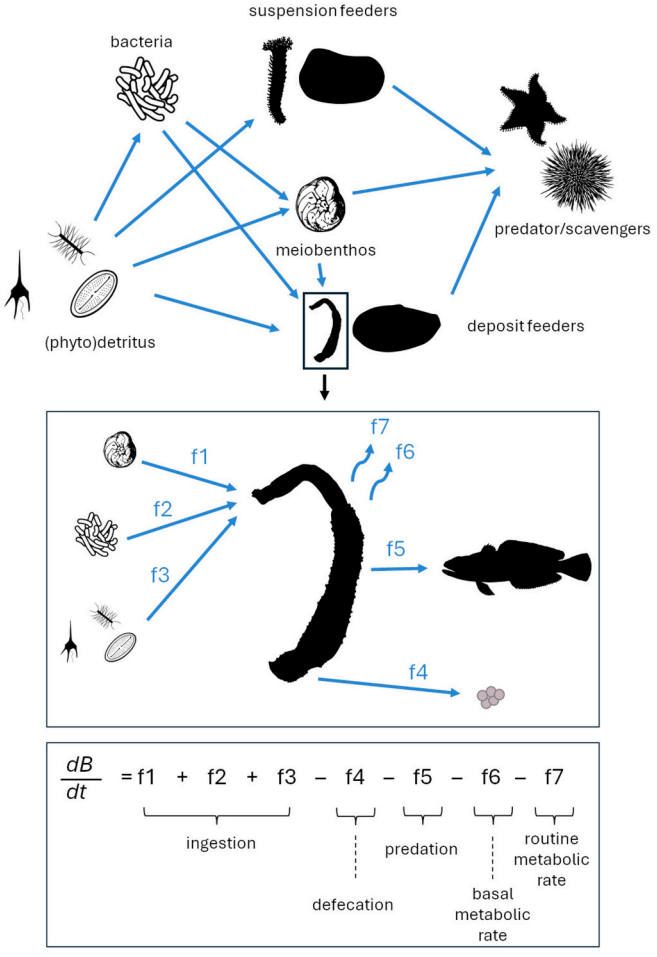

Fig. 4. Process rates that determine the rate of carbon storage within an assemblage. The top panel shows indicative food-web links between functional groups. The middle panel shows the energy fluxes through an individual organism. The bottom panel shows how the energy flux can be calculated from energy gains (f1-f3) and loses (f4-f7) from the organism (figure modified from Soetaert and van Oevelen (2009). Blue arrows indicate energy and therefore carbon fluxes. Icons represent functional groups, but not specific species (www.phylopic.org). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4.5. Functional groups

4.5.1. Definitions

Critical to understanding carbon pathways is a clear comprehension of the linkages between functional traits, functional groups, and ecosystem processes. Functional traits in biological oceanography are the morphological, physiological, or phenological characteristics of (marine) organisms that influence their fitness and ecological functions. These traits are essential for understanding marine responses to environmental change and their role in ecosystem processes (Zhang et al., 2023). Species with similar functional traits e.g., similar feeding strategies, can be grouped into functional groups, simplifying ecosystem function (Fig. 3), reducing the amount of information required to describe carbon pathways, and improving predictability (Martini et al., 2021). Functional groups in marine biology are used to categorize species according to common ecological characteristics and their roles in the ecosystem (see Barnes and Sands, 2017). These groups aid in comprehending the diversity, interactions, and impact of marine organisms on ecosystem processes (Functional Groups; Sohier, 2025). Hence, ecological processes in biological oceanography are driven by functional traits and groups of marine organisms. These processes include the functioning and structure of aquatic ecosystems, ecological patterns, and the response of marine organisms to environmental change (Martini et al., 2021; Zhang et al., 2023). It is important that these functional groups are standardised, to ensure comparability between studies (e.g. Table 5 and Table 6).

4.6. Standardisation

4.6.1. Phytoplankton functional groups

Morphological classification without taxonomic affiliation is an efficient functional approach for phytoplankton. The Morphologically Based Functional Classification (MBFC) and the functional groups outlined by Kruk et al. (2010) are defined by functional traits such as volume, maximum linear dimension, surface area, and the presence of mucilage, flagella, gas vesicles (aerotopes), heterocysts, or siliceous exoskeletal structures. These characteristics correlate with functional traits, e.g. growth rates, as maximum growth (in terms of doubling per day) decreases as cell volume ($\log_{10}V$) increases, affecting sinking rates. Higher sinking speeds are also associated with the presence of siliceous structures. Species that share similar morphological traits are grouped into morphologically based functional groups (MBFG). The findings indicate that MBFG could broadly represent ecological function.

The transfer efficiency of organic carbon can be used to distinguish between the roles of primary production and the ballast effect, e.g. from Coccolihophore $CaCO_3$ structures (Müller, 2019) or silicon from diatoms in high latitudes (Rixen et al., 2019).

4.6.2. Microbial functional groups

Integrating microbial food web processes into global biogeochemical models is vital for improving the accuracy of carbon cycling predictions in marine environments (Legendre and Le Fèvre, 1995). The functional groups that form part of the modern microbial food web include viruses, heterotrophic bacteria, pico-nanophytoplankton, mixotrophic and heterotrophic flagellates, and ciliates (Azam et al., 1983; Sherr and Sherr, 1994; Suttle, 2005; Wilhelm and Suttle, 1999).

Even though most of the global ocean is in the Southern Hemisphere, there is a lack of research on ocean microbiomes (Sarmento et al., 2025). A key bacteria functional trait (prokaryotes, including bacteria and archaea) is the degradation of dissolved organic carbon (DOC). More than 50 % of the carbon fixed by phytoplankton is processed by bacteria. Another significant bacterial function trait is vitamin metabolism; the entire food chain depends on vitamin B1 produced by microbes. Additionally, pollutant degradation traits related to carbon must be considered. There are also a variety of nitrogen and phosphorus cycling traits which interact with the carbon cycle (Pinhassi et al., 2022 and citations

Table 8
Methods for measuring POC.

Methods and references	Procedure	Strengths	Weaknesses
Filtration and Gravimetric Analysis (Schloss et al., 2012)	Water samples are filtered to collect particulate matter, which is then dried and weighed	Simple and cost-effective; provides direct measurement of total particulate matter	Non-specific to organic carbon; can include inorganic particles; time-consuming
	It can also include a incineration step where organic matter is combusted and inorganic matter content is assessed		Even when inorganic matter is accounted for, there is a variable relationship between organic mass and organic carbon content
Sediment traps (Flores-Melo et al., 2024; Honjo and Doherty, 1988; Larsson et al., 1986; Trull et al., 2001)	A collection vessel is typically attached to a mooring. Multiple collection vessels can be rotated to allow a time-series of samples to be collected	Detailed information on the amount of POC reaching various depths with a potential for good temporal coverage if deployed long enough using a rotating sediment trap	Resource intensive and expensive: requires the use of a research vessel to deploy and recover Sample resolution is limited by the number of collection vessels
	Samples then need filtering and analysing (as above)		Limited spatial coverage.
Optical measurement of carbon flux (Bourne et al., 2019)	Mooring deployed optical sediment trap	High resolution continuous measurements, with data instantly available	Resource intensive (see above) and requires calibrating
Filtration and Elemental Analysis (CHN Analysis) (Obermüller et al., 2013)	Water samples are filtered, and the particulate matter is analyzed for carbon, hydrogen, and nitrogen content using elemental analysers (spectrometers)	Specific and accurate for organic carbon; provides additional elemental composition.	Requires expensive equipment and skilled personnel; labour-intensive sample preparation
High-Temperature Combustion(Ratnarajah et al., 2022)	Filters with particulate matter are combusted at high temperatures, and the resulting CO2 is measured	High precision and accuracy; widely used and standardised.	Expensive equipment; requires careful calibration and maintenance
Chemical Oxidation(Scott et al., 2000)	Particulate matter is chemically oxidized, and the resulting CO2 is measured	Used to distinguish between organic and inorganic carbon. Further used to determine DOC	Complex procedure; potential for incomplete oxidation
UV Spectrometry (Ytow et al., 1996)		Rapid and non-destructive; can be used for real-time measurements	Indirect measure, can lead to inaccuracies if other substances are present. Lower sensitivity than the other methods, especially with turbid samples
Remote Sensing (Stramski et al., 1999)	Satellite or aerial imagery used to infer POC concentrations based on ocean colour	Provides large-scale and continuous spatial coverage; useful for temporal monitoring	Indirect measurement; requires validation and calibration with in-situ data; affected by cloud cover and sea ice

within). In terms of abundance, diversity and metabolic activity, bacteria dominate the ocean. Moreover, the issue of 'bacterial growth efficiency' in relation to ecosystem function must be addressed. This compares the fraction of assimilated carbon that is respired with the fraction that is used to increase bacterial biomass. In other words, its variability influences the carbon cycle (Azam and Malfatti, 2007). Bacteria can be quantified using flow cytometry, as described by (Gasol and Del Giorgio, 2000). Once the bacteria have been quantified, and it is considered that the method uses microspheres for biovolume calibration, multiplying the result by a carbon-per-cell factor will yield an estimate of bacterial biomass. Bratbak (1985) suggests an average value of 5.6×10^{-13} g C μm^{-3} as a factor for estimating bacterial biomass from biovolume.

Viruses, as a functional group, can account for the annual release of up to 0.63 Gt of organic carbon from marine sediments through viral lysis as a functional trait. Bacteriophages release organic matter that differs in both composition and nature. Viral lysis generates organic matter that is biologically recalcitrant or more refractory (Heinrichs et al., 2020; Weinbauer et al., 2011 and citations within). Viruses are responsible for up to 80 % of prokaryote mortality in water deeper than 1000 m (Danovaro et al., 2008). In the Antarctic the role of viruses on primary productivity was particularly noticeable during periods of phytoplankton accumulation (Biggs et al., 2025). Mortality due to viral lysis can be determined using techniques devised by Binder (1999), which measures the proportion of total bacterial mortality caused by viral lysis. An alternative method is to use the metric of viral production and the fraction of infected cells, as determined by the dilution method (Weinbauer et al., 2010).

The grazing activity of protists such as heterotrophic and mixotrophic nanoflagellates, and ciliates can be addressed using a fluorescence-based approach involving the use of fluorescently labeled bacteria (FLB), specifically *Brevundimonas diminuta*. These bacteria can be added to water samples and incubated for 24 h. The disappearance or reduction of the FLB during this period is used as an indicator of grazing activity. This approach has been used in Livingston Island, Antarctica (Vaqué et al., 2004).

The microbial hub (HUB) approach, introduced by (Legendre and Rivkin, 2008), is a method for studying microbial heterotrophic components of pelagic food webs. It is a powerful tool for studying the metabolism of pelagic communities (see **Respiration Rates**). The HUB focuses primarily on the photic zone of marine ecosystems. This method does not consider the ecological or biogeochemical functions of archaea, as these have not been properly documented or parameterized. In the model, the functional category "heterotrophic bacteria" or "bacteria" groups together archaea and bacteria. The approach involves grouping all heterotrophic microbes together in the HUB, while larger heterotrophic organisms are categorized into the METAZ, or metazoan compartment. Each food web flow is expressed as a ratio to community respiration. Summary respiration fluxes through, between and from the HUB and METAZ are calculated using fluxes derived from observations or obtained with models. Both the HUB and the METAZ have a dual role in the euphotic zone, receiving organic carbon from multiple food web sources and recycling this carbon to other food web compartments and their own respiration.

4.6.3. Benthic functional groups

The contribution of carbon accumulation (carbon proportion of dry mass), immobilization (net annual carbon accumulation), sequestration (estimation) have been considered to simplify the polar blue carbon by South Georgia benthic functional groups (Table 6).

The presence and composition of these functional groups positively influence carbon accumulation, immobilization, burial, and sequestration in the benthic ecosystem. The method involves obtaining ash-free dry (organic) mass. Carbon is considered immobilized in a subset of skeletonized animals (mainly calcareous) as skeletons provide greater shielding of organic matter from microbial breakdown on death. In these

Table 9
Main field methods for measuring primary production.

Number	Method	Strengths	Weaknesses
(1)	Light and dark bottle method (Gaarder, 1927) oxygen evolution (Latorre et al., 2023a, 2023b; Moreau et al., 2023)	Standard technique measuring oxygen production/ consumption with rich comparative literature It allows the assessment of community respiration rate along with net and gross primary production rates It is the easiest and cheapest technique available	Bottle effects (grazing, changing water chemistry, bacterial growth) The use of a fixed photosynthetic quotient to assess carbon fixation from oxygen production is problematic since this quotient is highly variable depending on several factors that we can not account for
(2)	carbon (^{13}C and ^{14}C) assimilation rate (Schloss and Ferreyra, 2002)	Direct measure of carbon fixation into tissues Well established technique that is good for comparative purposes	Bottle effects (grazing, changing water chemistry, bacterial growth) Intermediate between Gross Primary Production and Net Primary Production in photosynthetic organisms It needs more advanced equipment, is more labor intensive and more expensive Working with radioactive isotopes (^{14}C) require specialist facilities Low primary production rates may be below the detection limit for ^{13}C incubations unless large volumes of seawater are used
(3)	Nitrogen uptake (Kristiansen et al., 1992)	Known ratio of uptake relative to carbon fixation (Redfield ratio)	Bottle effects (grazing, changing water chemistry, bacterial growth) Intermediate between Gross Primary Production and Net Primary Production in photosynthetic organisms Dependent on light exposure levels Redfield ratio (C:N) in phytoplankton is highly variable depending on community composition, life stage of the bloom, physiological status, availability of trace metals, etc.
(4)	Variable fluorescence (Latorre et al., 2023b; McMinn et al., 2010)	In-situ measurements	Converting fluorescence to productivity requires laboratory calibration Highly variable relationship between carbon and chlorophyll-a content in phytoplankton limit the ability to transform

(*continued on next page*)

Table 9 (*continued*)

Number	Method	Strengths	Weaknesses
			measurements related to chlorophyll-a into carbon assimilation rates

cases, the carbon within the ash-free dry mass bound within the skeleton is calculated and added to the carbon proportion of skeletal mass (Barnes and Sands, 2017).

4.6.4. Macroalgal functional groups

In the southern marine ecosystems (southwestern Atlantic, 33°-35° S) macroalgae are classified based on seven morphological traits, which have been developed and further simplified in a diagram showing the classification tree (CART), where only three traits are used (shape, consistency and texture). The CART model is used to validate the morpho-functional groups (MFGs) by comparing its classifications with those made by experts, achieving a classification success rate of 99.6 %. These MFGs support easy recognition of algal assemblages and rapid ecological analysis. Once validated for high latitude ecosystems they should contribute to ecological studies and monitoring programs (Vélez-Rubio et al., 2021).

4.7. Habitat type

4.7.1. Definition

Habitats consist of a suite of environmental characteristics that provide suitable conditions for particular organisms to develop and survive. A combination of interacting environmental variables and parameters support assemblages with characteristic patterns of carbon uptake, storage and, in some cases, sequestration. Habitat classification is therefore an important tool for scaling knowledge of blue carbon pathways across regions (Fig. 3).

4.7.2. Measurement

Oceanographic, glaciological, geological, sedimentological, meteorological and biochemical factors collectively define the habitat types of Subantarctic and Antarctic Peninsula ecosystems. However, within these classifications numerous physical and chemical characteristics of the environment interact to determine the habitat and therefore the assemblage that can persist there. In marine coastal areas, some of the key predictors that define a distinct habitat are light (affected by ice cover, depth, and turbidity), water temperature, salinity, pressure, substrate type (hard versus soft substratum, or texture based on grain size distribution), topography (moraines, valleys, slope, rugosity), nutrient concentration (e.g. N, P, Fe, Si), hydrodynamic conditions (current direction and velocity, waves, particle transport, bed stress) and habitat age inferring the time since an area has been ice-free and available for colonization among others (Table 7). Additionally, disturbances such as ice impacts (e.g. scouring and melt water run-off) and stress factors as ocean acidification will influence habitat. These factors are expected to vary with climate change (Morley et al., 2020; Neder et al., 2022).

4.7.3. Standardisation

Due to the challenges of surveying habitats and the large number of variables and parameters characterising habitat type, it is important to identify key environmental (single or multiple) factors that can be used to scale across large areas.

Depth is one key variable, that is not only directly correlated with water pressure, but is strongly correlated with many other factors, and is widely available, either from direct measurements or bathymetric models. Local bathymetry is strongly correlated with species diversity and abundance, as species have specific depth ranges and assemblages exhibit marked patterns of depth zonation (e.g. Fig. 3 of Barnes and Kuklinski, 2010). In pelagic ecosystems, a reduced abundance tends to be observed with depth, principally due to limits of light penetration, and therefore available energy for primary productivity. In benthic ecosystems, the abundance and diversity of macroalgae, epifauna and infauna can increase to an optimal depth in response to factors such as, light attenuation, ice impact, wave disturbance, meltwater input, and downwards particle fluxes (Robinson et al., 2021). This complex interplay of factors shapes the ecological dynamics of an area and creates a mosaic of habitats. Factors change with depth and alter patterns of blue carbon capture, storage and sequestration, with primary capture and carbon storage highest on hard substratum in the shallows and sequestration highest in deep soft substrata (Bax et al., 2021; Quartino et al., 2020). Therefore, selected sampling at discreet depths can provide information on habitats and their characteristic assemblages. This allows for model-based scaling to less well surveyed regions. Improving bathymetric coverage should be a priority, particularly of newly ice-free areas, and bathymetric techniques that allow habitat assessment (e.g. swath bathymetry and back-scatter, (Lamarche et al., 2016), which facilitate predictive habitat modelling.

Habitat age of Antarctic and Subantarctic coastal regions describes the number of years habitats have been ice-free. Using satellite records of glacial retreat over the last 70 years, studies have measured the rate of assemblage colonization and succession (Barnes et al., 2020; Kim et al., 2024) correlating habitat age with assemblage structure, and standing stock of carbon (Zwerschke et al., 2022).

Suspended particulate matter (SPM) correlates with many other key factors and surface values can be estimated from drone or satellite surveys (Wójcik-Długoborska and Bialik, 2023). SPM affects water column turbidity, and therefore light penetration, photosynthetic activity, nutrient availability, and food dilution (Domack et al., 1994). It is also influenced by glacial proximity, and therefore meltwater input and sediment runoff (Neder et al., 2022). SPM is a key component of benthopelagic coupling transferring carbon into seafloor habitats and providing food for benthic species but also impacting substratum grain size and therefore habitat suitability. The sedimentation of SPM also directly determines the porosity of the sediment, the depth of the oxic layer and therefore the rate at which carbon will either be remineralised or remain buried long-term where it can be classified as sequestered (see **Sediment accumulation rate**).

Models utilising statistical autocorrelation analysis among parameters allow the combination of various environmental variables and parameters that can spatially differentiate habitats (Neder, 2023). As a result, environmental conditions are spatially mapped. Tools such as Geographic Information Systems (GIS) and geospatial modelling can then be used to produce habitat maps (Jerosch et al., 2018).

The application of habitat suitability models (see **Modelling blue carbon pathways**) can identify significant relationships between the environmental characteristics and predict the presence or abundance of a target species. Models allow the combination of different variables and parameters that shape the distribution of species or assemblages (Deregibus et al., 2023; Lagger et al., 2021; Neder, 2023). Using conversion factors enables biomass estimates for specific assemblages to be associated with habitat types. A comprehensive understanding of the link between habitat types, species distribution, and assemblage compositions is essential for accurately estimating the overall carbon dynamics of an ecosystem.

With ongoing and intensifying climate change, it is necessary to understand how habitat types are likely to shift over time and space and to predict many likely changes in biodiversity and therefore the altering structure of carbon pathways. Consequently, long-term monitoring of the rates of change are essential and temporal and spatial scales must be considered for the future budgeting of carbon.

4.8. Particulate organic carbon (POC)

4.8.1. Definition

POC is the proportion of organic material, such as carbon-containing compounds in suspended particles within a water column, generally of a size larger than 0.2 μm (Kharbush et al., 2020). These particles include microorganisms, plant material, and other organic detritus. POC measurements are crucial for understanding carbon cycling and **Primary productivity**, particularly in terms of carbon fixation, **Export and migration**.

4.8.2. Measurement

Various methods exist for measuring POC, each with its strengths and weaknesses (Table 8).

4.8.3. POC in blue carbon pathways

POC measurements can indicate changes in the ecosystem, such as shifts in primary productivity and the biological carbon pump (see **Export and migration**) or the impact of climate change. Hence these measurements contribute to the long-term monitoring of Antarctic ecosystems.

Furthermore, POC quantification is essential in constructing carbon budgets and understanding the role of the Southern Ocean in sequestering atmospheric CO_2, providing crucial data for studying biogeochemical cycles and nutrient dynamics. In addition, POC data can improve the accuracy of climate models, by providing data on carbon sequestration.

Table 10
Metabolic rate measurements (Cech and Brauner, 2011; Hochachka and Somero, 2002).

Metabolic rate	Description	Strengths	Weakness
Basal metabolic rate	Measurement of energy required for organisms maintenance.	Standardised physiological measure to compare the effect of environmental variability.	Difficult to ensure no routine processes are ongoing (e.g. feeding or locomotion)
Routine metabolic rate	Measurement including routine activities such as feeding and locomotion	Measures animals in their "field" state	Cannot partition different components of metabolic rate
Maximum metabolic rate	Measurement of the maximum metabolic rate of an organism	Allows the calculation of metabolic scope	The ecological relevance of methods is frequently criticised
Metabolic Scope	The difference between maximum and basal metabolic rates	Measures maximum aerobic capacity	Does not account for anaerobic metabolism
Net Primary Production	The difference between the oxygen consumed by photosynthetic organism and their oxygen evolution during photosynthesis	Reflects the balance between photosynthesis as carbon input, and respiration, providing a key measure of ecosystem productivity and health	Need to conduct experiments in the light and dark in order to partition respiration and photosynthesis.
Estimated from heart rate or growth rate in animals (Green, 2011)	Assumes a constant relationship between heart rate, temperature and oxygen consumption	Can measure heart rate in large free-ranging animals Can be calculated empirically from wild collected specimens	The calibration process can be complex

4.8.4. Standardisation

Different methods can yield varying results, require careful calibration and inter-comparison. However, combined use of multiple approaches can provide a comprehensive understanding of carbon dynamics in polar waters. In particular, it is important to settle on a clear size categorisation between dissolved organic carbon (DOC) and POC. A range of size criteria are used in the literature, from 0.2 to 1.0 μm, which is often based on the pore size of the most commonly used filters. We suggest standardisation on smaller (DOC) and larger (POC) than 0.2 μm, which leads to the inclusion of living prokaryotes in the size range 0.2 to 0.8 μm, leaving no gaps (the nebulous colloidal realm) between POC and DOC (Kharbush et al., 2020).

In particular, measurements of the mass of organic and inorganic carbon (see **Biomass**) in filtrate from water samples can be used to provide depth profiles, as well as to calibrate remotely sensed surface POC concentrations from satellites.

4.9. Primary production

4.9.1. Definition

Primary production takes two main forms. In shelf waters, autotrophs generate organic matter primarily through photolithoauthotrophy, using CO_2, H_2O, and solar irradiance as an energy source. In addition, chemoautotrophs fix carbon using inorganic electron donors (e.g., sulfide, ammonium, or methane) rather than light, contributing to carbon production, mainly in the euphotic ocean, but also in oxygen minimum zones and around hydrothermal vents(Middelburg, 2011). Although most hydrothermal vents, and methane seeps, are in deep water, where they occur in shallow waters they can be responsible for a high portion of the productivity (Gomez-Saez et al., 2017). Quantifying primary production, thus, provides information about the amount of seawater inorganic carbon transformed into organic carbon and fixed within body tissues, initiating the series of processes known as the biological carbon pump.

Marine phytoplankton contributes to nearly half of global primary production (PP), forming the foundation of marine trophic food webs, whereas, macroalgae become important primary producers in coastal marine environments. Less information is available for the microphytobenthic and epiphytic microalgal assemblages, at least for polar environments (Wulff et al., 2009). This community - mainly composed of diatoms, may play a substantial role as primary producers and constitute an important direct food source for both benthic and pelagic heterotrophs, particularly in areas with a usually low pelagic primary production (Ahn, 1997; Schloss et al., 2012).

4.9.2. Measurement

4.9.2.1. Phytoplankton. Several revisions have been published that compare the different phytoplankton analytic techniques (e.g. Regaudie-de-Gioux et al., 2014; Vernet and Smith, 2007)) and mathematical models determining final production rates (Behrenfeld and Falkowski, 1997; Platt and Sathyendranath, 2009). Here, we attempt to provide a concise review of the main approaches.

The primary field estimations of PP predominantly rely on four methods, all of which have been applied in Antarctica (Table 9).

In each approach, seawater samples are exposed to natural or artificial light, and various aspects of the photosynthetic process are measured. The first three methods quantify the outcomes, such as oxygen release and carbon or nitrogen assimilation, within the photosynthetic reaction, whereas the fourth method assesses the quantum performance of the "photosynthetic machinery" (Lutz et al., 2018).

Each of these methods has methodological constraints, that are in turn, prone to different biases (Table 9). In (1), (2) and (3), seawater is incubated for 2 to 24 h, introducing artifacts such as "bottle effects". Only method 1 is suited for assessing gross primary production (GPP),

Table 11
Main respirometry methods. (See Table 9, for methodological constraints relating to measuring primary production).

Measurement methods	Method and reference	Procedure	Strengths	Weaknesses
O_2	Winkler method (Strickland, 1972)	The classical Winkler titration	One of the most accurate techniques for measuring O_2 concentration in water. (μmol l^{-1}; (Coppola et al., 2013)	Labour-intensive Provides discontinuous measures
		The Spectrophotometric Winkler determination developed by (Labasque et al., 2004).		
	Electrodes	Polarographic oxygen electrodes	Continuous monitoring of O_2 tension in a solution, enabling the integration of respiration over different intervals of time or oxygen pressure. Enables parallel & simultaneous measurement of O_2 consumption of many samples. Rapid response times (<1S) Initial accuracy (2 % O_2 saturation)(Coppola et al., 2013) Precision of 1 μmol kg^{-1}	Perform poorly at low temperatures Requires regular calibration to account for drift
	Optodes	Principle: O_2 acts as a dynamic fluorescence quencher that decreases the fluorescence quantum yield of an immobilized fluorophore. Optode O_2 sensor spots can be fixed onto the inside wall of a transparent respiration chamber, thus allowing measurements to be conducted inside a sealed chamber	Allow parallel & simultaneous measurement of O_2 consumption of many samples, and easy, computer-assisted data-processing (Eleftheriou, 2013). Optode O_2 sensor spots can be fixed onto the inside wall of a transparent respiration chamber, thus allowing measurements to be conducted inside a sealed chamber Optode sensor spots are stable in the long-term Resolution of 1 μM and accuracy of 5 μM (Coppola et al., 2013).	Relatively slow response time, (although new sensors respond in <1 s., (Coppola et al., 2013).
	Closed cell respirometry	Sealed chamber in which oxygen is depleted	Technically simple	Oxygen concentration reduces and so conc. Must remain within the oxyregulation range of the species (Vaquer-Sunyer and Duarte, 2008; Wallace and Jones, 2008). Metabolites can build up in chamber
	Flow through respirometry		Complex apparatus with error inherent in flow control devices. Difficult to measure when metabolic rates are too low (Wallace and Jones, 2008).	Oxygen and metabolite concentrations remain constant (Killen et al., 2021).
CO_2	Infra-red gas analysers (Lighton, 2019).	Stimulated with light at 4.26 μm wavelength	More sensitive and less drift than oxygen analysers. Ideal for measuring metabolic rate of small organisms	Two gas calibration required. Non-linear response
	Eddy Covariance (Watts et al., 2022)	Direct measurement of CO_2 exchange in air-sea interface	Fast-response gas analysers Real-time assessment of fluxes rate	Difficult to compare due to global standardisation differences

net primary production (NPP) and community respiration rate (R) simultaneously, whereas methods (2) and (3) record an intermediate production rate between NPP and GPP without assessing R (Table 9X) (Vernet and Smith, 2007).

In method (3) phytoplankton growth is measured using the link between the ratios of carbon and nitrogen uptake. Carbon needs to be assimilated in a ratio of about 106:16 to nitrogen (known as the Redfield ratio) to form organic matter (DNA, proteins) and can be measured after adding $^{15}NH_4$ as a tracer to a sample. Uncertainties arise due to the variability in C:N ratio depending on phytoplankton physiological status, life stage and composition (Vernet and Smith, 2007). This method also needs to use a photosynthetic quotient to transform oxygen production into carbon fixation rate, which presents similar uncertainties, whereas method (2) has the advantage of directly assessing carbon fixation rates (Table 9).

The application of these methods further varies based on whether samples are incubated at a single light intensity (matching natural exposure in the sea at any given depth) or a gradient of light intensities (natural and artificial light source). The first case yields production rates (P) (mg C m^{-3} h^{-1}), reflecting the rate of production per unit volume and time at a specific site. The second approach enables the reconstruction of photosynthesis/irradiance curves (PI or PE or light-saturation curves) revealing photosynthetic parameters like α (slope of the light-saturation curve at low irradiances), and Pm (maximum production at saturating irradiance), Ek (saturation irradiance) and β (irradiance at the start of photoinhibition).

These parameters can be scaled through satellite-derived or biogeochemical models for extrapolating production information at larger spatial and temporal scales. Regardless, accurate measurements of visible-range irradiance (photosynthetic available radiation – PAR 400–700 nm wavelength) are crucial, in all but remote sensing or model applications (see **Modelling blue carbon pathways**).

Method (4), variable fluorescence, is distinctive as it does not always require sample incubation. Certain instruments allow for in situ profiling of fluorescence throughout the water column. This method involves measuring the fluorescence emitted by phytoplankton when exposed to short, varying-intensity flashes of light. Key instruments in this category include the “pump and probe,” the “pulse amplitude

modulated (PAM)," and the "fast repetition rate fluorometer (FRRF)." However, deriving actual PP estimates from these techniques pose challenges. Notably, variable fluorescence solely gauges the activity of photosystem II (PSII), which may not always correlate with overall photosynthetic apparatus' performance due to the uneven distribution of chlorophyll-*a* between PSI and PSII and non-photochemical quenching mechanisms. Transforming the fluorescence signal into the quantity of actual photosynthetic product requires fixed physiological factors (e.g., chlorophyll-*a* molecules per reaction centre in PSII), which currently relies on limited laboratory determinations, despite known variations based on phytoplankton type and physiological state (Lutz et al., 2018).

Remote sensing of ocean colour is an effective tool for regional and global PP assessment, offering extensive spatial and temporal coverage with daily estimations of phytoplankton biomass (Chl- *a* concentration), attenuation coefficient, and PAR. Satellites can also measure the extent of coastal macroalgae (Mora-Soto et al., 2020). Current algorithms range from simple empirical relationships between Chl- *a* and PP to complex models incorporating plant physiology, resolving various variables with depth and spectral irradiances. A drawback is that satellites only capture the upper ocean layer (first optical depth, often above the Chlorophyll maximum), limiting direct derivation of accessory information like photosynthetic parameters and biomass profile parameters from remote sensors.

4.9.2.2. Macroalgae. In general, ecological macroalgal investigations focus on "net primary production" (NPP), which denotes the portion of gross primary production remaining after deductions for respiratory losses. The specific methodology employed for measurement can result in different interpretations of this concept. Generally, NPP is quantified as the dry mass of plant material generated per unit area within a given unit of time (Reed et al., 2009). Algal biomass can be measured directly through quadrat clearance or calculated through statistical conversions from percentage cover (see **Biomass**).

In situ growth measurements of the brown alga *Himantothallus grandifolius* have been performed over 32 days (Dieckmann et al., 1985) and over a year (Drew and Hastings, 1992) by punching holes in the thalli at known distances above the basal meristem (Mann et al., 1979; Parke, 1948). Transplanting growing tips or whole thalli held by braded ropes on plastic racks onto concrete substrates has allowed in situ measurements of the growth of *Desmarestia* spp. (Fairhead et al., 2006) and several red macroalgal species (Schoenrock et al., 2013) over the course of six to nine weeks.

Through such methods, researchers can estimate the primary productivity of seaweed populations with greater accuracy, thus contributing to a comprehensive understanding of marine ecosystems (Allison, 2004; Johnson, 2020; see Biomass).

4.9.2.3. Microphytobenthos. Intact soft bottom assemblages are incubated in cores or chambers either in situ or under controlled light conditions in the laboratory (Glud et al., 2009; Gómez et al., 2009; Hoffmann et al., 2019; Woelfel et al., 2014; Woelfel et al., 2010; Wulff et al., 2008). The exchange of O2 and/or dissolved inorganic carbon, the incorporation of labeled carbon, O2-microsensor measurements and fluorometry (PAM) have been applied, in complementary approaches (Glud et al., 2009; McMinn et al., 2010). Transparent and black treatments are included to account for NPP, GPP and R (by adaptations of the classical light/dark bottles method). Recently, in situ chambers were deployed in the Antarctic and applied to assess Net Community Metabolism, Community Respiration and Gross Community Metabolism. These measured autotrophy and heterotrophy, as evidenced by respiration exceeding microalgal production (Braeckman et al., 2021). Hard substratum microphytobenthos and epiphytic microalgae can also be important contributors to the coastal primary production, particularly during early successional stages (Campana et al., 2018; Zacher et al., 2007a; Zacher et al., 2007b). Measurements of the functional attributes of these communities can be obtained by means of colonized artificial substrates, mimics and natural assemblages (Berlinghof et al., 2022; Campana et al., 2009; e.g. Hasegawa et al., 2007).

Laboratory measurements, carried out with clearly established light conditions (see Glud et al., 2009; Wulff et al., 2008), or in situ measurements, with sufficient coverage to overcome patchiness, can be used to assess local production rates (Braeckman et al., 2021). Data for underwater light intensity is available, allowing daily and/or seasonal production to be calculated, allowing scaling of data, particularly across latitudes.

4.9.2.4. Standardisation. It is important to set a clearly defined terminology so that studies carried out on different assemblages can be interpreted and compared (i. e. phytoplankton, macroalgae, microphytobenthos, ice algae)(see Glud et al., 2009; McMinn et al., 2012; McMinn et al., 2010). Since each method to assess primary production has its advantages and disadvantages there is not one that suits every need. Therefore, priority should be given to intercalibration exercises to allow easy and direct comparisons of primary production rates among different methods. Primary production rates should be represented in carbon mass units per unit area and time to allow for easy pooling of benthic and pelagic primary production rates. Finally, standard factors should be used to obtain carbon fixation rates in methods that need to transform the rates measured (e.g., oxygen production) into carbon mass (e.g., photosynthetic quotient).

4.10. Respiration rates

4.10.1. Definition

Aerobic metabolic rate (respiration rate) measures the O_2 consumption or CO_2 production of whole organisms or assemblages, as an assay for energy flux, and therefore carbon flux through food webs (Rowe et al., 2008; Fig. 4). Depending on the physiological state of organisms, different phases of metabolic rates can be measured (Table 10). In photosynthetic organisms, respirometry in the light measures net

Table 12
Key disturbance factors of polar blue carbon pathways.

Physical disturbance	Impact
Iceberg scour (Barnes, 2017)	Mass mortality, resetting from climax to pioneer assemblages. Higher frequency in shallows but fewer greater magnitude scours at depth. Sediment removal and destabilization, allowing higher remineralization. Maintains Beta and Gamma diversity.
Exploitation (Kock, 2007)	Harvesting of fisheries resources is currently well managed under CCAMLR but over-harvesting has disrupted high-latitude ecosystems in the past.
Human activity (Hughes et al., 2020)	Human presence impacts biodiversity through disturbance of wildlife and its behaviour, risking the introduction of invasive species or physical damage to the landscape.
Stressors	When stressors surpass species or populations threshold limit of resistance driving to increased mortality they became a disturbance.
Global warming (Morley et al., 2020)	Variable mortality and physiological response, impacting competitive balance and community structure.
Ocean acidification (Hancock et al., 2020)	Harder and more costly to produce skeletal structures. Greater dissolution of dead shells. Reducing inorganic carbon being buried below the oxic layer in sediment.
Reduced sea ice duration (Morley et al., 2020)	Increased iceberg scour, loss of pagophilic species, increased energy exchange at the surface, and potential to increase carbon capture from the atmosphere.
Sediment run-off (Fofonova et al., 2021)	Increased turbidity, reduction of primary production, food dilution, potential clogging of filter feeding mechanisms, impacting community structure (see **Sediment accumulation rates**).

primary production, which is the oxygen produced by photosynthesis minus the respiratory costs (see **Primary production**). Each technique has methodological strengths and weaknesses (Table 10).

4.10.2. Measurement

Metabolic rates represent a key assay for the flux measurement of carbon processing and cycling (Rowe et al., 2008; Fig. 4). It is important to constrain carbon fixation by photosynthesis and carbon storage in body tissues and skeletons as it is passed through the food chain of heterotrophic organisms (Rossi and Rizzo, 2020). The remineralisation of carbon, particularly through the microbial loop and by respiration are key processes that release carbon back into the carbon cycle and prevent it from passing directly along the pathway to sequestration in the sediment. However, given the prevalence of hypoxic conditions in marine environments, oxygen consumption can underestimate instantaneous rates of metabolism (Eleftheriou, 2013; Seibel, 2011).

Measurements of metabolic rate (Table 10) are logistically complex requiring access to the animals or assemblages to be measured. In the shallows, individual organisms or pelagic assemblages, can be collected and brought into the laboratory. However, collecting and measuring organisms from any depth requires special equipment capable of maintaining the pressure. To measure the respiration rates of benthic assemblages, chambers can be lowered to the sea floor or increasingly aquatic eddy covariance systems are being used to measure oxygen and carbon flux within the water column and the benthos (Berg et al., 2022) see **CO_2 fluxes**). This technology makes large-scale assemblage measurements possible and could be adopted widely as a standard method.

For photosynthetic organisms, the exchange of CO_2 and O_2 are the external manifestations of photosynthesis and respiration between algae and the water or air. The rates of the metabolic process in macroalgae can be estimated by measuring the rate of exchange of O_2 in water or CO_2 in air, or by mixing the radioactive tracer carbon, ^{14}C, with CO_2 or HCO_3^-, supply in water or air, and each method with its particular advantages and limitations (Lobban et al., 1988).

Most studies of gas exchange in water employ some version of the light- and dark-bottle technique, in which the algae or portions of them are enclosed in bottles filled with seawater (Table 11). Specifically, for respiration the bottle is completely blackened, and incubated under the time and specific conditions of interest (e.g. temperature). If oxygen is being determined by the chemical Winkler method, the incubation must be long enough for measurable change in the O_2 of the water to occur, or for the alga to accumulate measurable ^{14}C (Table 11). The Winkler method measures at the end of a fixed time, whereas the oxygen electrode technique allows continuous measurements, usually during 1 to 8 h. It is important to highlight that long incubations can generate some problems such as bacterial growth and oxygen super-saturation (Lobban et al., 1988).

4.10.3. Standardisation

Measurements of respiration, that are affected by many variables, are difficult to compare. Each measurement must be interpreted in terms of these many variables, temperature, age of the tissue, etc. For example, does a drop-in metabolic rate represent energy saving metabolic depression, or indicate that a limit has been reached and physiological systems are failing (Guppy and Withers, 1999).

Metabolic rates are widely used as a measure for testing responses to climate stressors, such as increasing temperature and lowered salinity. Hence, their adoption as a standard measure will allow comparisons with a wide body of research. To facilitate standardisation, it is important to standardise measurement (routine metabolic rate) and the units in which metabolic rate is measured (μmol O_2 g C^{-1} body mass). Body mass is typically measured as dry mass and therefore conversion factors are required to convert this into carbon (see **Biomass**).

4.11. Sediment accumulation rates

4.11.1. Definition

In order to define and constrain Sediment accumulation rates (SAR) as a metric, an understanding of several definitions and concepts is required. SAR is the rate at which particulate matter accumulates on the seafloor, causing the vertical accretion of the latter and the burial of carbon and other elements transported within the particle flux. Sediment accumulation is a reversible process with sediment subject to erosion. When expressed in terms of mass, SAR has units of mass per unit area, per unit of time. When expressed as linear accretion rather than mass accumulation, its units are length per unit time and are commonly referred as “Linear accumulation rates”.

Sediment accumulation rates are, related to, but not the same as particle settling rates in the water column, or even with deposition rates on the seafloor, since particles deposited on the seafloor undergo various processes, both biogenic and abiotic, that can dramatically alter their composition before an effective burial takes place. This metric is, however, dependent on particle “sedimentation (or settling) rates” as well as on particle composition, inflow and outflow via surface and deepwater, water column stratification, local currents and turbulence and in general the environmental and biological characteristics of the seafloor (Håkanson et al., 2004). **Burial rate** is an intrinsic component of SAR and is incorporated here. Higher sediment loads are expected in the near shore, due to higher melt water run-off as climate change leads to glacial retreat (Comiso et al., 2017; Cook and Vaughan, 2010; Meredith et al., 2018). However, the near-shore seafloor will also be subject to greater ice disturbance (see **Disturbance impacts**), reducing the chances of sediment accumulation.

4.11.2. Measurement

To measure SAR, sediment cores are extracted from the seafloor, and the layers within the core are analyzed (Baloza et al., 2022). Several natural radionuclides can be used to date the sediment collected in cores, depending on the time scale of interest. 210Pb, with a half-life of 22.3 years is an ideal tracer for dating aquatic sediments deposited within the past ~100–150 years (Arias-Ortiz et al., 2018). Assuming a constant flux of ^{210}Pb to the seabed, the excess ^{210}Pb in sediments can estimate recent SAR (approximately over the last 100 years) and assess mixing caused by bioturbation or physical processes (Appleby, 2001). For sediments with very low accumulation rates (on millennial scales), the ^{14}C method is applied (Hajdas, 2008). Artificial radionuclides, such as ^{137}Cs or ^{241}Am, are often used as independent time markers to constrain and validate ^{210}Pb radio-chronologies (Appleby, 2001). For measurements of sequestration potential (see **Defining Sequestration**) it is important to determine the depth of the oxygenated layer, as burial efficiency is strongly negatively correlated to exposure to oxygen (Sobek et al., 2009). SAR estimates need to be combined (multiplied) with organic carbon content of the deepest sediment layer to estimate organic carbon burial rate and therefore carbon sequestration.

4.11.3. Standardisation

To understand how carbon sequestration rates relate to sediment accumulation rates, depth stratified slices from sediment cores need to be dated using ^{210}PB for the last 100–150 years and 14C for older layers. Age determined organic and inorganic carbon content, sediment particle size, C:P:N ratios and stable isotopes, to help determine the origins of the carbon, should be calculated for each slice (Macreadie et al., 2019). To assess sequestration rates the depth of the anoxic layer and the age of the carbon below the oxygenated layer needs to be measured.

4.12. Carbon turnover rates

4.12.1. Definition

Carbon turnover describes the rate at which carbon is remineralised from carbon stores and forms a major component of carbon cycling,

controlling the percentage of carbon that is sequestered (Azam et al., 1991; Evans et al., 2021). It quantifies the breakdown of fixed carbon, but also the recycling of carbon through secondary and tertiary consumers, as respiration costs for maintenance (Evans et al., 2021 see Respiration rates) and producing body tissues (see **Secondary production**) and skeletons (see **Inorganic carbon stocks**).

In the pelagic realm, the majority of carbon fixed by primary producers is remineralised by break down of the phytoplankton through the microbial or viral loops (Evans et al., 2021). It is only if this carbon sinks to depths below the permanent thermocline that it can remain at depth where it can be stored for long enough that it will not be returned to the surface for more than 100 s or 1000s of years (Cavan et al., 2019).

Once POC (see **Particulate organic carbon**) settles onto the benthos, benthic carbon turnover becomes important to bentho-pelagic coupling, as the exchange of carbon between the water (column and interstitial) and sediments. The main drivers for this exchange are:

(1) inputs in the form of carbon deposition to the sediment by settling particulate matter (see **Sediment accumulation rates**). In sediment areas (shallow), microphytobenthic primary production may contribute to carbon accumulation (see **Primary production**).
(2) fluxes in the form of carbon remineralisation of decaying material by metazoans, protozoans and prokaryotes (i.e. the microbial loop - Bacteria and Archaea; Evans et al., 2021). In selected sediment areas, epifauna and large infauna may play an important role in re-mineralisation and respiration (see Respiration rates) and also through sediment ventilation and irrigation, mixing oxygen into sediments through bioturbation (Solan et al., 2019).

Both these fluxes can be expressed as rates of Carbon flux by mass over time and space e.g. g C m^{-2} yr^{-1}. If the carbon flux to the water column from the sediment is less than the input through sedimentation, the sediment acts as a sink.

Generally assuming some form of steady state, the overall turnover time from sediments will be a function of total carbon content over influx or outflux per annum - expressed as unit Carbon per unit area per unit time.

4.13. Measurement

4.13.1. Direct measures

The carbon fixed can be measured through primary production (see Primary Production), modified by respiration rates (see Respiration rates) as a proxy for microbial and viral breakdown (Evans et al., 2021). These result in sedimentation of POC (see **Sediment accumulation rates**) and determines the biomass that reaches organisms that store carbon both in the water column and on the seafloor (see **Biomass**). The flux can most easily be measured through respiration rates (see Respiration rates) or by tracking water chemistry (Henley et al., 2012).

4.13.2. Standardisation

To allow for direct comparisons across different sites and studies, all fluxes, inputs, and outputs should be reported in standardised units, as grams of carbon per square meter per year (g C m^{-2} yr^{-1}).

Carbon turnover rates are measured by combining many of the other metrics. It therefore relies on the standardisation of these input metrics, with consistent units.

4.14. Disturbance impact

4.14.1. Definition

Ecological disturbance refers to a discrete event (Pickett and White, 1985) leading to relatively sudden loss of biomass that will alter the stability, structure, performance, function or behaviour of an ecosystem, a community, or a population. This disturbance will alter relative survival, the availability of resources, or habitat suitability, therefore altering carbon pathways (Jentsch and White, 2019; Peters et al., 2011; Pickett et al., 1989). Consequently, disturbance is distinguished from stress, that affects the fitness of an organism population or species. (Burton et al., 2020). Multiple biological and non-biological factors can lead to disturbance, with both natural and anthropogenic origins (Table 12). Disturbance is an important driver of many other blue carbon metrics, particularly **Biomass**, **Species composition**, **Habitat type**, and **Functional groups**.

The frequency and magnitude of disturbance events define their impact, and are crucial to the ability of ecosystems to recover (e.g. (Zwerschke et al., 2021)). All ecosystems have evolved to cope with naturally experienced levels of disturbance, which often increase the Beta and Gamma diversity, increasing ecosystem complexity and stability, increasing the potential for carbon storage (Barnes and Sands, 2017; Jentsch and White, 2019; Marina et al., 2024b; Morley et al., 2022a; Robinson et al., 2021). When the disturbance frequency moves beyond the evolutionary norm of ecological disturbance, due to increased anthropogenic activity or changing climate, impacts will be seen on blue carbon pathways.

The magnitude and frequency of the disturbance determine whether the ecosystem will return to its previous state or shift to a new stable state (Zwerschke et al., 2021). Understanding how ecosystems respond to current levels of disturbance provides a framework for modelling the resilience of carbon pathways under predicted future disturbance regimes.

4.14.2. Measurement and Standardisation

Two main steps are required to standardise measurements of disturbance frequency.

1) Identify the key disturbance factor in each location of interest. Within the Antarctic, iceberg disturbance and sediment run-off are two of the main disturbance factors affecting biomass and species composition at individual to community levels respectively (Morley et al., 2020; Neder et al., 2024; Teixidó et al., 2007). Anthropogenic disturbance is likely to gain importance at lower latitudes, but increasing levels of human activity could also have a substantial impact.

2) Identify the spatial and temporal scale over which the disturbance acts. This requires a specific knowledge of the system components and the natural frequency of the disturbance so that measurements are taken at the right scale. Also to determine the smallest ecological entity affected by the disturbance (i.e. individual, population, community, ecosystem), and its affected attribute (e.g. mortality, growth, genetic structure, coexistence, resilience, connectedness).

4.15. Secondary production

4.15.1. Definition

Secondary production refers to the conversion of biomass, with losses, by heterotrophic organisms (those that consume organic matter) from the consumption of primary producers (such as phytoplankton and macroalgae) or other organic matter. The increase in heterotrophic complexity promotes a more efficient transfer of carbon to higher trophic levels (Steinberg and Landry, 2017), and, eventually, to sequestration in sediments.

4.15.2. Measurement

Secondary production is expressed as consumer incorporation of organic matter or energy per unit time. Measuring secondary production involves quantifying the growth (see **Growth**) and reproduction of heterotrophic organisms (including zooplankton, benthic invertebrates, and higher trophic levels like fish), that consume primary producers or organic matter. Some common methods to measure secondary production are reviewed in (Dolbeth et al., 2012).

4.15.3. Direct measures

The most direct way of measuring secondary production, is through cohort or size-based analysis, in which a group (cohort) of individuals of the same species and similar age or size are tracked over time. Ideally this would be reported in g C^{-1} unit $time^{-1}$. This tracking involves regular sampling of the population to measure changes in biomass, size and number of individuals, to estimate growth and mortality rates. In animals with skeletal structures annual growth rings can be validated and used to measure annual growth rates (Barnes, 1995). In many cases, this direct method is not practically feasible, and indirect methods are applied to estimate secondary production.

4.15.4. Indirect measures

Two examples of indirect methods can be applied: (1) using empirically established ratio of production to biomass (P/B) for a population (Brey, 1990) and (2) bioenergetic models. These models use energy budget equations to estimate secondary production, balancing energy intake and allocation and growth efficiency, e.g. Dynamic Energy Budget models (Kooijman, 2000) or Linear Inverse models (Soetaert and van Oevelen, 2009).

4.15.5. Standardisation

Due to the complexity of measuring growth rates in the field modelling is essential to scale from regions with higher resolution data, typically around research stations (see **Growth Rates** and **Modelling blue carbon pathways**).

4.16. CO_2 air-sea fluxes

4.16.1. Definition

Air-sea CO_2 fluxes refer to the exchange of carbon dioxide (CO_2) between the atmosphere and the ocean, playing a key role in the Earth's climate system and carbon cycle. Measuring CO_2 fluxes between the ocean and the atmosphere is a crucial step for understanding and estimating coastal and marine blue carbon, as well as its connection to climate change. CO_2 fluxes occur when there is an imbalance between surface waters and the atmosphere CO_2 concentrations. This difference between the partial pressure of CO_2 in seawater and the overlying air represents the thermodynamic driving potential for the CO_2 transfer across the sea surface sea-air layer. The sea-air pCO_2 difference (seawater minus air) positive values indicate the oceanic areas where there is a net release of CO_2 into the atmosphere, and the negative values indicate regions where there is a net uptake of CO_2 (Feely et al., 2001). Normally the imbalance in pCO_2 is generated by CO_2 uptake in surface waters by phytoplankton during photosynthesis or by upwelling of old waters masses enriched in CO_2, generating situations when the ocean acts as a sink or source of CO_2 (e.g., (Gray et al., 2018). The sea-air pCO_2 difference controls the direction of the CO_2 flux while the magnitude of the flux depends mainly on wind speed over the ocean and to a lesser extent on the magnitude of the pCO_2 difference (Nicholson et al., 2022; Nightingale et al., 2000; Wanninkhof et al., 2009).

Monitoring air-sea CO_2 flux is the first step to assessing the potential role of marine ecosystems as carbon sinks. These fluxes are also driven by the solubility of CO_2 in seawater which depends on the salinity and especially seawater temperature. Less saline and cold waters, like the ones in the Southern Ocean, can capture and transport large quantities of dissolved CO_2 without any biological activity; this is called the solubility carbon pump (Ito and Follows, 2003); it represents the largest fraction of CO_2 capture by the Southern Ocean (Henley et al., 2020). On the other hand, when primary producers uptake CO_2 in surface waters during photosynthesis, it enters what is called the biological carbon pump (Azam, 1998) where the carbon is removed from surface waters, by biological activity, and transported into deeper layers of the ocean even reaching the seabed and marine sediments where carbon may be sequestered. Over the last decades our understanding of the biological carbon pump has grown noticeably, including the activity of other groups beyond phytoplankton and metazoan zooplankton: the viral shunt (Weitz and Wilhelm, 2012), the microbial pump (Jiao and Azam, 2011), and the fungal shunt (Klawonn et al., 2021).

Air-sea CO_2 fluxes are a crucial step determining the marine carbon cycle hence it is key to monitor them to assess the potential role of marine ecosystems as carbon sinks. Besides, air-sea CO_2 fluxes depend on several climate change-related processes, such as wind patterns, ocean warming and shifts in ocean circulation, among others.

4.16.2. Measurement

4.16.2.1. Direct measures. Measuring CO_2 fluxes (e.g., mmol C m^{-2} d^{-1}) involves employing various techniques to capture the dynamic exchange at the air-sea interface. One method is the eddy covariance technique (Watts et al., 2022), which directly measures the turbulent exchange of CO_2 between the two mediums. This method utilizes fast-response gas analysers installed on towers or buoys to continuously monitor fluctuations in CO_2 concentration, allowing for real-time assessment of flux rates. However, differences in global standardisation of the method make results difficult to compare (Table 11).

Another approach involves the deployment of floating chambers or drifting platforms that enclose a known volume of water, capturing the CO_2 emitted or absorbed during a specific timeframe (Lorke et al., 2015). By analysing the changes in CO_2 concentration within these chambers, flux rates can be estimated.

The most common method to determine CO_2 fluxes, assess surface water pCO_2. This can be achieved by collecting seawater samples close to the surface and obtaining its pCO_2 (e.g., (Höfer et al., 2019)) or by instruments equipped with gas sensors can directly assess seawater pCO_2 (Moreau et al., 2013; Moreau et al., 2015; Schloss et al., 2007). These sensors can be deployed or mounted in ships (Mo et al., 2023), biogeochemical floats (Gray et al., 2018) and autonomous surface vehicles (Sutton et al., 2021) greatly enhancing our ability to increase the spatial coverage of our observations in remote locations like the Southern Ocean. Similarly, gas sensors can be deployed in oceanographic moorings to monitor seawater pCO_2 with a high temporal resolution (Shadwick et al., 2021; Vellojin et al., 2022). Along with seawater pCO_2 measurements atmospheric measurements of pCO_2 and wind speed are needed to assess air-sea CO_2 fluxes. The combination of all these methods is needed to generate composites that better register the natural variability in air-sea CO_2 fluxes.

4.16.2.2. Indirect measures. Remote sensing technologies, such as satellites and aerial drones, are increasingly significant tools for studying the role of large-scale CO_2 fluxes monitoring. Satellite sensors can simultaneously detect sea surface temperature (infrared), chlorophyll concentration (visible spectrum), and sea surface height (lidar sensors), contributing valuable data to estimate flux rates over extensive oceanic areas (Liu et al., 2022).

Furthermore, oceanographic models and machine learning techniques help simulate CO_2 fluxes by integrating various parameters such as sea surface temperature, wind speed, and biological activity. These models enable researchers to extrapolate flux estimates on broader spatial and temporal scales.

Further standardisation should involve combining these diverse methodologies allowing for a comprehensive assessment of CO_2 fluxes between the ocean and the atmosphere. Furthermore, fieldwork can also include net and gross primary production (see **Primary Production**) and community respiration measurements (see **Respiration rates**) to quantify the role of the photoautotrophic and micro-heterotrophic biological carbon community pump has in CO_2 dynamics (Latorre et al., 2023a). This multidisciplinary approach enhances our understanding of the intricate complex interactions occurring at the air-sea interface and provides essential insights for climate change research and the sustainable management of marine ecosystems.

4.16.3. Standardisation

Over the last years the spatial coverage of CO_2 data for high latitudes in the southern hemisphere has improved considerably due to the deployment of biogeochemical floats in the Southern Ocean (e.g., Mazloff et al., 2023). Therefore, our current efforts should be more focused on generating year-round, high-resolution, uninterrupted pCO_2 records in areas where these datasets are lacking like Antarctic coastal waters. These records are essential to validate and improve parametrizations as well as characterize uncertainties in satellite data and models (Swart et al., 2019). Simultaneously, efforts to monitor atmospheric pCO_2 should be maintain like for example the NOAA Global Monitoring Lab (https://gml.noaa.gov/about/research.html#carboncycle).

Standardisation of wind products and gas exchange parametrizations used when calculating CO_2 air-sea fluxes needs to improve since the selection of these parameters significantly increase (~600 %) the uncertainties associated with the estimation of CO_2 air-sea fluxes (Henson et al., 2024).

4.17. Dissolved organic carbon (DOC)

4.17.1. Definition

Dissolved organic carbon (DOC) in marine environments refers to the complex mixture of organic compounds, such as proteins, carbohydrates, and lipids, that is dissolved in seawater, representing a fraction of the total organic carbon (TOC), which is also a fraction of the dissolved organic matter (DOM), which includes other key biogeochemical cycles (e.g. Fe, N, P; Henley et al., 2020). These carbon pool plays a crucial role in the marine carbon cycle, influencing the ocean's biological, chemical, and physical characteristics (Lønborg et al., 2020). Marine DOC is produced through various processes, including organic matter input from terrestrial sources, exudation from marine organisms, and microbial degradation of organic material (Samui et al., 2020; Thomas et al., 2001). Terrigenous inputs, such as riverine discharge and run-off, contribute organic carbon to the marine environment. Autotrophic organisms, like phytoplankton, also release organic compounds through exudation, adding DOC to the mix. Microbial degradation of particulate organic matter further contributes to the pool of DOC.

4.17.2. Measurement

Marine DOC is mostly produced in the euphotic zone, by phytoplankton carbon fixation, with much of it recycled through the microbial loop or degraded at the ocean surface by UV radiation (Sarmiento and Gruber, 2006). Hence, measurements need to describe both its distribution and dynamics. Common methods include high-temperature combustion, where the carbon is oxidized to carbon dioxide, and the resulting gas is measured. UV-absorbance and fluorescence spectroscopy are also employed, capitalizing on the absorbance and fluorescence properties of DOC. These techniques provide insights into seawater DOC concentration and composition. Some other new indirect techniques consider remote sensing images for the development of an artificial neural network based model to estimate DOC in open ocean accounting for optical water classes, sea surface temperature, mixed layer depth, absorption coefficient of Coloured Dissolved Organic Matter, and chlorophyll-a (Bonelli et al., 2022).

Marine DOC serves as a significant carbon sink. This has implications for the global carbon cycle and climate regulation. While the carbon stored in marine DOC is vulnerable to microbial degradation, some fractions can persist for extended periods, effectively sequestering carbon in the deep ocean. Understanding the dynamics of marine DOC as a carbon sink is crucial for comprehending the overall carbon balance in the oceans and its impact on climate change mitigation. Moreover, the fate of marine DOC has implications for nutrient cycling, microbial ecology, and overall marine ecosystem health.

4.17.3. Standardisation

Innovation will be key to scaling up measurements of DOC and their fluxes in the Southern Ocean and therefore gaining a greater understanding of the variability (Boyd et al., 2024). The use of autonomous measuring platforms will be essential to provide high resolution spatial and temporal measurements (Boyd et al., 2024). Numerical models of the fate of DOC will help to identify priority areas for these models.

4.18. Growth rates

4.18.1. Definition

The growth rate is defined as the increase in a size and/or **Biomass** estimator through a specific period of time. Within the framework of carbon estimations, it can also be considered as the increase of carbon storage in any level of biological organisation (body tissue, population or community biomass). **Primary** and **Secondary production** of multicellular organisms are major components of growth.

4.18.2. Measurement

Widespread methods to estimate the growth of individual organisms consist of relatively simple mathematical approaches. Growth is often reported as absolute (gain per day), relative (percentage increase in size) or specific growth rate (percentage increase in size per day, SGR) (Lugert et al., 2016). For example, SGR has been applied to assess the growth of diverse taxa such as fish and macroalgae, by means of the function.

Nevertheless, and since growth rate varies along the ontogeny of an organism— typically, organisms grow at a faster rate when young, and growth progressively diminishes or ceases as they age—a mathematical equation or growth model, such as von Bertalanffy growth function, is applied to empirical data to quantify growth (Brey, 1999). Often, this calculation is closely tied to biomass estimation. Methods based on von Bertalanffy growth function have been applied to a diverse taxonomic range of organisms (fish, mammals and invertebrates), by recording a size increment such as area, weight, length, width, among others, over time (Von Bertalanffy, 1948; Von Bertalanffy, 1957).

Reporting of ecological relationships with length (e.g. size at first reproduction) is well established (Lugert et al., 2016; Wiencke, 1990). However, depending on the organism under study, different measures can be used as proxies for growth. In addition to length, the most commonly used include: height or width of the organism or a part of it (such as shell length), weight or mass, growth rings, etc. The choice of the growth proxy will depend on data availability, ease of measurement, variability of the proxy, and biological relevance to the species under study. It is important to select appropriate measures for the biological characteristics and life cycle of the organism under study.

A special case to be considered are calcifying organisms such as coralline algae and a diverse variety of invertebrates. They play a very important role in the carbon cycle, as their carbonate structures, often composed of $CaCO_3$ or other mineralized materials, remain in the environment and can be buried for geological periods of time, being sequestered into sediments (Feng et al., 2023; Filgueira et al., 2019; McCoy and Kamenos, 2015). In coralline algae, calcification rate is directly related to photosynthetic rate (McCoy and Kamenos, 2015) so both non-photosynthetic and photosynthetic tissues need to be evaluated. For invertebrates with carbonate structures, it is indeed important to consider the growth rates of both the soft tissues and the exoskeleton as they are both proxies for growth. Furthermore, the growth of the soft tissues and the exoskeleton may not occur at the same rate.

The variable used to estimate growth can be obtained through direct estimations from experimental studies under standardised controlled conditions or from field sampling utilising repeated measurements of the same organism.

4.18.3. Measurements in the laboratory

Organisms can be maintained in laboratory aquaria under controlled levels of nutrients, food and environmental conditions. In this way, desired variables such as weight, size, etc., can be measured at various time points throughout the study. As an example, macroalgae specific

growth rates can be obtained by cultivation of even small portions of the thalli (Fortes and Lüning, 1980) as well as using the entire organism (Wiencke, 1990). For calcifying primary producers such as coralline algae, crust thickness, vertical growth and annual or seasonal growth bands are considered proxies for growth (McCoy and Kamenos, 2015).

The growth rate of invertebrates with $CaCO_3$ exoskeletons is usually measured by labelling calcium in tissues with stains, such as calcein, alizarin red or tetracycline hydrochloride (Achilleos and Smith, 2023; Clarke et al., 2004; Sato-Okoshi and Okoshi, 2008). These chemicals are incorporated into growing $CaCO_3$ structures, creating a growth mark that brightly fluoresces upon excitation. The staining does not affect the organism's growth, and the mark serves as a reference to monitor its growth over time.

4.18.4. Measurements in the field

The techniques of capturing, tagging and recapturing individuals (Achilleos and Smith, 2023) or using 3D Photogrammetric Reconstruction (Prado et al., 2021) are usually applied. Repeated measurements of marked individuals can be used to track growth in their environment (e.g. Parke, 1948; Peck and Bullough, 1993). These non-destructive methods that can be applied depending on the size or robustness of the organisms. For instance, the punching hole method (Parke, 1948) consists of measuring the progressive distance between perforations of macroalgal thalli over time and it is relatively widespread to assess macroalgal growth (e.g. Matsson et al., 2021; see Primary production).

Another method for collecting growth-related variables in the field, albeit a destructive approach, entails extracting and dissecting organisms. This allows for measurements of growth-related proxies in each organism and age determination. For instance, in fish, otoliths are frequently used to determine age by analysing growth rings patterns since they contain a complete record of growth from hatching to capture (La Mesa and Eastman, 2024; White, 1991). Similarly, in molluscs and certain crustaceans, the growth rings, or bands, on their shells, eyestalks or gastric mill, offer valuable insights into their age and growth patterns (Choi et al., 2023; Lomovasky et al., 2020). However, this method may not be universally applied since it is species-specific and deposition rates need to be calibrated (e.g. Becker et al., 2018).

The population growth rate (i.e. the rate of increase or per capita growth rate: (r) is defined as the birth rate (b) minus the death rate (d) divided by the initial population size (N_0) and it can also be expressed as a percentage. The specific growth rate (r) has been estimated from exponential and logistic models and it expresses the contribution of each individual to the population growth (i.e. biomass increase, per unit of time, per unit of biomass) and it can be highly dependent on the biomass descriptor (Grimaud et al., 2017). For primary producers, species-specific growth rates can be calculated using chlorophyll-a measurements, cell counts, carbon incorporation (e.g., ^{14}C) and in vivo fluorescence (see **Biomass** and **Primary production**).

At higher organisation levels, such as phytoplankton or microphytobenthos, species-specific growth rates are calculated using monocultures of dominant species or key organisms. Indeed, deterministic models have been largely applied to represent the effects of temperature and other environmental factors such as light or nutrients (Grimaud et al., 2017). Furthermore, conceptual models for communities/assemblages' growth have been developed to account for these effects, see (Schloss et al., 2002). Despite high nutrient concentrations prevailing in Antarctic coastal sites, the physical factors affecting the underwater radiation and the depth of vertical turbulent mixing play a key role in limiting phytoplankton growth (Schloss et al., 2002). However, an unusually adequate light, mixing environment driven by anomalously cold air temperature and local eastern winds, have also been attributed as drivers of phytoplankton blooms (Schloss et al., 2014).

4.18.5. Standardisation

When available, species-specific growth rates should be combined with field sampling and be used to estimate local- and even global-scale key metrics such as primary production (Duarte et al., 2022). Temperature is a key factor influencing growth rate at every level of organisation, from individuals to communities (e.g. (Grimaud et al., 2017) and understanding its effects should therefore be prioritised.

Particularly for Antarctic organisms, seasonality of the growth processes should be considered, as it can be highly seasonal and either be restricted to a short period of adequate light, nutrients and food supplies or be decoupled and fuelled by stored reserves (Peck, 2018; Wiencke, 1990).

Calcifying organisms play a key role in inorganic carbon burial and immobilization (Feng et al., 2023; Filgueira et al., 2019; McCoy and Kamenos, 2015). Nevertheless, when calculating the carbon balance, it is important to quantify not only the carbon sequestered as $CaCO_3$ but also the CO_2 released in respiration (see **Respiration rate**) and biogenic calcification resulting in the construction of carbonate structures like exoskeletons, crusts, among others (Filgueira et al., 2019; see Inorganic carbon stocks).

In general, community level estimations of growth rates are more appropriately defined as production measurements, based on the change of biomass or photosynthesis estimators (oxygen, fluorescence, chlorophyll) over time (e.g. Underwood, 2001; see Primary production).

As growth is nonlinear, it is probably more appropriate to compare growth using single parameters from the growth function in a statistical analysis (Brey, 1999). The Growth Performance Index (ϕ'), derived from the Bertalanffy growth function, makes growth comparable between populations and species by removing individual variation and is defined as the point of inflection on the von Bertalanffy growth curve (Brey, 1999). By calculating ϕ' for different species or populations, researchers can standardise growth and comparatively evaluate between different groups or species, facilitating the analysis of patterns, trends, and differences in growth performance (Reed et al., 2021). Growth performance is calculated from the equation where k is the growth co-efficient and L_∞ is asymptotic size.

$$\phi' = log(kL_\infty)$$

To standardise assessment of the environmental drivers and forcing factors affecting growth rate continuous monitoring using automated sensors for parameters like chlorophyll fluorescence or optical density in the case of plankton, will give an indication of the growth rate. Taking into account the environmental conditions conforming an habitat type in the sampling design is crucial and the level of spatial and temporal resolution depends on the species and population under study (see **Habitat type**) For instance, for a species with an extensive distribution spanning diverse environments, the calculation must be performed separately for each specific environment. Applying habitat suitability models contribute to determining species distribution (see **Modelling blue carbon pathways**).

4.19. Downward particle flux

4.19.1. Definition

In the context of blue carbon pathways, downward particle fluxes (DPF) describe the rate at which POC settles through the water column, from carbon fixation in the surface waters to the seafloor. The rate at which the gravitational and the various biological pumps transport inorganic and organic solids from the surface to the seafloor (see **Export and migration**), will determine their residence time in the water column and therefore the proportion that is remineralised (see **Carbon turnover rates**) and is a key factor in the rate at which carbon effectively accumulates in the sediments (see **Sediment Accumulation Rates**).

The incorporation of particle sinking into an ecosystem and nutrient cycling model is crucial, as sinking speed estimates are key to nutrient and biomass fluxes. Mao et al. (2023) suggested that phytoplankton cell sinking rates under different marine conditions are closely related to cell

size and carbon biomass (Bienfang, 1981).

It must be noted that, except on short time scales or where settling rates are very fast, in general the carbon fluxes reported by particle traps are substantially different (often lower) than **Sediment Accumulation Rates,** given the biological and chemical transformations that POC may undergo once it reaches the seafloor and until it is buried for significant periods of time. The former can, under certain conditions, be in fact, greater owing to lateral transfer (**Export and migration**).

4.19.2. Field measurements

4.19.2.1. Direct measurement. Sediment traps or particle traps are the most widespread method for measuring DPF (Alurralde et al., 2020; Honjo et al., 2008; Isla et al., 2002; Steinberg et al., 2001). Sediment traps can be deployed using different methodologies, including either being surface-tethered or anchored to the bottom. When sediment traps are deployed close to the seafloor, resuspension and nepheloid layers must be taken into account as they bias measurements of the flux of carbon involved in the downward 'pumps'.

Sediment traps are subject to a long number of biases that are not entirely resolved. In most field conditions encountered in marine environments, a passive, truly vertical collection of particles is precluded, and the final trapping of particles is rather the result of a water exchange process at the trap's mouth, governed by turbulence and lateral shear. Early studies (Gardner, 1980a; Gardner, 1980b) on the hydrodynamics of particle collectors determined the cylindrical shape to be the most efficient geometry. Aspect ratios (ratio of cylinder's height and diameter) higher than 2.5 are preferred. It is a good idea to monitor contextual parameters such as inclination of the trap from the vertical (inclinometers) or the current speed (current meters), both of which can substantially bias the trap collection efficiency. Freely drifting traps (e.g. Miquel et al., 2015) are an alternative that removes most of the horizontal shear. Another approach to minimize hydrodynamic biases due to flow over the trap mouth, consists in the use of neutrally buoyant traps (Buesseler et al., 2007).

Another critical parameter is the fixation agent used on trap samples (Knauer et al., 1984). Very short deployments can afford to avoid any preserving agent at all, while long-term ones need then to avoid or slow down the bacterial remineralization of organic matter and deter grazing by swimming animals. The most widely used is diluted (approx. 2 %, in filtered seawater) and buffered formaldehyde, which nonetheless precludes certain biochemical analysis on the samples.

The nekton, or so-called 'swimmers' (see e.g. Pagès et al., 2007), i.e. those organisms that are deemed to have entered the traps actively, must be carefully removed because they are not part of the passive, gravitational flux that traps are expected to collect. But, to further complicate things, part of the large zooplankton can actually be part of the sinking flux, i.e., corpses (see Ivory et al., 2014).

4.19.2.2. Indirect measurement. An indirect measurement, that can also be used to attempt to calibrate trap fluxes relies on the ^{238}Uranium to ^{234}Thorium radionuclide disequilibrium (Buesseler et al., 2007). ^{238}U is very soluble and thus has a conservative behaviour in seawater, whereas ^{234}Th is highly particle reactive and so comparisons of the ratio of ^{238}U:^{234}Th can indicate the deficiency of ^{234}Th in the surface waters and therefore the flux towards the seabed, which combined with POC determination provides an estimation of POC flux (Coppola et al., 2002).

Table 13
Units for measuring faecal pellet production and export.

	Faecal pellet measure	Units
Production rate	daily carbon excreted per individual	mgC ind^{-1} d^{-1}
Export	Total carbon	mgC L^{-1} or m^{-3} mgC m^{-2} d^{-1}
	Total number of intact pellets	number L^{-1} or m^{-3} number m^{-2} d^{-1}
	Total volume of intact (and broken pieces)	ml L^{-1} or m^{-3}

4.19.2.3. Laboratory measurements. The SETCOL (settling columns) is one laboratory method that can help to assess the role of phytoplankton functional groups and the potential influence of different environmental conditions such as temperature or light on settling rates. The average sinking rate of the population is calculated by measuring how the vertical distribution of the biomass changes over a given period, using the SETCOL equations. While the SETCOL method is low-cost, comparisons with a novel video-based method suggests that SETCOL may underestimate sinking speed (Du Clos and Gemmell, 2024).

4.19.3. Standardisation

Comparison between direct, indirect and laboratory measurements to estimate the downward particle flux is not complicated. Therefore, the used methods should be very well documented. In addition to the methods described above innovative use of optical measuring devices is allowing particle sinking rate to be measured in-situ (Giering et al., 2020). These can be deployed on CTD's and other commonly used ocean sampling equipment allowing measurements throughout the water column. This information can be used to scale up the temporal information gained from sediment traps. Interpretation of optical measurements can be complicated (Giering et al., 2020) but a focus on calibration of such devices will greatly increase the capability for measuring downward particle flux. In the end, the downward particle flux should be expressed in units of carbon per unit of area per time.

4.20. Species composition

4.20.1. Definition

Species composition refers to the identity and abundance of different species (or taxa when the organism cannot be identified to species level) within an assemblage, community, or ecosystem in a particular spatial and temporal distribution. A known species composition enables biomass estimation (see **Biomass**) and assemblage function (see **Functional groups**) influences processes such as carbon fixation, transport, storage, and sinking (Fig. 3).

4.20.2. Measurement

Assemblage properties such as richness, diversity, and structure have shown a strong correlation with carbon fixation, storage, and sequestration (Barnes and Sands, 2017; Morley et al., 2022a). Therefore, standardisation of methods and metrics is crucial for accurate C budget assessments.

Species composition can be assessed by three main metrics:

- **Species richness**: is the inventory list of species present in the system, measured on quantitative and qualitative samples that requires species identification to the lowest possible taxonomic level. It can be expressed with different indexes: (a) S: species number, (b) The Margalef index (I) that relates the species number to the total individuals $I = \frac{S'-1}{LnN}$ sampled, facilitates comparisons between different sample sizes.

Where S' = total number of species and N is the total number of individuals in the sample.

- **Diversity:** measures both, species present (richness) and their relative abundances within samples. The metric requires species identification and determination of abundances expressed in terms of densities (individuals or colonies per area, surface, or volume), percentage cover, or ideally, their biomass expressed in terms of carbon. Diversity can be expressed by indexes that reduce the dimensionality of the information to a single number-index. Several

Table 14
Methods for measuring IRs.

	Method	Strengths	Weaknesses	Citation
Ingestion or feeding rate	Gut content analysis along with estimation of digestion time	It measures in situ feeding rates. It is cheap and samples for this method are easy to collect It only requires low maintenance and well-established equipment such as nets and dredges	It is only applicable for carnivorous organisms. Organisms collected for gut content analysis may regurgitate/defecate it due to stress during its capture. It is highly dependent in the correct estimation of digestion time for each prey type It is biased towards preys with hard parts that are recognizable as gut items. It underestimates feeding on preys without hard parts. Processing gut content samples is labour intensive.	(Feigenbaum and Maris, 1984) (Paffenhöfer, 1988)
Ingestion or feeding rate	Gut fluorescence method	It measures in situ feeding rates. It is relatively cheap and samples for this method are easy to collect	It is only applicable for herbivorous organisms. Organisms collected for gut content analysis may regurgitate/defecate it due to stress during its capture. It is highly dependent in the correct estimation of gut clearance rate Logistically more complex.	(Mackas and Bohrer, 1976)
Clearance rate	Laboratory (incubation in chamber with known conc. of particulate food) Field (sealed chamber over natural assemblage with natural food concentration)	Reproducible and easy to control Undisturbed natural assemblage, likely to measure closer to natural clearance rate	May not measure "natural" feeding rates Logistically complex. Measures clearance rate of mixture of species	(Cheng et al., 2018) (Hansen et al., 2011)
Filtration rate (utilising clearance rates and pumping rates)	Laboratory (direct observations e.g. of bryozoans) Field (Direct observations e.g. of sponges	High resolution No manipulation and measured under natural conditions	Technically challenging Technically challenging	(Best and Thorpe, 1983; Kowalke, 1999) (Yahel et al., 2005)
Measuring change in food mass consumed	Laboratory	Accurate estimates of consumption	Potential errors due to mass loss during feeding	(Morley et al., 2016)

indexes have been developed and proposed, each with particular advantages and limitations, offering value for specific assemblages and highlighting different information such as the dominance of species, evenness or richness relative to abundance (Roswell et al., 2021; Santini et al., 2017). Among numerous indexes, and despite its drawbacks the most used across spatial scales for an extensive period, enabling valid comparisons among studies, has been the Shannon-Wiener (H′) index (Magurran, 2013). An improvement to deal with the non-linearity of the diversity index has been the introduction of Hill numbers, although the ecological relevance of this transformation is being debated (Ricotta and Feoli, 2024).

- **Structure:** This metric is complex and can be expressed in various ways based on quantitative and semiquantitative samples, making comparisons between studies challenging. Determining the assemblage structure requires the same measures as diversity. It relies on species richness and their relative abundances, resulting in multidimensional information rather than a single index. Typically, two or three dimensions are sufficient to capture the assemblage structure (Azovsky, 2009). Since this information is not expressed into a single number but as a multivariate approach, we recommend that basic information such as species and their relative abundances be available for further analysis and comparisons across spatial and temporal scales by reanalysing sample sets together.

4.20.3. Standardisation

As mentioned above, measurement of species composition will need the combination of **Species composition** and the determination of their abundance as well, ideally, their biomass expressed in terms of carbon (see **Biomass**), within certain boundaries of the ecosystem, for example, by depth, area, or habitat type. A variety of methods can be applied to assess species composition including:

a) The morphological identification of species/taxa from live catches (nets, cores, grabs) together with counts to determine abundances in the visible range or under the stereo- or optical microscope. The target community includes plankton, nekton, and benthos. Abundance per cubic meter can be measured using horizontal net hauls (e.g., multinet) which allows the sampling of multiple layers, separated by depth bands or hydrology. Mesh size is crucial, with a smaller mesh size recommended for accurate plankton analysis. Cell concentration has been widely recognized as inadequate for the estimation of the phytoplankton community (Olenina et al., 2006), and biovolume is considered more appropriate, as it integrates cell number and cell volume. Cell volumes can be calculated from cell size and shape using appropriate geometric formulas. For small-size communities (i.e. phytoplankton, microphytobenthos, zooplankton, in- and meiofauna) automated imaging methods such as *Planktoscope* (Pollina et al., 2022) or *Zooscan* (Grosjean et al., 2004) can be applied using identification and measurement software to determine the species, their abundances, and biovolumes. The application of (semi-)automated methods requires an exhaustive calibration for species identification, in each region, which requires an appropriate

level of expertise. For example: flow-cytometry (e.g., Imaging FlowCytobot, IFCB; (Olson and Sosik, 2007) allows for the characterization of cell types and the determination of abundance for picoplankton, bacteria, and archaea. These types of techniques use three-dimensional image data classification and object recognition methods (e.g., Convolutional Neural Network, CNN) for species identification. Traditional morphological identification can be supplemented with optical semi-automated methods using laser light scattering (Laser Optical Plankton Counter; Herman et al., 2004) or high-resolution images of particles (Underwater Vision Profiler; Picheral et al., 2022). These are less time-consuming methods with broader spatial coverage for size classes and dominant fractions in a community, contributing to total abundance, though calibration is essential for reliability.

b) Molecular studies like (meta-)barcoding applied to live catch samples, and environmental DNA (eDNA) from seawater or sediment samples can identify species, from DNA present in the sample that can be amplified with taxa-specific or universal primers (Zaiko et al., 2018). Unlike conventional methods, eDNA metabarcoding offers the advantage of being non-invasive and is useful for targeted early detection of species identified as high risk invasive species, as well as elusive or threatened taxa (Taberlet et al., 2018). However, the sequences of many species are still missing from databases, or misidentified, (Cowart et al., 2018) and at best eDNA will only identify a sub-set of the species that are there.

c) Indirect (non-invasive) observational methods for the identification of species and simultaneous determination of abundances (see **Biomass**).

d) Passive acoustics to identify vocal fauna such as marine mammals and UAVs for terrestrial surveys.

Balancing the strengths of each methodology is crucial for obtaining a comprehensive understanding of the complex marine ecosystem. The classical morphological identification of microscopic species can be challenging or even impossible, as taxonomic investigations are still necessary to clarify uncertainties in the identification and nomenclatural position of several taxa. For all these methods and the resulting metrics, a thorough understanding of the species composition in the study area is essential, if not imperative, to accurately recognize, discern, and interpret the ecosystem's changing status.

4.21. Faecal production rate

4.21.1. Definition

Zooplankton and benthic animals excrete waste products as both particulate and dissolved material. Faecal pellets (FP) are released by zooplankton (both protozoans and metazoans) and benthic filter feeders (bivalves, ascidians), coupling pelagic and benthic systems. Faeces constitute an important part of particulate organic matter (POM), which includes POC. The FP-fraction of the POC can be exported to the deep sea by passive (gravitational sinking of FP) and active (i.e. vertical migration, see **Export and migration**) fluxes and constitute an important part of the Biological Carbon Pump (BCP; see **Export and migration**). The efficiency of the BCP depends on several factors and processes that boost or hinder the vertical flux (e.g. microbial loop remineralisation and copepod recycling, reviewed by Turner, 2015).

The relative contribution of FP-carbon to total carbon flux is highly variable in time and space, and depends on the abundance and composition of plankton functional groups (phyto-, zoo-, and bacterioplankton, see **Functional groups**) in the upper layers of the ocean (Gleiber et al., 2012). For example, a diet of diatoms is one of the most likely to result in attributes that enhance zooplankton-mediated export flux: such a diet is categorized by high FP production rate (FPP), large pellet size and relatively low assimilation efficiency in copepods (Besiktepe and Dam, 2002) and krill (Cadée et al., 1993). An efficient grazer response has been suggested to result in high FPP in the upper part of the ocean, followed by a major fragmentation/remineralization of particles in the twilight zone. This results in FP-dominated, but low-POC, fluxes to the deep sea (Coale et al., 2004; Ebersbach et al., 2011). The processes involved in FP flux are multiple, although it seems to be mainly biologically driven (Boyd and Trull, 2007). Flux can be described by a power-law function of POC flux attenuation with depth, where the attenuation exponent "b" (in $F=F_{100}(z/100)^{b}$, see (Martin et al., 1987), is highly variable depending on multiple biological, physical, and chemical factors and processes (Rivkin and Legendre, 2001; Smetacek et al., 2004). Although, there is strong consensus that most POC is recycled in the upper part of the ocean, a tight coupling of primary production and zooplankton consumers can lead to the export of high amounts of fast sinking FP, which can increase the POC export efficiency (Stukel et al., 2011). Studies using sediment traps and large-volume water samplers have concluded that FP makes up the bulk of the POC flux in many areas of the world oceans (Bishop et al., 1977; Sampei et al., 2004; Turner, 2002; Wassmann et al., 2000) and in the Humboldt current system off Chile (González et al., 2007; González et al., 2000). Thus, FP from the water column are a major food source for benthic communities (Graeve et al., 2008), both as a source of POC and as the faeces break down, as DOC. The faeces of benthic filter feeders are also important component of bentho-pelagic coupling of carbon from the water column to the seafloor assemblage (Tatián et al., 2008).

4.21.2. Measurement

Faecal pellet production and export can be measured by area, volume or individual and as a number or a mass of carbon (Table 13).

The proportion of carbon ingested by zooplankton (e.g. copepods) and benthic filter feeders that is released in form of FP, is highly variable (see **Ingestion Rates**). The carbon ingested has different fates, either being included in new tissue, respired, or released as dissolved or particulate products. Some scientific evidence suggests that ingested food has highly variable assimilation efficiency in copepods (e.g. 90 to 20 %, see Besiktepe and Dam, 2002). This is often associated with absorption efficiency (the proportion of ingested food absorbed across the gut walls of metazoan consumers) and is usually assumed to be within a narrow range, 67–74 %, in marine ecosystems models or in bioenergetics calculations for copepods and appendicularians (Bochdansky et al., 1999). This coincides with the idea that the remaining, unassimilated food, would be released in some form of waste product. For example, studies show that from total carbon ingestion, ca. 24–30 % can be egested as FP by copepods (Conover, 1978) and euphausiids (González et al., 2016).

4.21.3. Direct measurements

Direct measurements to estimate ingestion rate (IR) and FPP have several standard requirements:

4.21.4. Laboratory

Capturing healthy individuals for incubations requires specific collection-procedures (e.g. low-speed, and short zooplankton tows, with effort allocated mainly during night-time for vertically migrating groups). Zooplankton without (salps, appendicularians, etc.) or with (euphausiids, copepods, etc.) hard keratin-skeletons, require different net-tow procedures. For example, more gentle (low-speed), vertical net-tows for the former and high-speed, oblique tows for the latter functional groups of zooplankton.

-To estimate FPP in copepods: A low speed-rotation, plankton-wheel incubation system reduces the chance of sedimentation of the

Box 1
Total Carbon (TC) assessment:

Inorganic carbon estimation can be estimated directly as 12 % of the mass of carbonates. However, as mentioned before, huge differences may arise when including inorganic carbon (IC) in blue carbon assessments and whether the CO_2 release during $CaCO_3$ formation is considered or not:

$TC = OC + IC$
Where OC is organic carbon

In the first equation the CO_2 release due to the complexity of carbonate water chemistry is not included and CO_2 release is not taken into account. In the second equation the protective role of carbonates is considered as well as CO_2 release.

$TC = OC + IC\text{- }IC * \psi$
Where ψ is the ratio of CO_2 flux to $CaCO_3$ precipitation

However, the time-scales over which IC (months to centuries) and PIC* ψ (seconds) operate are likely to be substantially different and the complexities of how the seawater carbonate equilibrium is shifting needs to be better understood.

assayed food (e.g. phytoplankton). Short incubation is required because the copepod gut empties after 1 to 3 h. For example, a gut passage time of 107 min was reported for the copepod *Neocalanus plumchrus*, when fed with 0.45 μg Chl-a L^{-1} (Dagg and Walser Jr, 1987), and a range from 10 to 300 min for *Acartia tonsa* when incubated with a wide range of food concentrations (Besiktepe and Dam, 2002).

-**To estimate FPP in ascidians**: Use a seawater bath at controlled temperatures and provided with aeration by air pump. Animals are then put inside the system in separate containers. Faeces are collected after 24 h (considering the gut passage time). Faeces are dried and ashed (5–24 h at 450 °C) and then weighed to estimate dry mass and ash free dry mass.

4.21.5. Field

-To estimate FP-export: Sediment traps can be deployed using different methodologies, such as surface-tethered, anchored to the bottom, neutrally buoyant and others. To minimize hydrodynamic biases due to flow over the trap mouth, the use of neutrally buoyant sediment traps is encouraged. The influence of active animals within traps is best minimized by using traps that limit zooplankton access to the sample collection chamber, and to calibrate the trap catch efficiency, U—Th radionuclide decay rates and selective particle-scavenging have been proposed (Buesseler et al., 2007).

4.21.6. Standardisation

Priorities to allow standardisation should focus on reducing methodological uncertainties and filling knowledge gaps:

- Carbon and nitrogen content of the zooplankton FP is a key factor, which has high spatial and temporal variability. Understanding how and why FP elemental composition (C, N or C/N ratio) varies across different functional groups of zooplankton (i.e. copepods, euphausiids, appendicularians, salps) and across latitudes will greatly improve our ability to scale results between regions.
- A more detailed understanding of the effect of mineral ballasting (organic matter, calcium carbonate or silica) on the sinking rate of FP, is required.
- A better understanding of the main drivers affecting gut assimilation rate, will improve estimates of the fraction of ingested material that is egested as faeces (FPP).
- The role of the zooplankton diel vertical migration (DVM) in the transport of FP to deeper layers of the ocean requires more research (see **Export and Migration**). Factors such as (i) the gap in zooplankton sampling periodicity (day/night and seasonal) during oceanographic data acquisition; (ii) difficulties in sampling the deep sea and (iii) the contribution DVM in FP export in a gradient of productive areas from oligotrophic to eutrophic (Hernández-León et al., 2024) and through the course of a phytoplankton bloom (Butler and Dam, 1994) need to be assessed.

4.22. Ingestion rates

4.22.1. Definition

Ingestion rates (IR) (normally in unit of carbon per unit of time and predator) measure the amount of captured food which is consumed by a predator. They represent the amount of energy ingested by a predator which part is not assimilated (i.e., egestion or faecal production) and the rest is divided between secondary production (growth and reproduction) and metabolic consumption accounting for basal (organism maintenance) and active (swimming) metabolism (Smith and Hollibaugh, 1993); see **Faecal production rate** and **Export and migration**). Therefore, ingestion rates are an important component of measurements of the flux of fixed and stored carbon through the food web (Barnes and Tarling, 2017; Coppari et al., 2019). The trophic transfer of carbon by assimilation is a function of ingestion rates, modified by how much of this carbon is recycled, through metabolic and other remineralisation processes.

4.22.2. Measurement

4.22.2.1. Direct - laboratory. IRs may be assessed in situ by analysing the gut content of an organism (Table 14), but more often they are measured in the laboratory, by direct observation of food passing into the mouth, e.g. for bryozoans (Best and Thorpe, 1983), by calculating the clearance rate by measuring the reduction in the concentration of suspended food particles over a set period (e.g. (Cheng et al., 2018). For other functional groups the quantity of food ingested is commonly measured by counting or weighing the food ration offered and the uneaten food remaining and or of produced faeces (Tatián et al., 2008). These techniques are challenging when they can be controlled in the laboratory and become very difficult to conduct in the field.

(Hansen et al., 2011) developed a technique to seal a container over a section of undisturbed mussel bed and measure the clearance rate of the enclosed mussel assemblage. Rather like chambers used to measure benthic respiration and carbon flux (see **Respiration rate** and **CO_2 air sea fluxes**) these techniques cannot partition consumption by the component species. Hansen's chamber allows filtering rate to be measured in real time with a built in fluorometer, which could be confirmed later by analysis of water samples.

Filtering rate, in the field, can also be measured by following the movement of dye through filter mechanisms, combined with the measurements of particles in water samples before and after passing through animal filter mechanisms (Yahel et al., 2005).

4.22.3. Filtering rates

IR, as a percentage of body carbon, was negatively correlated with animal size, i.e. varying in the northern Humboldt Current off Chile between 4 % in euphausiids (17 mm) and 123 % in small calanoid copepods (0.8 to 1.7 mm) (González et al., 2000). In the pelagic,

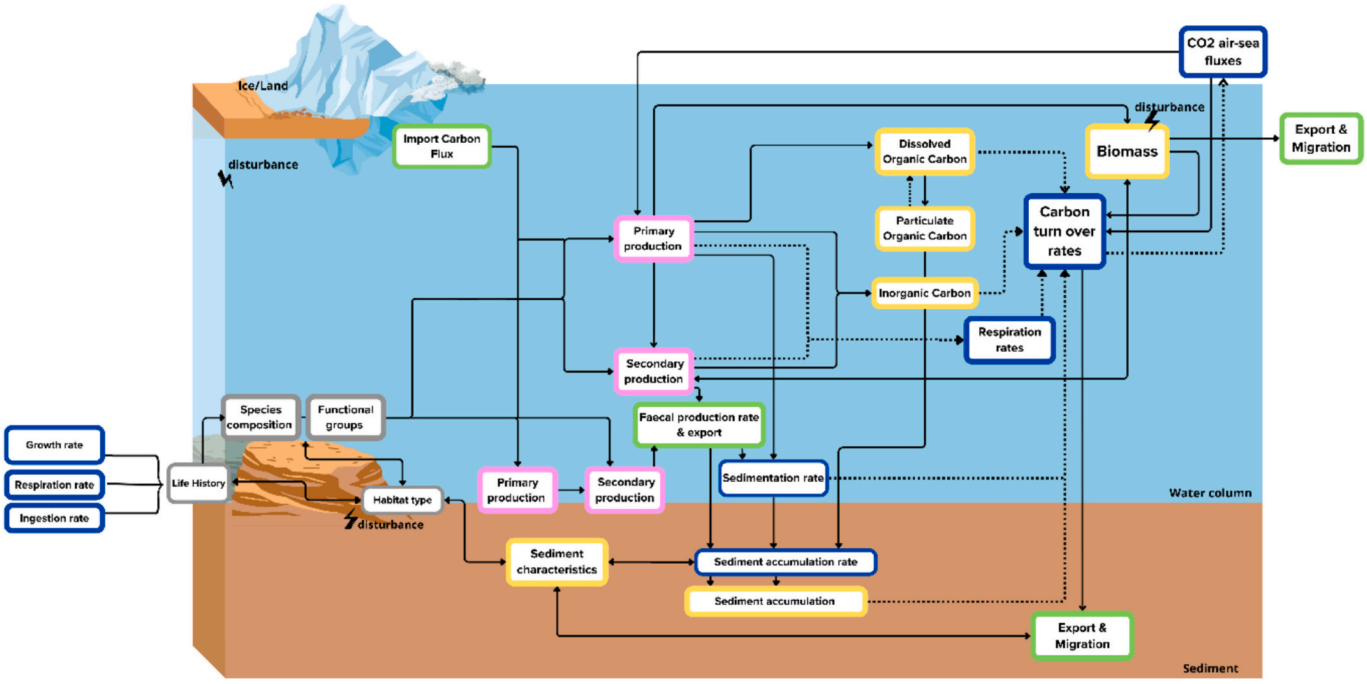

Fig. 5. Showing the conceptual framework for modelling carbon flow among the metrics prioritised in this manuscript. Arrow directions indicate carbon pathways, and colours represent carbon incorporation (pink), cycling (blue), storage (yellow), and external fluxes (green). Metrics that influence the overall carbon ecosystem life-stage, disturbance-response & time-dependent (gray). Solid lines indicate the main flow towards sequestration, while dashed lines indicate pathways releasing CO2 to the atmosphere by respiration, remineralisation, degradation or dilution. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

zooplankton consumption of carbon, fixed into phytoplankton, is a key process that alters the speed and efficiency of carbon flux from surface waters towards the sea floor, altering the proportion of carbon that is re-mineralized through the microbial loop (Azam et al., 1994). Consumption by nekton can also result in carbon transfer across ecosystem boundaries (Hyndes et al., 2014; see Export and migration).

At the seafloor ingestion rates determine how much of the fixed carbon is taken up by benthic organisms, which are often heavily calcified, with inorganic carbon having a high sequestration potential within the sediment (Coppari et al., 2019); see **Inorganic carbon stocks**). Marine animal "forests", are important for bentho-pelagic coupling and therefore the blue carbon budget (Coppari et al., 2019; Rossi and Rizzo, 2020).

IR could be used as an indicator of changes in blue carbon pathways as they vary in response to a wide range of environmental factors, including prey fields (Garrido et al., 2007), environmental conditions (including stressors; (Aelion and Chisholm, 1985), and predator fields (Nelson et al., 2004). However, current methods are too difficult to be scaled across locations and ecosystems and direct measurements of ingestion rates are not suggested as a priority, recommending indirect measures based on factors such as growth.

4.23. *Inorganic carbon stocks*

4.23.1. *Definition*

The biogenic inorganic carbon (PIC) fraction located in shells and carbon skeletal components of organisms are eventually deposited in the seafloor. The most common molecule is calcium carbonate mainly found in two crystalline forms, aragonite and calcite.

For many years Blue Carbon studies across different ecosystems had neglected or did not consider the inorganic carbon fraction. Only recently, have the importance of carbonates been considered. This could

Table 15
Summary of the different methods that could be applied to model carbon pathways. Base data: minimum data needed to apply the method.

Method	Base data	Output	Software	Case-study
Complex food web	Minimum: species composition; predator-prey interactions; species body mass. If available: biomass; ingestion rate	Carbon flows	R packages: multiweb (Saravia, 2022), fluxweb (Gauzens et al., 2019)	(Marina et al., 2024a; Rodriguez and Saravia, 2024)
Linear Inverse Modelling	Functional groups; biomass; inorganic carbon; life history (metabolic rates)	Carbon flows; carbon cycling	R package: LIM (Soetaert and van Oevelen, 2009)	(Braeckman et al., 2024)
Hierarchical Modelling of Species Communities Hierarchical Modelling	Community data (species occurrence or abundance data presence-absence, abundance data); environmental data; functional traits (functional groups), phylogeny	Species' responses (e.g. abundance) to the environment; the role of functional traits and phylogenetic relationships in those responses	R package: HMSC (Tikhonov et al., 2020)	(Ovaskainen et al., 2017)
Habitat Suitability	Species occurrences (presence mandatory, absences optional), Environmental parameters in raster format	Habitat suitability maps, Distribution maps, Projected changes maps	R packages: Biomod2(Guéguen et al., 2025). ENMeval (Muscarella et al., 2014)	(Guillaumot et al., 2021; Neder et al., 2024)

be due, at least in part, to the inherent difficulties including carbonates in the carbon estimations.

4.24. Measurement

4.24.1. Direct Measurement

The most simple and available method is to measure carbon loss on ignition, in which samples (both organisms and sediments) are dried, either lyophilized or with an oven at 50–65 °C and then burned at 450–500 °C for 5 h to estimate organic matter content (see **Biomass**). If the sample is burned again at 900–950 °C for 5 h, and the residual mass after burning will measure the carbonates.

A more precise method is mass spectrometry coupled with an elemental analyser. Two subsamples are needed to distinguish between organic and inorganic carbon. For the determination of organic carbon, a freeze-dried sample undergoes fumigation with HCl to remove carbonates. After acid fumigation, each sample is dried again. The second half of the sample is used to estimate total carbon content. Inorganic carbon is calculated as the difference between the total percentage carbon concentration determined in the non-acidified subsample and the organic carbon determined in the acidified subsample.

4.24.2. Indirect measurement

An appropriate PIC estimation could be considering one atom of carbon in a $CaCO_3$ molecule, then proceeding with the calculation, where 12 % of $CaCO_3$ mass is carbon. This can be estimated as a net uptake of atmospheric CO_2. Indeed, this relation has been calculated and reported in many studies (Barnes et al., 2021; Souster et al., 2020).

4.24.3. Complexities and uncertainties

However, the biogenic $CaCO_3$ production and the IC chemistry in sea-water are much more complex. There is still a debate about net balance of carbon storage and how to consider carbonates in carbon stocks during biogenic $CaCO_3$ production, including the carbon capture and the reduction of CO_2 solubility in sea water that causes the liberation of CO_2 to the atmosphere. As a general estimation, one mole of precipitated $CaCO_3$ will release 0.6 mol of CO_2 to the atmosphere, the ratio (ψ) CO_2 flux:$CaCO_3$ precipitation (Box 1). However, this coefficient is dependent on many factors, such as temperature, which impacts on carbonate saturation state (Feely et al., 2004). In high latitude areas the released factor should be 0.8 due to low temperatures. This implies that for each precipitated molecule of $CaCO_3$ 0.8 to 0.85 of carbon is released to the atmosphere (Smith, 2013). On the other hand, $CaCO_3$ dissolution has the opposite potential, with the sea acting as a CO_2 sink in a reverse relation.

Since carbonate production releases CO_2, it should be subtracted from the total inorganic carbon stock and studies that included PIC into carbon stocks used different calculation methods due to these different approaches. In terms of total stored carbon, the most negative assessment is to directly subtract PIC from the total carbon estimation (Howard et al., 2018). Carbonates are in this case exclusively considered as a source of atmospheric CO_2. In contrast, some studies have highlighted potential advantages that carbonates can provide to carbon storage and sequestration and these should be also considered. For instance, when carbonates are fixed and stored in living organisms, a function that is consistent across calcifying taxa, this facilitates the storage of organic carbon for a longer period. Therefore, these studies considered the PIC (12 % of $CaCO_3$ mass) together with organic carbon (OC) in the total carbon assessment of stored carbon (Barnes et al., 2021; Souster et al., 2020). In sediments, carbonates can also protect the particulate OC by adsorption of the OC to the mineral surfaces. Thus, carbonates contain and preserve organic matter through both intracrystalline and non-intracrystalline structures. This serves as an efficient pathway for the preservation of organic matter, making remineralization more difficult and delayed. Consequently, this process promotes carbon sequestration (Tambutté et al., 2007).

4.24.4. Standardisation

Due to the high complexity of the carbonate cycle, and the numerous uncertainties over the actual flux of oceanic CO_2 from the ocean to the atmosphere, it becomes challenging to establish a straightforward and standardised estimation method. As a result, there is still a debate about whether certain ecosystems, such as coral reefs or other blue carbon ecosystems, act as CO_2 sources or as CO_2 sinks (Macreadie et al., 2017; Saderne et al., 2019). The use of different methods to estimate PIC, can result in variations of up to an order of magnitude for both, biomass and sediment carbon storage and therefore depending on the calculation method the system could performs as a carbon source or sink. The outcomes of these calculations depend entirely on the time scale over which they are made and whether these benthic ecosystems are accumulating biomass (storing more carbon over time) or not. These complexities need to be resolved.

4.25. Life histories

4.25.1. Definition

The life histories of species encompass all stages of their existence from early development (ontogeny) through maturity to eventual death. Organisms with very long lifespans can store carbon long term (hundreds of years). Life stages contribute, to varying degrees, to the carbon cycle, from carbon capture during growth (see **Primary production**, **Secondary production and Growth rates**), to carbon sequestration post-mortem, illustrating the integral role of life histories in the global carbon dynamics.

Understanding how organisms store and use energy, as well as how carbon is stored, cycled, and sequestered, depends on understanding species (or population) life histories. The connection between pelagic larvae and benthic species highlights the interdependence of the benthic and pelagic environments (bentho-pelagic coupling). This coupling is crucial for carbon transfer into seafloor sediments, where it can be buried (Bax et al., 2021); see **Sediment accumulation rate**). Understanding and quantifying these life histories is therefore critical for carbon turnover assessments and predicting the effects of climate change, with long-term studies revealing patterns and shifts over time. While adult organisms store the most carbon in their bodies, other life history stages, especially reproductive cycles and energy allocation between growth and reproduction, also critically influence population dynamics and carbon pathways (Kooijman, 2010). This distinction is crucial as it directly influences an organism's carbo allocation to growth or reproduction, and therefore, its overall role in the ecosystem's carbon cycle. For example, some species, like certain cephalopods (e.g., (Rocha et al., 2001)), have short lifespans and invest heavily in reproduction relative to growth, while others, such as sponges, live longer and invest small amounts of energy into reproduction over many decades (e.g. Dayton, 1990). The reproductive strategy adopted affects not just the individual's lifespan and carbon storage but also population genetics, species connectivity, and the overall dynamics of carbon flow through ecosystems.

4.25.2. Measurement

4.25.2.1. Direct measurement. The energy stored in somatic and gonad tissue can be directly measured (see **Biomass**). Long-term measurements are particularly useful because they can provide measures of the system's inter-annual variability and, if taken over many decades, can detect signals of long-term change. Proximate values from analysis of tissues and energy stores can be input into models, such as Dynamic Energy Budget models ((Kooijman, 2010); see **Modelling blue carbon pathways**), which can be used to predict how environmental variability will affect reproductive investment and growth. There are many life history parameters, including age to first reproduction and even reproductive allocation that lack basic information.

Measuring the early stages of a species' life, particularly the larval phase before they join the adult population, presents complex challenges. Measuring characteristics from larvae, from release to settlement, is still primarily done through plankton trawls, measuring development, distribution and abundance. However, an increasingly popular method is the use of environmental DNA (eDNA) extraction from water samples ((Darling, 2019), see **Species composition**). This method effectively confirms species presence, independent of the developmental stage, but is less reliable for estimating their abundance compared to direct collection techniques like plankton trawls (Bradley et al., 2022).

4.25.3. Standardisation

For realistic standardisation to maximise blue carbon context standardisations of life history should focus on measurements of carbon allocation to reproductive versus somatic tissue, and the models that allow the dynamics to be understood (Kooijman, 2010). Conducting these assessments year-round offers the most comprehensive understanding of how seasonal changes and environmental factors like temperature, nutrient availability, or pollution impact carbon allocation affect gonadic and somatic carbon allocation. However, year-round surveys are resource intensive and directing sampling effort to spawning periods may be a good compromise.

4.26. Modelling blue carbon pathways

Estimating blue carbon dynamics requires modelling to quantify carbon sequestration, storage, and export, which involves mapping carbon stocks and fluxes (Fig. 5). Subantarctic and Antarctic regions present specific challenges, including limited data availability, temporal variation, and spatial heterogeneity. Particularly in remote areas or in ecosystems with limited spatial extent, difficulties arise in (a) accessing the area for habitat-specific carbon measurements, (b) capturing long-term changes due to a lack of continuous monitoring, and (c) assessing the variability within and between ecosystems complicates generalization, particularly across regions. Models will therefore play a key role in advancing our understanding of carbon allocation dynamics, enabling predictions of the effects of environmental changes on these processes.

The previous sections have introduced different models for estimating the individual metrics contributing to carbon pathways. Integrating these metrics allows for a comprehensive assessment of overall carbon contribution across marine ecosystems, addressing (i) Carbon Input: Combining primary and secondary production with biomass accumulation. (ii) Carbon Cycling: Linking functional groups, ingestion, faecal production, respiration rates, and carbon turnover. (iii) Carbon Storage or sequestration: Connecting sediment characteristics, accumulation, burial rates, and disturbance impacts with long-term sequestration. (iv) External Fluxes: considering export/migration and air-sea CO_2 fluxes to assess their impact on the overall carbon budget (Fig. 5).

Interdisciplinary and integrative approaches for modelling carbon pathways (Table 15) are explained in the following section.

4.26.1. Carbon flows in complex food webs

Depending on the available data, carbon flows in complex food webs can be estimated using several methods. When information is limited, allometric scaling approaches based on predator body mass (Brown et al., 2004; O'Gorman et al., 2010) or predator-prey body mass ratios combined with predator's search space dimensionality (Pawar et al., 2012) offer a practical way to estimate interaction strengths. These methods provide per capita estimates of flux magnitudes between predators and prey (Marina et al., 2024a; Rodriguez and Saravia, 2024). When applied across the entire trophic network—assuming a complete map of trophic interactions is available—these approaches can identify species critical for ecosystem carbon flux. This is essential for quantifying marine food web contributions to blue carbon sequestration.

However, when more comprehensive data are available, the Fluxweb method (Gauzens et al., 2019; Jochum et al., 2021) enables a more detailed analysis of carbon fluxes. In addition to body size, this approach requires essential data, including species biomass, diet composition, and assimilation efficiency to achieve more precise flux estimates. By incorporating metabolic theory, this methodology quantifies energy transfer between trophic with greater accuracy.

4.26.2. Linear Inverse Modelling (LIM)

Linear inverse models (LIM) are increasingly applied to estimate carbon flow in food webs (Niquil et al., 2023). These models are based on quantitative data sources (e.g. biomass, respiration rates, physiological rates) combined with a topological flow network (Vézina and Platt, 1988). LIM relies on the principle of mass conservation of mass, where the sum of inflows and outflows through the food web compartments equals the rate of change in their standing stocks. More details on the modelling technique can be found in Soetaert and van Oevelen (2009).

In remote areas like Antarctic and Subantarctic ecosystems, where sampling is challenging, LIM arises as a powerful tool. This modelling approach allows the estimation of missing carbon flows, which are typically derived from data on similar systems. These values are used as ranges for constraints, eliminating the need to select a specific value. Instead the optimization method (likelihood approach) chooses the most appropriate one, making LIM particularly well-suited for data-scarce environments.

In order to apply LIM for estimating carbon flows the following steps are required: 1) define the carbon flows to be estimated and, consequently, the ecosystem compartments (see **Functional groups**) and their level of aggregation; 2) establish the set of linear equalities, which represent mass balance constraints for each compartment (see **Biomass** and **Inorganic carbon stocks**); and 3) establish the set of linear inequalities, incorporating metrics such as metabolic rates and/or physiological efficiencies, expressed either as ratios between flows or ratios between a flow and a biomass. Finally, one must either select a single solution or define each carbon flow by the range of its possible solutions (see (Niquil et al., 2020) for details on solving methodologies).

Although case-studies applying LIM for estimating carbon flows are abundant in northern high-latitude marine ecosystems (e.g. (Dunlop et al., 2016; Oevelen et al., 2009; Pint et al., 2024), few exist for Antarctic and Subantarctic ecosystems (Braeckman et al., 2024; Sailley et al., 2013), highlighting the need for more research in these regions.

4.26.3. Bayesian Hierarchical modelling and HMSC

Hierarchical Modelling of Species Communities (HMSC) is a suitable statistical framework for analysing community data. All the models within this approach are multivariate hierarchical generalised linear mixed models fitted with Bayesian inference (Ovaskainen and Abrego, 2020). HMSC integrates species occurrence or abundance data with environmental covariates, phylogeny, and species traits using a Bayesian approach (Ovaskainen et al., 2017). HMSC can quantify species-specific responses to climate-driven variables, thereby assessing the impact of climate change on blue carbon stock. Specifically, HMSC can be used to study whether the abundance (see **Biomass**) of different species changes according to the environment and whether these responses are modulated by species traits or phylogeny. HMSC could also be implemented to estimate how the biomass of different functional groups changes with the environment and predict these changes under plausible future scenarios. Given that the Antarctic Peninsula is a hotspot of environmental change, HMSC could help us move beyond the study of functional redundancy to identify whether certain functional groups are being favoured or disadvantaged by environmental changes and predict potential disruptions in blue carbon pathways.

4.26.4. Habitat suitability models

Models are efficient tools for inferring the current status of

ecosystems, as well as predicting future shifts in response to climate change. Among these tolls habitat suitability models, also known as niche models (ENM) or species distribution models (SDMs), are particularly useful for understanding the spatial distribution of taxa and providing policy visualisations for spatial management. SDMs simplify ecosystem complexity by identifying species' environmental associations based on physiological tolerance and geographic range, evaluating habitat suitability across time and space, and predicting species' responses to environmental change (Elith and Leathwick, 2009; Peterson et al., 2011; Soberon and Peterson, 2005). By linking species presence/absence to environmental factors SDMs also highlight data gaps in regions with limited data availability. Additionally habitat suitability can help identify habitat types where a certain assemblage of species occurs, consequently impacting carbon pathways (Deregibus et al., 2023; Ferrier and Guisan, 2006; Neder et al., 2024).

Various platforms and studies support the development and application of both individual and ensemble SDMs through programming and georeferencing software (Araújo and New, 2007; Guéguen et al., 2025). These models help predict changes under diverse scenarios, including habitat loss, restoration, or climate change impacts. In Subantarctic and Antarctic regions, SDMs have been applied to identify habitat suitability and potential species presence, which can in turn estimate blue carbon pathways by inferring habitat type, biomass, colonization patterns, hotspot areas, and life history traits (Deregibus et al., 2023; Guillaumot et al., 2021; Jerosch et al., 2019; Lagger et al., 2021; Neder et al., 2024; Pertierra et al., 2020; Reyna et al., 2024, among others)(see **Habitat type**).

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.earscirev.2025.105372.

Data availability

No data was used for the research described in the article.

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