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Fluxes of carbon in the upper ocean: regulation by food-web control nodes

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ABSTRACT: We present a new approach to assess the role of upper ocean pelagic food webs on the partitioning of phytoplankton production (P_T) into its 3 principal component fluxes: remineralization to CO_2 (i.e. respiration, R), transfer to the pelagic food web (F), and downward export (E_T); E_T is the sum of its particulate (POC) and dissolved (DOC) organic carbon components ($E_T = E_{DOC} + E_{POC}$). Although it is well known that there are relationships between the size and trophic structure of the planktonic community on the one hand, and the export of organic carbon (OC) from the euphotic zone and its potential sequestration below the permanent pycnocline on the other hand, the causative mechanisms for these relationships are not well understood. Here, we propose that the fluxes of OC in the upper ocean depend on the coexistence of a relatively small POC pool, which is responsible for the fluxes P_T, R, F and E_{POC}, and a much larger DOC pool, which sustains both bacterial production and E_{DOC}. In our model, phytoplankton, microbial heterotrophic plankton, and large zooplankton are the 3 food-web control nodes of the 5 carbon fluxes (P_T, R, F, E_{DOC} and E_{DOC}). The phytoplankton node controls the downward flux of phytodetritus (mostly from large phytoplankton), which is often the major component of E_{POC}. The microbial heterotrophic plankton node is responsible for most of the remineralization of OC to CO_2 and the uptake and release of DOC. This node therefore controls the size of the DOC pool that can be exported downwards. The large zooplankton node controls both the transfer of POC to large metazoans and part of the downward POC flux (E_{POC}; faecal pellets and vertically migrating organisms). We implemented our model by estimating export as $E_T = P_T - R$ at 8 sites in different regions of the World Ocean. The functional relationship between E_T and P_{new} was highly significant ($r^2 = 0.85$): In contrast to other approaches, where export is calculated as a fraction of P_T, we estimate E_T as the difference between 2 independent variables (i.e. P_T and R); hence our approach produces some regional values $E_T < 0$ – these regions are net heterotrophic. Overall, our approach improves our understanding of carbon cycling and export in the upper ocean.

KEY WORDS: Bacteria · DOC · Export · Food web models · Heterotrophy · Microbial heterotrophic plankton · Phytoplankton · Zooplankton

INTRODUCTION

Quantification of the rates, patterns and mechanisms that control the photosynthetic uptake of carbon by marine phytoplankton (procaryotic and eucaryotic photoautotrophic plankton) and the fate of the resulting organic carbon (OC) has been a central objective of biological oceanographic research on the upper ocean during the past 2 decades (Knauer 1993, Fasham et al. 2002). This is, in large part, because the pelagic food web plays significant roles in regulating the exchange of CO_2 between the lower atmosphere and the upper ocean, the downward export of OC, and the transfer of OC towards marine renewable resources. Here, the 'upper ocean' is defined as the whole water column above the permanent pycnocline (discussed in the next section). Although it is well known that there are rela-

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tionships between the size and trophic structure of the planktonic community, and between the export of OC from the euphotic zone and its potential sequestration below the permanent pycnocline (e.g. Boyd & Newton 1995, 1999, Rivkin et al. 1996, Legendre & Michaud 1998, Fasham et al. 1999, Vézina & Savenkoff 1999), the causative mechanisms for these relationships are not well understood. In this paper, we propose a conceptual basis for the food-web regulation of carbon fluxes in the upper ocean.

Prior to the early 1970s, marine pelagic ecosystems were generally thought of as being largely dominated by the herbivorous food chain, going from large phytoplankton to zooplankton to fish (e.g. Ryther 1969). We now know that marine ecosystems are a complex array of interacting living organisms that range in size over several orders of magnitude (from free viruses <0.1 µm equivalent spherical diameter to baleen whales ca. 30 m long). Almost 3 decades ago, Vinogradov et al. (1972) and Pomeroy (1974) proposed that small autotrophic and heterotrophic microbes are important and at times the dominant components of water column production and respiration. Ten years later, Azam et al. (1983) developed a conceptual model in which free-living heterotrophic bacteria (ca <1 µm) and picophytoplankton are ingested by small (3 to 10 µm) heterotrophic flagellates, which are in turn consumed by larger (20 to 200 µm) flagellates, ciliates and micrometazoans. Heterotrophic bacteria use the DOC released by phytoplankton and small grazers for growth: this almost closed system of heterotrophic bacteria, phytoplankton, flagellate grazers, and microzooplankton predators was called the 'microbial loop'. Within the microbial loop, microheterotrophs release inorganic nutrients for which the bacteria and phytoplankton compete. Rassoulzadegan (1993) proposed a distinction between the microbial loop where phytoplankton play little or no role and the 'microbial food web' in which small (<5 µm) phytoplankton play a significant role and from which there is a flux of matter and energy to higher trophic levels. The microbial food web therefore includes small phytoplankton and planktonic microbial heterotrophs (i.e. heterotrophic bacteria, protozoa and small metazoans). In the literature, it is not always clear whether the authors consider phytoplankton as part of the microbial food web. In order to avoid any confusion, we call the heterotrophic component of the microbial food web 'microbial heterotrophic plankton'. Legendre & Rassoulzadegan (1995) subsequently described a 'multivorous food web', in which the microbial and herbivorous trophic modes are equally important. In their model, there is a continuum from the herbivorous food web, through the multivorous and microbial food webs, to the microbial loop.

In this paper, we build upon recent advances in our understanding of the structure and functioning of pelagic food webs to (1) develop the conceptual basis that describes the dominant trophic relationships regulating carbon fluxes in the upper ocean, and (2) implement our conceptual model using published food-web variables for planktonic communities from 8 different regions of the World Ocean. Our conceptual model does not replace the approach of directly estimating carbon dynamics and fluxes (e.g. from bottle incubations, sediment traps, ^{234}Th), but it is instead a tool for quantifying integrative system properties.

INTERACTIONS BETWEEN DOC and POC

OC in seawater ranges in size from dissolved and colloidal compounds to baleen whales (ca. 30 m). This continuum is functionally divided into particulate (POC) and dissolved (DOC) organic carbon using filtration, and depending on the study and author, DOC or DOC + colloidal OC is the fraction passing through a 0.2 or 0.4 µm or GF/F (nominally 0.8 µm) filter (Kepkay 2000). POC consists of both non-living (detritus) and living (organisms) components, whereas the DOC pool is normally considered as non-living, although this functionally defined pool may also include free viruses (Fuhrman 1999) and very small bacteria (Li & Dickie 1985, Li 1990, Longhurst et al. 1992). In this context, it is important to note the tendency in the recent literature to use 'biogenic carbon' as equivalent to 'organic carbon'. They are not the same, because living organisms fix carbon (i.e. biogenic carbon) into both organic matter and inorganic $CaCO_3$.

Export from the euphotic zone and remineralization below

The fraction of the OC that sinks (e.g. POC) or is mixed or advected (i.e. DOC) below the euphotic zone may be ingested, metabolized, or remineralized (respired) in the underlying disphotic zone (also called the 'twilight zone'), above the permanent pycnocline. In the euphotic zone, there is enough light for net photosynthesis to occur, whereas in the disphotic zone, there is enough light for animal vision but not for net photosynthesis. The disphotic zone extends down to about 1000 m in the clearest oceanic waters; its depth range approximately corresponds to that of the mesopelagic layer (150 to 1000 m). The permanent pycnocline is a persistent barrier to deep vertical mixing. It is typically centred at ca. 1000 m depth at low and middle latitudes, but is poorly developed or absent at high latitudes where deep convection occurs (which transports

large quantities of dissolved inorganic carbon downwards). In water columns shallower than 1000 m, where the permanent pycnocline is absent, it is replaced in our conceptual model by the maximum depth of winter mixing. This is because, as was shown by Tian et al. (2000) at a 355 m deep station in the Gulf of St. Lawrence, net-downward export takes place when carbon is transferred, typically during the spring-to-autumn period, below the depth of maximum wintertime vertical mixing. The carbon thus exported may be returned to the euphotic zone, buried in local sediments, or transported towards oceanic areas, where it may be sequestered.

Most of the POC exported from the euphotic zone is remineralized above the permanent pycnocline (see below). It is possible to approximate the mid-water OC remineralization by combining published empirical equations that describe the flux of organic particles at depth z [$E_{POC}(z)$] as a function of phytoplankton production (P_T). Betzer et al. (1984) proposed the following equation for $E_{POC}(z)$:

$$E_{POC}(z) = 0.409 P_T^{1.41} / z^{0.628} \quad (1)$$

Wassmann (1990) proposed the following equation to describe the POC flux out of the euphotic zone [E_{POC}(eu)] in the boreal North Atlantic for sites and times when the depth of the euphotic zone varies:

$$E_{POC}(\text{eu}) = 0.049 P_T^{1.41} \quad (2)$$

Combining Eqs. (1) and (2) gives

$$E_{POC}(z) / E_{POC}(\text{eu}) = 8.35 z^{-0.628} \quad (3)$$

Eq. (3) shows that ca. 15 and 10% of E_{POC}(eu) will reach the permanent pycnocline when it is located at 500 and 1000 m, respectively.

There are comparatively few estimates of DOC export (Copin-Montégut & Avril 1993, Carlson et al. 1994, Williams 1995, Emerson et al. 1997, Alldredge 2000), and although equivalent empirical models to estimate the downward DOC flux are not available, it is reasonable to assume that DOC is remineralized at least as, if not more, rapidly than POC in the disphotic zone (e.g. the exported DOC is mostly consumed above 400 m in the Sargasso Sea; Carlson et al. 1994, Hansell & Carlson 2001).

The CO_2 that is derived from the OC which is remineralized above the permanent pycnocline can be mixed back to the surface waters and re-equilibrate with the atmosphere within decadal timescales. Because the OC below the permanent pycnocline is isolated from the upper ocean by the density barrier, and is also below the depth of migration of most large pelagic grazers, it would not be transferred back to the surface waters through vertical diffusion or biological processes. Hence, the OC that is transferred below the permanent pycnocline would be sequestered there for centuries (the residence time of deep waters in oceans is ≥1000 yr) to several millennia (if buried in sediments). Depending on the pathways and timescales of the transit of DOC and POC from surface to depth, different proportions of the OC will be respired or reach either large metazoans (where it will be ultimately respired) or deep waters. Thus the transfer of OC to large metazoans and to depth is of significance to fisheries and carbon sequestration, respectively.

Cycling of OC

Fig. 1 identifies the main processes involved in the circulation of OC within and out of the euphotic zone that are mediated by the main components of the food web. The sizes of boxes do not reflect the relative magnitudes of the DOC and POC pools. The left- and right-hand sides of the figure show the pools and fates of OC originating from large (>5 µm) and small (<5 µm) phytoplankton, respectively. The central part shows the pools and flows of DOC. Following Sherr & Sherr (1988), we use a 5 µm threshold between large and small phytoplankton, as it approximately corresponds to the smallest size of particles effectively grazed by most crustacean zooplankton (Fortier et al. 1994). In Fig. 1, carbon is exchanged between the inorganic (i.e. CO_2) and organic pools by photosynthetic uptake and respiration. Respiration is not specified for phytoplankton because field measurements using $NaH^{14}CO_3$ generally provide estimates of phytoplankton net production. Hence, all the respiratory CO_2 in the figure comes from heterotrophic organisms.

The >5 µm phytoplankton on the left-hand side of Fig. 1 either sink to depth as phytodetritus or are grazed generally by mesozooplankton and microphagous macrozooplankton (see next paragraph). Another fate of >5 µm phytoplankton is grazing by protists (e.g. Jeong & Latz 1994, Sherr & Sherr 1994), which is at times significant (e.g. Neuer & Cowles 1994). Mesozooplankton feed on both >5 µm phytoplankton and microbial heterotrophic plankton of suitable size. Part of the carbon taken up by mesozooplankton is rapidly egested as faecal pellets, the remainder being partitioned among respiration, excretion of DOC and assimilation in their own body masses. Mesozooplankton are consumed by large metazoans, which ultimately remineralize the ingested carbon. The main contributions of zooplankton to the downward flux of OC typically occur during the vertical migrations and from the sinking of faecal pellets for POC fluxes and from excretion and leakage from sinking faecal pellets for DOC (DOC_{total}) fluxes. Diel vertical migration by zooplankton transfer OC to the dis-

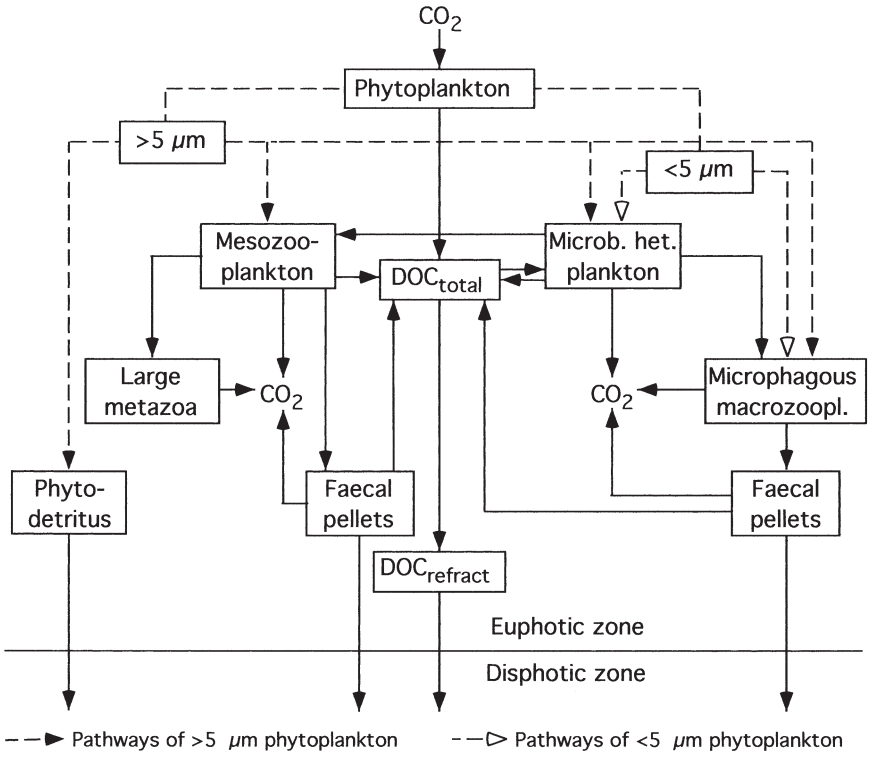

Fig. 1. Main processes involved in the circulation of organic carbon (OC) in the pelagic marine environment. The size of the DOC_{total} (total dissolved OC) box does not reflect the relative magnitude of the DOC and POC (particulate OC) pools in oceans (see Figs. 2 & 4). The left and right-hand parts of the figure describe the fate of carbon originating from large (>5 µm) and small (<5 µm) phytoplankton, respectively; the central part illustrates the DOC pool. $DOC_{refract}$: refractory DOC; arrows: carbon fluxes; CO_2 fluxes out of OC compartments: respiration. Some important biotic and abiotic processes are not represented: downward carbon transport by vertically migrating organisms (biotic); photochemical (UV) oxidation of DOC in surface waters (abiotic); and formation of detrital POC from DOC by exopolymer condensation. The predation of large metazoans on some microphagous macrozooplankton is not represented, for simplicity

photic zone, where the organisms respire part of the OC ingested within the euphotic zone. Seasonal migrations transfer OC below the permanent pycnocline, where there is respiration by metazoans and microheterotrophs and microbial degradation and remineralization of carcasses (e.g. Longhurst & Harrison 1988, Longhurst et al. 1990, Hays et al. 1997, Morales 1999, Steinberg 2000, Al-Mutari & Landry 2001, Hidaka et al. 2001). For simplicity, vertical migrations are not represented in Fig. 1. The faecal pellets of copepods sink but, because of their relatively low settling velocities (ca. 100 m d^{-1}), they are usually largely ingested (coprophagy) or fragmented (coprohexy) by zooplankton, or degraded by bacteria in the upper few hundred metres. This results in the release of most of the faecal carbon as DOC or its remineralization to CO_2 above the permanent pycnocline (see references in Fortier et al. 1994). Many crustacean zooplankton can feed on both phytoplankton and non-phytoplankton prey (e.g. ciliates and flagellates; Dam et al. 1994, Ohman & Runge 1994, Pond et al. 1996) and seasonally switch from herbivory to omnivory. Because of the switch in trophic mode, the downward POC flux may be similar during (mostly phytodetritus) and after (mostly faecal pellets) the spring phytoplankton bloom in some regions (Rivkin et al. 1996, 1997).

The <5 µm phytoplankton, on the right-hand side of Fig. 1, are grazed by either microbial heterotrophic plankton, mixotrophs (organisms that are both autotrophic and heterotrophic to various degrees; Stoecker 1998, Stickney et al. 2000), or microphagous macrozooplankton (e.g. salps, doliolids, appendicularians and pteropods; Fortier et al. 1994). Because microphagous macrozooplankton can ingest particles several orders of magnitude smaller than their own size, they can efficiently feed on the whole size range of phytoplankton and some components of microbial heterotrophic plankton. In the case of mucous web feeders, such as salps and appendicularian tunicates, a portion of the ingested OC may be egested as rapidly sinking faecal pellets, the remainder being respired or incorporated into biomass. The distribution of and predation on these microphagous macrozooplankton are poorly known relative to the same for crustacean zooplankton

(e.g. copepods); thus the absolute magnitude of their contribution to the pelagic food web fluxes remain largely unquantified. Therefore, most of the OC flux through mucous web feeders is thought to be mediated by rapidly sinking faecal pellets (up to 2700 m d^{-1}; Fortier et al. 1994), which often reach the permanent pycnocline relatively intact (i.e. before the POC is converted to DOC and released to the surrounding seawater; Jumars et al. 1989). Much of the carbon grazed by microbial heterotrophic plankton is respired, the remainder being either released as DOC or eaten by mesozooplankton or microphagous macrozooplankton The predation of large metazoans on some microphagous macrozooplankton is not represented in the figure, for simplicity.

In the centre of Fig. 1, the large pool of DOC_{total} is supplied from many sources, including phytoplankton exudation and lysis, sloppy feeding of mesozooplankton on phytoplankton, excretion by mesozooplankton and microbial heterotrophic plankton, leakage from sinking faecal pellets and viral lysis of bacteria (Jumars et al. 1989, 1993, Fuhrman 1992, Strom et al. 1997, Urban-Rich et al. 1999, Nagata 2000, Anderson & Ducklow 2001). The relative importance of these different sources varies spatially and temporally. The fraction of the DOC that is used by microbial heterotrophic plankton (labile DOC: DOC_{labile}) is thought to be small relative to DOC_{total} (Carlson & Ducklow 1995, Carlson et al. 2000, Kepkay 2000). DOC_{labile} is functionally defined here as the fraction of DOC that has a turnover time of hours to days (Carlson & Ducklow 1995, Nagata 2000). The relatively large pool of DOC that is not assimilated by bacteria in the euphotic zone (functionally defined here as refractory DOC, $DOC_{refract}$, although some authors distinguish between semi-labile and refractory DOC) is available for downward transport in those regions and at times of the year when deep convective mixing occurs. When bacterial activity or growth is limited by top-down control of bacterial stocks, availability of inorganic nutrients or low temperatures (Zweifel et al. 1995, Palulski et al. 1996, Rivkin & Anderson 1997, Thingstadt et al. 1997, Church et al. 2000), the bacterial DOC uptake is limited so that the amount of unused DOC available for export may increase.

Three processes which transform DOC are not represented in the figure because they do not directly involve the food web: photochemically (i.e. UV) driven degradation of refractory coloured organic matter to DOC_{labile}; photooxidation of DOC to CO_2 (Bushaw et al. 1996, Moran & Zepp 1997); and condensation of exopolymers (colloidal OC and DOC) into transparent exopolymers (TEP), followed by aggregation and sinking of macroscopic particles (e.g. marine snow). The first 2 processes are usually important only in the upper few 10s of metres of the water column.

Fig. 2 summarizes the interrelationships among the CO_2, DOC and POC pools in the euphotic zone, where CO_2 is taken up and converted to OC by phytoplankton photosynthesis. A large proportion of this OC is respired back to CO_2 in the euphotic zone and a small fraction of the DOC is oxidized to CO_2 in the surface layer by UV radiation. The remaining OC is partitioned between the DOC and POC pools, and continuously redistributed by abiotic and biotic exchange processes. The latter include the formation of detrital POC by exopolymer condensation of DOC, uptake of DOC mainly by heterotrophic bacteria (some protists and

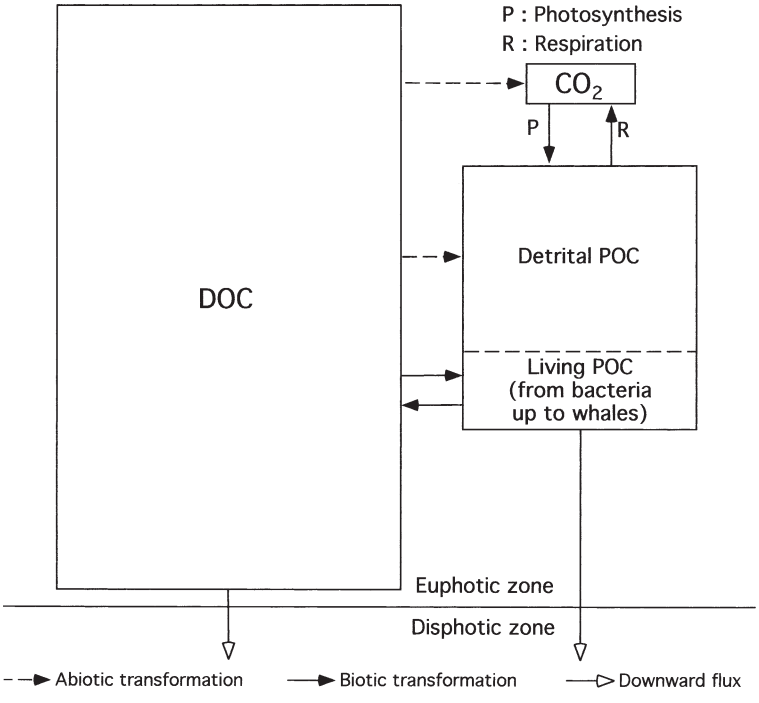

Fig. 2. Interrelationships between the CO_2, DOC and POC pools in the euphotic zone of oceans. The relative sizes of the 2 main rectangles (3:1) reflect the fact that the pool of DOC in oceans is much larger than that of POC, i.e. 200 to 700 versus 20 to 30 Gt, respectively, and the partition of the POC rectangle reflects the relative importance of the detrital and living POC pools, i.e. 20 versus 1 to 11 Gt, respectively (Kepkay 2000, his Figs. 1 & 2). Inorganic carbon is fixed by phytoplankton from dissolved CO_2; a large proportion of the resulting organic carbon is respired back to CO_2 within the euphotic zone, the remainder being exchanged between pools by abiotic and biotic processes; both DOC and POC can be exported below the euphotic zone. Abiotic transformations: UV oxidation of DOC to CO_2 and exopolymer condensation of DOC to POC. Biotic transformations: respiration and production of DOC (all living organisms), photosynthesis (phytoplankton), and the use of DOC and POC as a food source (heterotrophic organisms). Arrows: carbon fluxes

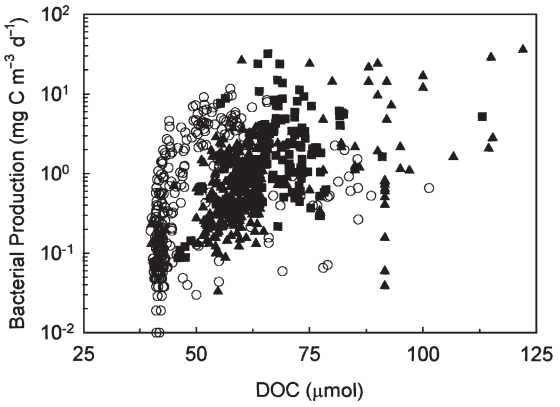

Fig. 3. Scatterplot of bacterial production (BP) as a function of DOC concentration for polar (>55° latitude; ○), temperate (20 to 55° latitude; ▲) and tropical (20°N to 20°S; squares) regions of the World Ocean. The figure is based on concurrently collected literature data on DOC concentrations and BP. We excluded data from estuarine and coastal sites, because of the influence of potentially large concentrations of DOC of fluvial and terrigenous origins in these regions (Hedges et al. 1997, Opsahl & Benner 1997). BP was extrapolated from hourly to daily rates by multiplying by 24. For data reported in areal units, average volumetric values were computed by dividing by the integration depth. For data reported in volumetric units, vertical profiles were converted to areal values by trapezoidal integration over the depth of the euphotic zone, after which the integrated values were divided by the integration depth. Sources for the data used in this figure are available from the authors upon request

invertebrate larvae also take up limited quantities of dissolved and colloidal OC, but the ecological importance of non-bacterial uptake is thought to be trivial; Manahan & Richardson 1983, Manahan 1990, Flood et al. 1992, Tranvik et al. 1993, Shilling & Manahan 1994), and production of DOC by the metabolic activity of all living organisms. Although there is continuous exchange between the detrital and living POC pools, for simplicity these fluxes are not shown in Fig. 2. The OC exported to depth may consist of both DOC and POC, in proportions that vary spatially, temporally, and with the physical characteristics of the upper ocean (Copin-Montégut & Avril 1993, Carlson et al. 1994, Ducklow et al. 1995, Guo et al. 1995, Tian et al. 2000).

Bacterial activity and DOC

An important aspect arising from the above discussion is whether the availability of DOC_{labile} controls *in situ* bacterial activity, as widely thought (e.g. Ducklow & Carlson 1992), or conversely, bacterial activity (stock size and uptake rate) determines the size of the DOC pool (e.g. Ducklow et al. 1999). The relationship between bacterial activity and the oceanic DOC pool has been typically inferred from short-term incubations, where the changes in bacterial abundance or production and the uptake of DOC or radiolabelled carbon substrates are concurrently estimated. Fig. 3 shows a scatterplot of bacterioplankton production (BP) as a function of concurrently measured DOC concentration in the World Ocean. Even though there is a strong positive relationship between BP and [DOC], the figure does not define the underlying interactions between [DOC] and BP. This is because correlative relationships can result from direct interactions between variables, or forcing exerted by external variables. Moreover, *in situ* DOC reflects the balance between DOC production by the whole pelagic food web and its uptake by microbial heterotrophic plankton, so that the observed DOC corresponds to the fraction that had not been used by microbial heterotrophic plankton at the time of sampling. In other words, the relationship shown in the figure does not unequivocally support either the hypothesis that the availability of DOC_{labile} controls *in situ* BP or the converse where bacterial activity determines the size of the DOC pool.

Heterotrophic bacteria require an exogenous source of reduced carbon for their anabolic (i.e. growth) and catabolic (i.e. respiration) needs. BP is related to DOC concentration by the bacterial growth efficiency (BGE), which is defined as the ratio of BP to the total amount of DOC assimilated by the bacteria per unit time (B_{DOC}):

$$\mathrm{BGE} = \frac{\mathrm{BP}}{B_{\mathrm{DOC}}} \quad (4)$$

Eq. (4) shows that BP could be a function of B_{DOC} and BGE:

$$\mathrm{BP} = B_{\mathrm{DOC}} \times \mathrm{BGE} \quad (5)$$

or, alternatively, that B_{DOC} could be a function of BP and BGE:

$$B_{\mathrm{DOC}} = \frac{\mathrm{BP}}{\mathrm{BGE}} \quad (6)$$

According to Eq. (6), the bacterial uptake of DOC is a positive function of BP, which means that BP could modify [DOC]. This relationship is supported by results of the several studies showing that DOC may not always control BP. For example, Zweifel et al. (1993) enriched predator-free seawater cultures from the Baltic and the northwest Mediterranean seas with inorganic nutrients. Bacterial growth (μ_B = BP/BB [where BB is bacterial biomass]) was phosphorus-limited, and the addition of inorganic N and P resulted in a strong decrease in [DOC] compared to the unenriched controls. In another study, Thingstad et al. (1997) used a modelling approach to explain the seasonal accumulation of DOC in the surface waters of several marine areas. They showed that μ_B is limited by competition with phytoplankton for inorganic nutrients, and that BB is maintained at low levels by top-

down control by bacterivores. Hence, the availability of inorganic nutrients (first example) or food-web mechanisms (second example) instead of the availability of DOC may limit BP. Hence, bacteria can control the size and characteristics of the DOC pool. It follows that, in regions and at times when bacterial growth is limited by mineral nutrients (or temperature), bacterial activity controls [DOC] instead of DOC controlling BP.

NEW APPROACH

Food-web control nodes

Fig. 1 depicts the commonly accepted view of OC cycling in the pelagic environment. Because of the large number of processes that are involved, and the complexity of interactions, it is difficult to derive a clear understanding of the key food-web processes that regulate the fluxes of carbon among the pools of CO_2, DOC and POC. In Fig. 4, we consolidate into a small number of compartments and fluxes the processes illustrated in Figs. 1 & 2. However, unlike Fig. 2, Fig. 4 illustrates only processes that involve the pelagic food web, i.e. the abiotic transformations and detrital POC are not explicitly represented here. On the right-hand side of Fig. 4, the vertical fluxes among living POC compartments, and between the DOC and living POC pools are the same as in Fig. 1, but the remineralization of OC (to CO_2) from individual trophic compartments is combined into an overall remineralization term. Similarly, living POC includes the same trophic compartments as depicted in Fig. 1, i.e. phytoplankton (<5 and >5 µm-sized cells), microbial heterotrophic plankton, large zooplankton (mesozooplankton and microphagous macrozooplankton), and large metazoans. The effects of vertically migrating organisms are included in the downward POC flux. On the left-hand side of Fig. 4, the DOC pool (DOC_{total} in Fig. 1) is partitioned into DOC_{labile} (shown as an arrow from DOC_{total} to microbial heterotrophic plankton in Fig. 1), and $DOC_{refract}$. Overall, the pools of CO_2, DOC and POC are involved in 5 major carbon fluxes: CO_2 uptake, respiration of OC back to CO_2 (remineralization), transfer of OC to the pelagic food web, and downward export of DOC and POC.

Table 1 summarizes the input and output of carbon to and from the various trophic compartments specified in Fig. 4. The centre column shows that the 5 carbon fluxes in the upper ocean are controlled by 3 trophic compartments, i.e. phytoplankton, microbial heterotrophic plankton, and large zooplankton. We call these 3 trophic compartments 'food-web control nodes'. The following numbered paragraphs discuss specific roles of the 3 nodes in the regulation of upper-ocean carbon fluxes. Although these roles are presented separately, there is a complex array of interactions and feedbacks among nodes.

Specific roles of the three nodes

1. Phytoplankton node. The magnitude of phytoplankton production sets upper limits to both the overall activity of the pelagic food web and the quantity of OC exported downwards. The size structure, nutritional status and taxonomic composition of the phytoplankton community largely determine the partitioning of photosynthetic carbon among the DOC pool, microbial heterotrophic plankton, large zooplankton, and sinking phytodetritus. The fraction of primary production released as DOC by phytoplankton during photosynthesis (i.e. exudation) is generally 10 to 15%, but it may be much higher in some regions (e.g. in the oligotrophic North Pacific Ocean; Karl et al. 1998). Small-sized phytoplankton are mostly grazed by

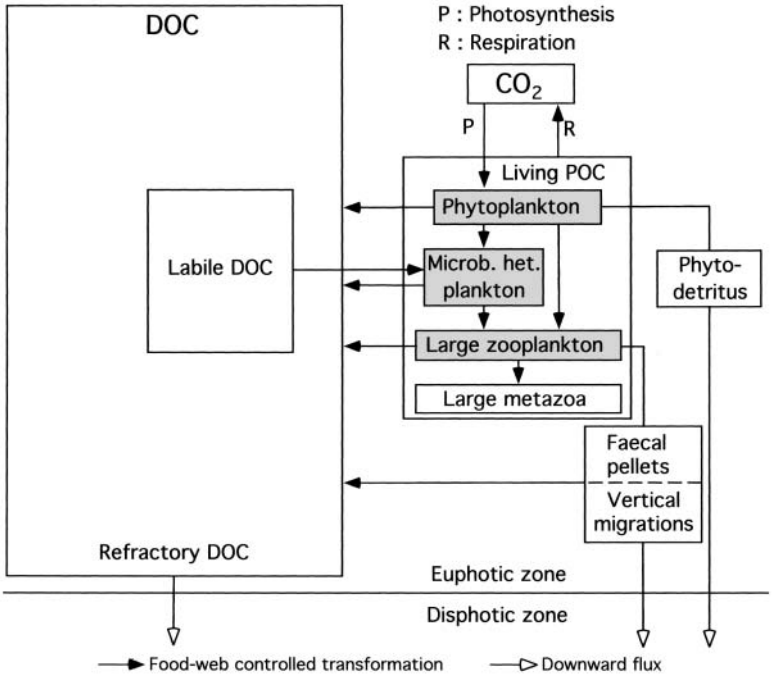

Fig. 4. Food-web-controlled interrelationships between the CO_2, DOC and POC pools in the euphotic zone of oceans: consolidation of the processes illustrated in Fig. 1 into a small number of compartments and fluxes, within the context of Fig. 2. In contrast with Fig. 2, this figure illustrates only the processes that involve the pelagic food web. Arrows: carbon fluxes. Shaded boxes: 3 food-web control nodes (phytoplankton, microbial heterotrophic plankton and large zooplankton) of the 5 carbon fluxes (i.e. phytoplankton production, respiration, transfer to the pelagic food web, and downward export of DOC and POC)

Table 1. Input and output of carbon to and from the various trophic compartments specified in Fig. 4. Output column: DOC = DOC_{labile} + $DOC_{refract}$; CO_2 = respiration

Compartment	Input from	Output to
Phytoplankton (P)	CO_2	MHP, Z, DOC, phytodetritus
Microbial heterotrophic plankton (MHP)	P, DOC_{labile}	Z, DOC, CO_2
Large zooplankton (Z)	P, MHP	M, DOC, CO_2, faecal pellets
Large metazoans (M)	Z	CO_2
Vertically migrating zooplankton	Z	CO_2, DOC, disphotic zone
Phytodetritus	P	Deep waters
Large faecal pellets	Z	DOC, disphotic zone
Labile DOC	P, MHP, Z	MHP
Refractory DOC	P, MHP, Z	Disphotic zone

microbial heterotrophic plankton (and, under specific conditions, by microphagous macrozooplankton), whereas larger cells are generally eaten by large zooplankton, or if ungrazed, they sink to depth as phytodetritus. The latter bifurcation is influenced by the taxonomic composition and size structure of the phytoplankton assemblage, i.e. some large or gelatinous phytoplankton taxa are not ingested by zooplankton, and others readily aggregate and sink out of the euphotic zone (Boyd & Newton 1995, 1999, DiTullio et al. 2000, Armstrong et al. 2001).

2. Microbial heterotrophic plankton node. Microbial heterotrophic plankton largely control heterotrophic respiration (2.1) and the pool of DOC (2.2) in the upper water column. When the microbial heterotrophic plankton (i.e. bacterial) activity is limited by inorganic nutrients or grazing, these factors influence the assimilation and ultimately the concentration of DOC and its subsequent export below the euphotic zone (2.3).

2.1. Heterotrophic respiration: Over the annual cycle, the bacterial component of microbial heterotrophic plankton is responsible for most of the heterotrophic respiration in the water column (Sherr & Sherr 1996, del Giorgio & Cole 1998, 2000, Rivkin & Legendre 2001 and references cited therein). Consequently microbial heterotrophic plankton affect several important euphotic zone processes. For example: (1) Microbial heterotrophic plankton activity can influence the air-sea exchange of CO_2, i.e. in general, most of the carbon fixed by phytoplankton is rapidly respired back to CO_2 by microbial heterotrophic plankton. (2) Microbial heterotrophic plankton set an upper limit to the transfer of OC to large metazoans and substantially modifies the total amount of OC that can be exported from the euphotic zone. This is because, as seen in Eqs. (7) and (8) (below), only the fraction of primary production that is not respired (primarily by microbial heterotrophic plankton) is transferred to metazoans or exported.

2.2. Upper-water column DOC: From our current understanding of the DOC cycling (Jumars et al. 1989, Fuhrman 1992, Nagata 2000 and references therein), microbial heterotrophic plankton and herbivorous zooplankton are important sources of DOC (see Figs. 1 & 4). Although lysis of bacteria by viruses releases bacterial DOC (and dissolved organic nitrogen; McCarthy et al. 1998), and it is clearly an important mortality term, the contribution of this process to overall carbon cycling in the ocean is poorly quantified (Fuhrman 1999, 2000, Middelboe & Lyck 2002), and based upon recent modelling studies, it is probably not a major factor mediating the flow of carbon (Anderson & Ducklow 2001). The above analysis of the interactions between heterotrophic bacteria and the DOC pool showed that, by taking up and either converting to biomass or respiring part of the available DOC, bacteria influence both the size and composition of the DOC pool. Hence, microbial heterotrophic plankton have a unique role in the biogeochemical cycling of OC. Whereas nearly all pelagic organisms release DOC, only microbial heterotrophic plankton take up ecologically significant quantities of DOC, so that microbes control the concentration of DOC and partition the DOC pool into labile and refractory components. The quantity of DOC that is available for export to depth (i.e. $DOC_{refract}$) by regional downward transport and basin-scale thermohaline circulation is directly proportional to the production of DOC by the whole food web and inversely proportional to the DOC taken up by microbial heterotrophic plankton. Since the downward export of DOC can equal or exceed that of POC, this represents a potentially important mechanism for the transport of carbon into the ocean interior (Copin-Montégut & Avril 1993, Carlson et al. 1994, Williams 1995).

2.3. DOC export: When microbial heterotrophic plankton activity is limited by factors other than the availability of DOC, e.g. inorganic nutrients or grazing, a smaller fraction of ambient DOC would be taken up

and subsequently transferred to protistan and metazoan grazers than would otherwise occur under conditions of OC limitation. This is because food-web processes are accompanied by strong remineralization of DOC back to CO_2, which is exchangeable with the atmosphere. Therefore, low microbial heterotrophic plankton activity would lead to greater downward export of DOC than under conditions where DOC is taken up by microbial heterotrophic plankton. It follows that the availability of inorganic nutrients and grazing pressure may control the uptake of DOC by microbial heterotrophic plankton (especially bacteria), and thus influence the transfer of OC to the ocean's interior.

3. Large zooplankton node. Large zooplankton contribute to the general cycling and downward export of OC by influencing the export of phytodetritus (3.1), producing fast-sinking faecal pellets (3.2), vertically migrating to depth over daily and seasonal periods (3.3) and transferring OC from phytoplankton and microbial heterotrophic plankton to the ocean's renewable resources (3.4).

3.1. Export of phytodetritus: Sinking phytodetritus is a major flux to the deep ocean. This can occur when there is a mismatch between the growth of large phytoplankton and their grazing by herbivorous mesozooplankton. In such a case, and where conditions are appropriate, the large algal cells may aggregate and sink out of the euphotic zone (e.g. Alldredge et al. 1995, Passow & Alldredge 1995, Alldredge 1998). The mismatch between phytoplankton production and zooplankton grazing both increases the downward POC flux and decreases zooplankton-mediated DOC production (e.g. sloppy feeding, excretion, and faecal pellet leaching). Because of the high sinking velocity of large aggregates of phytodetritus, these often represent the major component of the downward POC flux.

3.2. Fast-sinking faecal pellets: In some locations and times, the downward POC flux largely consists of fast-sinking faecal pellets (Fortier et al. 1994). These pellets are produced by actively feeding large gelatinous zooplankton (e.g. salps; Fortier et al. 1994). Because these organisms can be locally very abundant (Madin et al. 1996, Andersen 1998, Gorsky & Fenaux 1998), their production of faecal pellets may both significantly increase the downward POC flux and reduce the release of faecal pellet derived DOC in the upper waters (Steinberg et al. 2000).

3.3. Vertical migrations: The downward OC transport in the form of vertically seasonally migrating organisms may be important in some ocean regions (e.g. Morales 1999). The OC remineralized to CO_2 or released as DOC below the permanent pycnocline during deep seasonal migrations of large zooplankton may remain in the deep ocean for long periods (100s of years) and be thus sequestered. This is not the case for the OC respired by zooplankton that vertically migrate to several 100 metres on diel cycles, because the resulting CO_2 may be returned to surface waters, where it can re-equilibrate with the atmosphere.

3.4. Renewable resources: The larval stages of many of the finfish and shellfish that are important marine renewable resources belong to the large zooplankton node. In addition, the growth of most large metazoans, including finfish and marine mammals and birds, depends on the transfer of carbon from the small components of the food web via large zooplankton. Hence, the production of large zooplankton is one of the factors that regulate the ocean's renewable resources.

Much of the current focus of biological oceanography on the biogeochemistry of carbon is developing within the context of the role of oceans in the regulation of atmospheric CO_2 concentrations, the progressive exhaustion of exploited wild living marine resources, and the rapid development of marine farming. The above items 1 through 3.3 are of significance to the ocean's mediation of global climate processes, and items 1, 2.2, 3.1 and 3.4 are of significance to the continued sustained exploitation of renewable marine resources and to marine farming. It follows that the food-web control node model of carbon fluxes in the upper ocean is relevant to ongoing research on several global environmental problems.

QUANTIFICATION OF THE FOOD-WEB CONTROL NODES MODEL

Model equations

The above discussion shows that the 3 food-web nodes control the 5 major carbon fluxes in the illuminated region of the upper ocean. Three of these fluxes are phytoplankton production (P_T), euphotic-zone remineralization of OC to CO_2 (i.e. respiration; R) and transfer to the pelagic organisms (F). The 2 other fluxes are the partitioning of downward export out of the euphotic zone (E_T) into exported DOC (E_{DOC}) and POC (E_{POC}), where E_{POC} includes OC transported downwards by vertically migrating organisms. The partitioning of P_T among R, F and E_T is summarized in the following general equation:

$$P_T = R + F + E_T \quad (7)$$

Subscript T stands for total and, where appropriate, the fractions are specified. Over the long-term steady state (i.e. multiyear), the OC that is incorporated into the pelagic food web (F) is either respired in the upper ocean or exported downwards. Hence, F is ultimately

partitioned between R and E_T, and Eq. (7) can be rewritten as

$$P_T = R + E_T \quad (8)$$

By rearranging Eq. (8), E_T can be computed as follows:

$$E_T = P_T - R \quad (9)$$

This equation shows that E_T is the same as net community production (NCP). Because E_T is composed of E_{DOC} and E_{POC}, Eq. (8) is rewritten as follows:

$$P_T = R + E_{DOC} + E_{POC} \quad (10)$$

Fig. 4 shows that both the microbial heterotrophic plankton and large zooplankton nodes contribute to R. If follows that resolving Eqs. (8) & (9) should include these 2 food web control nodes. However, because the bacterial component of microbial heterotrophic plankton accounts for most of the euphotic zone respiration (Rivkin & Legendre 2001, Robinson et al. 2002), we are assuming here that R in Eqs. (8) & (9) can be approximated without including the respiration of protistan and large zooplankton.

Testing the model

Eqs. (8), (9) & (10) allow the computation of OC export from the food-web characteristics of P_T and R. One way to test the food-web control nodes model is by comparing export estimated as $E_T = P_T - R$ with that determined from new production, trap fluxes or ^{234}Th disequilibrium. Many empirical models relate P_T and export (or E_{POC}) (Suess 1980, Betzer et al. 1984, Bishop 1989), but the relatively poor performance of these models in some situations suggests that factors additional to P_T may control E_{POC} (e.g. Bishop 1989, Boyd & Newton 1995, Karl et al. 1996, Buesseler 1998).

The estimation of E from P_T and R is conceptually simple and thus attractive. Although R has been directly estimated for relatively few regions of the World Ocean (Williams 1998, 2000), it may be possible to compute R from food-web characteristics. For example, it has been suggested that the bacterial component of the microbial food web is responsible for most of the heterotrophic respiration in the water column (Williams 1984, Hopkinson et al. 1989, Sherr & Sherr 1996, del Giorgio & Cole 1998, 2000 and others). However, because of methodological constraints, bacterial respiration (BR) is often estimated from BGE and BP.

Since the fraction of B_{DOC} that is not used to synthesize bacterial biomass is ultimately respired (i.e. B_{DOC} = BP + BR), Eq. (4) can be rewritten to compute BGE as

$$BGE = \frac{BP}{BP + BR} \quad (11)$$

Hence,

$$BR = \frac{BP}{BGE} - BP \quad (12)$$

We have shown (Rivkin & Legendre 2001) that BGE is a highly significant ($p < 0.001$) inverse function of temperature (T):

$$BGE = 0.374\ (\pm 0.04) - 0.0104\ (\pm 0.002)\ T \quad (r^2 = 0.54,\ n = 111) \quad (13)$$

Hence, BR can be directly computed from concurrent estimates of BP and T as

$$BR = \frac{BP}{0.374 - 0.0104T} - BP \quad (14)$$

Using a data set that was completely independent from the one used to develop Eq. (14), we found that, over a wide range of observed BP (0.2 to 415 mg C m^{-3} d^{-1}), T (–1.4 to 29°C) and R_T (1.8 to 2300 mg C m^{-3} d^{-1}), there was a significant relationship between BR computed from Eq. (14) and measured R. The slope and r^2 of 1.10 and 0.88, respectively, suggest that, for a wide diversity of conditions and scales, BR is an accurate proxy for R, and it can be estimated from T and BP.

IMPLEMENTATION OF THE MODEL

Comparing the model with independent data

The implementation of our model requires the computation of E_T (Eq. 9) from concurrent estimates of P_T and R (where R is computed from Eq. 14). Because $P_T - R$ is an estimate of both NCP and export (Eq. 9), we compare our computed E_T with both NCP estimated from new production (P_{new}; i.e. Laws et al. 2000) and E estimated from ^{234}Th disequilibrium (E_{TH}). Because heterotrophic stocks and processes in the upper ocean are grossly under-sampled compared to those of phytoplankton or even vertical carbon fluxes, there is only a limited number of regions where comprehensive process studies have been carried out. We have compiled information on these variables for 8 sites in different regions of the World Ocean (Table 2).

Table 2 includes sites from polar, temperate and tropical ocean areas, and contains field values for the depth of the euphotic zone (z_{eu}), T, P_{new}, P_T, BP, E_{TH} and computed values for BR ≈ R (Eq. 14) and $E_T = P_T - R$ (Eq. 9). Values for z_{eu}, T, P_{new}, and P_T come from Table 3 of Laws et al. (2000). The rates of P_{new} and P_T they reported were converted from N-based to C-based values using the Redfield C:N ratio. The BP rates reported by Ducklow (1999; his Table 1) include all the sites described by Laws et al. (2000), except HOT, the Peruvian upwelling system and the Northeast Water Polynya (NEW). As far as we know, there

Table 2. Observed depth of the euphotic zone (z_{eu}; m), temperature (T; °C), new (P_{new}) and total (P_T) phytoplankton production, bacterial production (BP) and downward export estimated from ^{234}Th disequilibrium (E_{TH}), and computed bacterial respiration (BR, Eq. 14) and export ($E_T = P_T - R$, Eq. 9), at 8 sites in the World Ocean. All rates were vertically integrated over the euphotic zone (mmol C m^{-2} d^{-1}). The values of P_{new} and P_T are those reported by Laws et al. (2000; their Table 3); they were converted from N-based to C-based values using the Redfield C:N ratio. Unless otherwise indicated, BP values are from Ducklow (1999; his Table 1). na: data not available

Site	z_{eu}	T	P_{new}	P_T	BP	BR	E_T	E_{TH}	
								Mean	Range
N. Atlantic, subtropical (BATS)	140	21	3.7	38.7	5.8	31.7	7.0	2.6	1 to 6
N. Pacific, subtropical (HOT)	150	25	5.8	39.1	na	na	na		
N. Atlantic, temperate (NABE)	35	12.5	46.2	91.5	22.9	71.0	20.5	36	7 to 77
Equatorial Pacific, normal	120	24	15.1	122.6	23.8	167.2	–44.6	2.8	1 to 8
Equatorial Pacific, ENSO	120	27	5.8	79.7	14.7	142.7	–63.0	2	1 to 4.5
Arabian Sea	65	25	13.8	91.9	21.4	166.4	–74.5	10	1 to 26
Ross Sea	40	0	77.8	114.6	4.6	7.7	106.9	15.6	8 to 22
N. Pacific, subpolar (PAPA)	120	6	19.0	44.8	4.7	10.3	34.5	5.8	2.8 to 7.7
Peru upwelling, normal	25.5	16.8	159.8	405.4	42.5[a]	170.8	234.7	na	
Peru upwelling, ENSO	17.8	17.4	120.7	408.7	29.6[a]	124.0	284.7	na	
N. Atlantic, polar (NEW)	50	0	16.8	29.8	0.82[b]	1.4	28.5	39	13 to 70

[a]Data from the upwelling system off of Chile (McManus & Peterson 1988)
[b]Bacterial production was computed as the product of bacterial biomass and growth rates. Data from Smith et al. (1995), Yager (1996) and Yager & Deming (1999)

are no published or reported BP data for HOT (Hawaii Ocean Time-series) (see Karl & Lukas 1996, Karl 1999 and http://hahana.soest.hawaii.edu/hot/methods/pprod.html). In addition, because there are no published PB data for the Peruvian upwelling system, we used instead those for the Chilean upwelling (McManus & Peterson 1988, Ducklow & Carlson 1992). BP in the NEW was computed from published bacterial growth rates and bacterial biomass (Smith et al. 1995, Yager 1996, Yager & Deming 1999). Values of E_{TH} are from Buesseler (1998), Charrette et al. (1999) and Buesseler et al. (2001).

In Table 2, temperatures range from 0 to 28°C, with euphotic zone depths of 35 m (for the North Atlantic Bloom Experiment) to 150 m (HOT site). BP varies among sites by ca. 60-fold, and computed BR (Eq. 14) by ca. 150-fold. The highest and lowest rates of both BP and BR are in the upwelling region and the NEW, respectively. As explained above, 1 test of our food-web control nodes model is to compare $E_T = P_T - R$ with P_{new} or E_{TH}. New production (as computed by Laws et al. 2000) ranges between 3.7 and 160 mmol C m^{-2} d^{-1} (43-fold) at BATS and the upwelling system, respectively. In contrast, E_T (Eq. 9) ranges between –74 and –44 mmol C m^{-2} d^{-1} in the Arabian Sea and the Equatorial Pacific, respectively, to 284 mmol C m^{-2} d^{-1} in the upwelling system. By virtue of their respective methodologies, P_{new} and the collection of settling particles in interceptor traps or isotope disequilibrium must be positive. In contrast, our approach of computing E_T as the difference between 2 independently determined properties allows the possibility of locally negative values. If we consider only those E_T values that are positive, the range is between 7 and 284 mmol C m^{-2} d^{-1} (41-fold) at BATS and the Peruvian upwelling system, respectively. There is a very strong linear relationship between E_T and P_{new} (major axis Model II regression, $r^2 = 0.85$; Fig. 5):

$$E_T = -60 + 2.4P_{new} \quad (15)$$

This indicates that when $P_{new} > 43$ mmol C m^{-2} d^{-1} then $E_T > P_{new}$. The relationships between (1) E_T and E_{TH} and (2) P_{new} and E_{TH} are very weak ($r^2 = 0.01$ and 0.12, respectively).

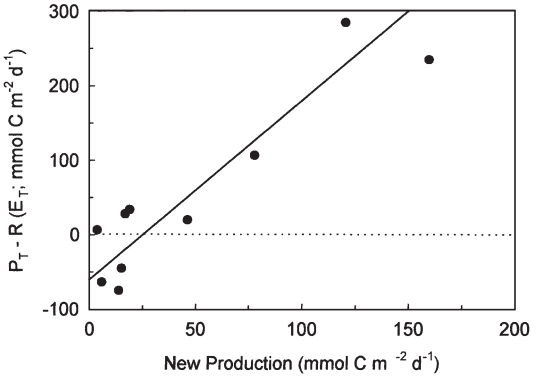

Fig. 5. Scatterplot of computed euphotic-zone $E_T = P_T - R$ (Eq. 9) as a function of observed (euphotic-zone) P_{new} (Table 2), and major axis Model II regression (95% confidence interval): $E_T = -60$ (–116 to –29) + 2.4 (1.7 to 3.5) P_{new} ($r^2 = 0.85$). Regression (solid) and zero (dashed) lines are shown for visual reference

Unexpected relationships

Two aspects of the relationship between E_T and P_{new} require further exploration: (1) the negative values E_T in the Arabian Sea and Equatorial Pacific, and (2) the systematically higher values of E_T than those of P_{new} when the latter is >43 mmol C m^{-2} d^{-1}.

Negative E_T values

There is presently an extensive, yet unresolved debate on metabolic balance in oligotrophic oceans, i.e. whether large ocean areas are carbon sinks (del Giorgio et al. 1997, Duarte & Agusti 1998, Alvarez-Salgado et al. 2001, Duarte et al. 2001) or sources (Williams 1998, Williams & Bower 1999). Rates of heterotrophic respiration higher than those of local primary production (i.e. $P_T < R$, and negative NCP) have been reported for several ocean areas, including the Arabian Sea, the Equatorial Pacific and the tropical North Atlantic. This is consistent with our computed E_T for the Arabian Sea and the Equatorial Pacific (Table 2). Negative E_T values mean that the heterotrophic demand for OC exceeds the local rate of primary production. There are 2 possible explanations for this: heterotrophic metabolism is partly sustained by lateral or atmospheric input of OC, or DOC production (and release) by phytoplankton was not included in the reported rates of primary production (this is usually the case). In the latter case, P_T (i.e. dissolved + particulate production) could be up to 50 to 75% higher than particulate primary production (Karl et al. 1998).

Higher E_T than P_{new}

As noted above, both E_T and P_{new} provide estimates of NCP (Hansell & Carlson 1998). Hence, the 2 quantities should be similar when integrated over broad spatio-temporal scales. However, P_{new} is always >0, whereas E_T can be <0 locally or regionally (Table 2). Given that $E_T \approx P_{new}$ globally, and $E_T < P_{new}$ in some areas, it follows that $E_T > P_{new}$ in other areas (i.e. when $E_T = 0$, $P_{new} = 25$ mmol C m^{-2} d^{-1}) According to Eq. (15), $E_T = P_{new}$ only when the latter is about 43 mmol C m^{-2} d^{-1}.

CONCLUSIONS

The conceptual model developed in this paper provides an alternative approach to the analysis and estimation of food-web-controlled carbon fluxes in the upper ocean. This new approach is based on the recognition that the pools of CO_2, DOC and POC in the upper ocean are involved in 5 major carbon fluxes (i.e. CO_2 uptake, respiration of OC back to CO_2, transfer of OC to the pelagic food web, and downward export of DOC and POC), and the linking of these 5 fluxes to 3 food-web control nodes (i.e. phytoplankton, microbial heterotrophic plankton and large zooplankton). Operationally, the flux of carbon through the phytoplankton node is partitioned into community respiration, transfer to the pelagic food web, and downward export out of the euphotic zone (Eq. 7). This partitioning is controlled by the microbial heterotrophic plankton and large zooplankton nodes. When the aim of the study does not include large metazoans, the flux to the pelagic food web vanishes (Eq. 8). Even if total export (DOC + POC) is controlled by the microbial heterotrophic plankton and large zooplankton nodes, it can be estimated without considering the latter node because microbial heterotrophic plankton is responsible for most of the community respiration (Eq. 9). However, it is essential to consider large zooplankton when assessing the flux of OC to large metazoans.

Further partitioning of total downward export could proceed as follows: Because the partitioning of downward export into POC and DOC (Eq. 10) is controlled by the microbial heterotrophic plankton node, its estimation would require considering that node only. Because the exported POC includes phytodetritus, faecal pellets and vertically migrating organisms, the partitioning of POC export would require consideration of the large zooplankton node. Hence, the approach to food-web-controlled carbon fluxes proposed and illustrated in the present study is to progressively partition the fluxes into more detailed components. A first-order partitioning can be obtained by analysing the food-web properties of 3 control nodes.

We implemented our model by estimating export as $E_T = P_T - R$ (Eq. 9) at 8 sites in different regions of the World Ocean. Because we estimate E_T as the difference between 2 independent variables (i.e. P_T and R), our approach can and does produce local or regional values of $E_T < 0$. This is not possible with approaches where export is calculated as a fraction of P_T, which is a fundamental distinction between our and other current methods of computing export (e.g. Laws et al. 2000 and references cited therein). Our approach allows the identification of areas where net community production is negative and which are thus net heterotrophic. Our results contribute to ongoing debates on the possible net heterotrophy of some ocean regions, and underestimation of primary production. Overall, our approach improves our understanding of carbon cycling and export in the upper ocean.

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