Deep-Sea Research II 56 (2009) 941–953

Contents lists available at ScienceDirect

Deep-Sea Research II

journal homepage: www.elsevier.com/locate/dsr2

Predicting plankton net community production in the Atlantic Ocean

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ARTICLE INFO

Article history:
Accepted 2 October 2008
Available online 17 November 2008

Keywords:
Empirical prediction
Marine plankton
Respiration
Net community production
Trophic scale
Ocean biogeography

ABSTRACT

We present, test and implement two contrasting models to predict euphotic zone net community production (NCP), which are based on ^{14}C primary production (PO^{14}CP) to NCP relationships over two latitudinal (ca. 30°S–45°N) transects traversing highly productive and oligotrophic provinces of the Atlantic Ocean (NADR, CNRY, BENG, NAST-E, ETRA and SATL, Longhurst et al., 1995 [An estimation of global primary production in the ocean from satellite radiometer data. Journal of Plankton Research 17, 1245–1271]). The two models include similar ranges of PO^{14}CP and community structure, but differ in the relative influence of allochthonous organic matter in the oligotrophic provinces. Both models were used to predict NCP from PO^{14}CP measurements obtained during 11 local and three seasonal studies in the Atlantic, Pacific and Indian Oceans, and from satellite-derived estimates of PO^{14}CP. Comparison of these NCP predictions with concurrent in situ measurements and geochemical estimates of NCP showed that geographic and annual patterns of NCP can only be predicted when the relative trophic importance of local vs. distant processes is similar in both modeled and predicted ecosystems. The system-dependent ability of our models to predict NCP seasonality suggests that trophic-level dynamics are stronger than differences in hydrodynamic regime, taxonomic composition and phytoplankton growth. The regional differences in the predictive power of both models confirm the existence of biogeographic differences in the scale of trophic dynamics, which impede the use of a single generalized equation to estimate global marine plankton NCP.

This paper shows the potential of a systematic empirical approach to predict plankton NCP from local and satellite-derived P estimates.

1. Introduction

Global C cycle models highlight the importance of the marine biota in controlling ocean and atmospheric CO$_2$ (e.g., Stephens et al., 1998), hence the accurate determination of the balance between plankton production and respiration in the ocean is important for C budgets and global change predictions (del Giorgio and Duarte, 2002).

Net community production (NCP), i.e. the difference between gross primary production (GP) and total (algal plus heterotrophic) community respiration (R), summarizes the metabolism of a biological community. However, the interpretation or extrapolation of instantaneous measurements of NCP in terms of basin scale ecological and biogeochemical processes critically depends on our knowledge of the spatial and temporal scales of plankton food-web dynamics. Unfortunately, the measurement of plankton GP, R and NCP is relatively time consuming, which has severely hampered the development of representative regional, annual or global databases from which to derive the relevant scaling properties (Robinson and Williams, 2005) and to improve our estimate of the global annual GP:R balance.

To overcome the paucity of direct measurements, some studies have compiled different data sets to produce empirical relationships between GP and R, with which to predict GP:R balances from GP (e.g., Williams, 1998; Duarte and Agustí, 1998; Duarte et al., 2001; del Giorgio and Duarte, 2002; Agustí and Duarte, 2005). These relationships show that R is less variable than GP, but disagree on the predicted 'threshold' rate of GP at which R exceeds GP, and hence the extrapolation of these models to predict the net metabolism of the open ocean from GP estimations has generated an active debate. del Giorgio and Duarte (2002) extended this empirical approach by integrating the range of

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0967-0645/$ - see front matter © 2009 Published by Elsevier Ltd.
doi:10.1016/j.dsr2.2008.10.006

models to constrain the "representative mean value of respiration for the surface layer of the ocean". They used the linear equation of Williams (1998) and the non-linear equation of Duarte and Agustí (1998) to produce a range of estimates of global respiration from the annual average of primary production in each of the biogeographic provinces in the open ocean defined by Longhurst et al. (1995). However, this solution to the debate assumes that any generalized GP:R equation is valid for all provinces of the open ocean.

The empirical approach to dealing with ecological complexity establishes predictive power as the key criterion to discriminate between conflicting hypotheses (e.g., Peters, 1991), and usually depends on comparisons among systems (e.g., del Giorgio et al., 1999), which gives "the resulting models generality and established patterns against which to evaluate other systems" (Pace, 2001). However, due in part to the limited data available, the conflicting empirical marine plankton GP:R relationships (Williams, 1998; Duarte and Agustí, 1998) were derived from the unspecific aggregation of published GP and R data, disregarding the geographic, temporal, structural and functional differences between the ecosystems included, and no systematic validation exercise was performed.

Under these circumstances, the idea that R is universally scaled to GP, so that any empirical GP:R relationship derived from short-term measurements may be extrapolated with annual averages of production across the pelagic biomes of the World ocean (del Giorgio and Duarte, 2002), assumes that GP always controls R (but see Serret et al., 2006), and rests on two alternative scenarios:

1. A prevalence of steady-state conditions throughout the ocean, that is, that the connection between the processes of production and consumption of organic matter always occurs locally in both space and time with no relevant role played by ecosystem structure, or allochthonous inputs of organic matter.
2. If allochthonous organic matter or ecosystem structure do influence the net ecosystem metabolism, then the absolute constancy, or at least the absence of any systematic temporal or regional variation, of these factors throughout the World ocean.

However the accumulation, transport and consumption of dissolved organic matter (DOM) in the water column are relevant processes (Hansell and Carlson, 1998) that disconnect the local production and consumption of organic matter at short (e.g., Blight et al., 1995; Serret et al., 2001b), seasonal (e.g., Scavia and Laird, 1987; Serret et al., 1999) and regional scales (e.g., Duarte et al., 2001; Robinson et al., 2002; Serret et al., 2006). Likewise food web organization (including the biomass, species and activity of the heterotrophs), and not only the magnitude of GP, has been found to influence the net metabolism of plankton ecosystems both experimentally (McGrady-Steed et al., 1997; Schindler et al., 1997) and from the observation of across-system patterns (Serret et al., 2001a). Finally, it is well established that neither plankton community structure nor DOM dynamics remain constant throughout the year nor the World ocean; they vary systematically with the hydrodynamic regime and primary productivity (e.g., Kiørboe, 1993; Teira et al., 2001a), thus producing characteristic seasonal cycles of, and regional differences in, primary production (Longhurst, 1998), community structure (Tamigneaux et al., 1999; Tremblay and Legendre, 1994; Boyd and Newton, 1999) and DOM accumulation and depletion (Hansell and Carlson, 1998; Teira et al., 2001b), that are reflected in seasonal (e.g., Serret et al., 1999) and regional (e.g., Serret et al., 2001a, 2006) variations of the net ecosystem metabolism (Jansson et al., 2000; Hanson et al., 2003).

In previous studies (Serret et al., 2002, 2006) we suggested that such a systematic seasonal and regional covariation of hydrodynamics, primary production, allochthonous inputs and trophic functioning gives rise to biogeographic differences in the trophic dynamics and net ecosystem metabolism of the open ocean. From the published NCP data in the open ocean, we proposed the existence of net autotrophic (Bender et al., 1999), seasonally compensated (Serret et al., 1999), locally balanced (Serret et al., 2002) and subsidized (Duarte et al., 2001; González et al., 2001; Serret et al., 2001a, 2002) pelagic ecosystems. Although the fundamental food-web processes are common to all these ecosystems, important differences exist in their relative importance, and especially in the spatial and temporal scale of their interaction. These differences imply that, if GP:R relationships can be used for prediction of NCP, no single relationship can be expected to be universally valid. For predictive purposes, different, system-dependent, GP:R relationships should apply to different areas/times of the ocean. Given that these trophic biomes need to integrate local and remote processes influencing net community metabolism, a partition based on the phytoplankton growth (e.g., Longhurst et al., 1995) may be incomplete (Serret et al., 2006). However, the paucity of the regional R database prevents the delineation of a complete trophic–biogeographic partition of the ocean from the spatial and temporal variation of GP and R.

The empirical relation between two ecological processes whose interaction varies with time and space is valid only over a limited domain of scales where the interactions remain invariable (Wiens, 1989; Strayer et al., 2003). The characteristics of plankton community organization and the paucity of R measurements complicates the use of changes in pattern-process relationships to recognize the relevant scale transitions (Ludwig et al., 2000), but predicting ecosystem rates from instantaneous measurements of processes will only be possible when the functional scales of both the modeled and predicted ecosystems are the same. Consequently, exploring the geographic and temporal ranges where a particular empirical GP:R relationship is valid, will constrain the long-term and large spatial scales of trophic functioning. This approach has been preliminarily explored in Serret et al. (2001a, 2002, 2006), but progress towards global implementation requires improving the potential of models to predict NCP.

This study examines the validity of the empirical approach to NCP prediction, and the sensitivity of P:R relationships to the scale of marine plankton trophic dynamics. To this aim, our specific objectives are (1) to present and test two contrasting predictive models of marine plankton NCP based on empirical relationships with ^{14}C-derived primary production, and using data from ecosystems differing in the relative importance of local vs. remote processes in their net ecosystem metabolism, (2) to explore the potential that the analysis of the regional and seasonal validity of these models creates for the study of the scale over which they function, i.e. for progress towards a trophic–biogeographic partition of the ocean, and (3) to predict the seasonal variability and annual balance of NCP in the biogeographic provinces (Longhurst et al., 1995) included in the original models, and to study the importance that regional differences in functional scale (context) have in the extrapolation or prediction from NCP measurements. We assume that, beyond differences in taxonomic composition and functional diversity, some common processes govern the trophic organization of planktonic communities, giving rise to ecosystem-level patterns of NCP across oceanic biomes; and that these processes can be summarized in the relationship between primary production, plankton community structure (as summarized by phytoplankton size, e.g., Kiørboe, 1993) and community respiration. Our main hypothesis is that the scale of trophic-level dynamics of pelagic planktonic ecosystems varies predictably between habitats.

2. Methods

2.1. Model construction

GP, NCP and R were determined from in vitro changes in dissolved oxygen concentration after 24 h light and dark bottle incubations (Serret et al., 2001a, 2002). This is the same method used in published plankton GP, NCP or R empirical models (Williams, 1998; Duarte and Agustí, 1998; Duarte et al., 1999; Duarte et al., 2001; Serret et al., 2001a, 2002; Arístegui and Harrison, 2002). NCP and R rates are calculated from the difference between the light (under irradiance conditions simulating those of the original sampling depth) and dark incubated and zero time O_2 concentrations, respectively: NCP = measured ΔO_2 in light bottles (mean of $[O_2]$ in 24-h light−mean initial $[O_2]$); R = measured ΔO_2 in dark bottles (mean initial $[O_2]$−mean $[O_2]$ in 24-h dark); GP is calculated, not directly measured, from the sum of the measured changes in dissolved oxygen concentration in the incubated light and dark bottles: GP = NCP+R. Primary production was determined as the uptake of ^{14}C-bicarbonate into particulate organic carbon (PO^{14}CP) (Serret et al., 2006).

Since GP and R are methodologically dependent variables, GP:R empirical relationships are prone to spurious correlations and provide poor empirical power (Berges, 1997; Sokal and Rohlf, 1995). Additionally, whenever GP is measured, R and NCP are too, hence a GP:R relationship adds no real predictive power. On the other hand, while PO^{14}CP and NCP are measures of related physiological properties, they are methodologically independent, thus giving empirically fitted curves the predictive potential for the substitution of the more difficult to measure NCP by the easier to measure PO^{14}CP (Sokal and Rohlf, 1995). Additionally, only the immense dataset of PO^{14}CP measurements, and satellite-derived estimates of primary production (currently calibrated using PO^{14}CP measurements), will ultimately allow a global prediction of NCP.

We therefore developed two predictors for the euphotic zone integrated NCP from its relationship with integrated PO^{14}CP over two latitudinal (ca. 30°S–45°N) transects of the Atlantic Ocean (Atlantic Meridional Transect (AMT)-6 and -11 cruises) (Serret et al., 2001a, 2002, 2006) (Fig. 1). For the AMT6 model we used data from three productive biogeochemical provinces (NADR, CNRY and BENG. Longhurst et al., 1995) and two oligotrophic, net heterotrophic, and hence locally subsidized, provinces (NAST-E and ETRA) (Serret et al., 2001a; Robinson et al., 2002) of the eastern Atlantic Ocean. For the AMT11 model we used data from the productive NADR, CNRY and also the equatorial upwelling within the ETRA, but on this occasion the low production data utilized in the model come from the oligotrophic and isolated central part of the South Atlantic mid-ocean gyre (SATL) where the net metabolism of the plankton communities remained locally balanced (Serret et al., 2006). The two datasets from the ETRA (Longhurst et al., 1995) are assigned as representative of highly productive (AMT11) and oligotrophic (AMT6) communities following the distinction by Pérez et al. (2005) of an equatorial divergence area and a typical tropical structure within the ETRA. Such division is based on the distribution of microbial plankton abundance, production and respiration, and is therefore appropriate for this study.

As our objective is prediction, and following the recommendations given by Sokal and Rohlf (1995), the ordinary least-squares (o.l.s.) linear regression model was used instead of the model II reduced major axis, despite both PO^{14}CP and NCP rates being subject to measurement error.

2.2. Model validation and implementation

2.2.1. Comparison of predicted NCP with measured NCP

2.2.1.1. General validation. We compiled data from 12 published and one unpublished studies of GP, R and PO^{14}CP in coastal and oceanic systems of the Atlantic, Pacific and Indian Oceans. Depth integrated NCP was predicted from PO^{14}CP using the PO^{14}CP:NCP

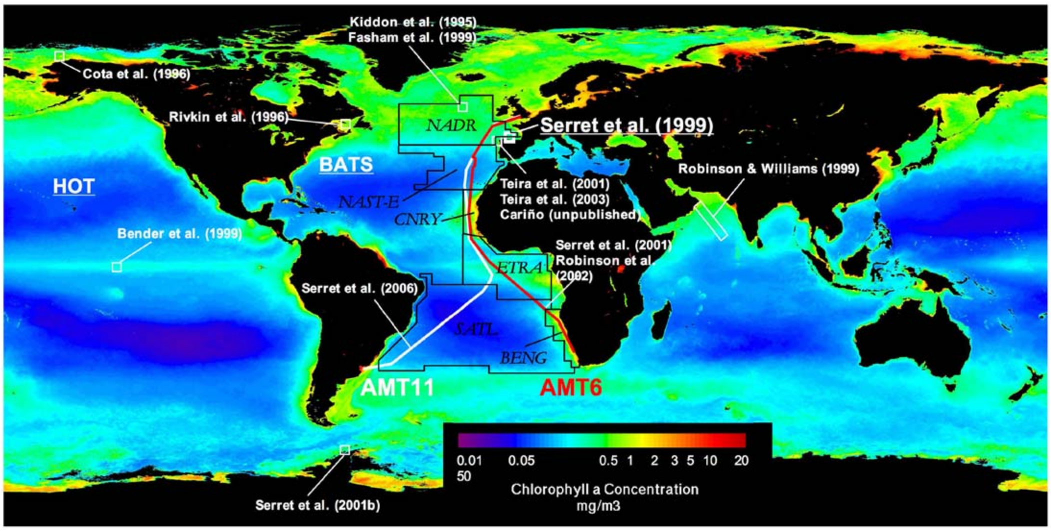

Fig. 1. AMT6 and AMT11 cruise tracks overlaid over SeaWiFS chlorophyll *a* September 1997–August 2000 composite image. Image provided by the SeaWiFS Project, NASA/Goddard Space Flight Center and ORBIMAGE. The approximate boundaries of the biogeochemical provinces (Longhurst, 1998) traversed are shown: Benguela Current Coastal (BENG), Eastern Tropical Atlantic (ETRA), Canary Coastal (CNRY), North Atlantic Subtropical Gyral (NAST-E), North Atlantic Drift (NADR) and South Atlantic Gyral Province (SATL). Also shown are the approximate positions of the published data used in this study, as well as the US JGOFS Hawaii Ocean Time-series (HOT) and Bermuda Atlantic Time-series Study (BATS) sites. The underlined studies (Serret et al., 1999; HOT and BATS) correspond to those where the most complete validation of our models is performed.

relationships presented here, and compared with concurrently measured depth integrated NCP.

2.2.1.2. Seasonal cycle of NCP in the S Bay of Biscay. Uncertainties about the temporal scales of GP:R linkage in different pelagic ecosystems imply that the snap-shot, unspecific validation above is not a powerful test. The best comparative data set for validation purposes would be a seasonal study of integrated NCP. One of the few published seasonal studies of photic zone integrated NCP and PO^{14}CP in the Atlantic Ocean is an 18 month survey at three stations across the coastal transitional zone (depths of ca. 70, 250 and 1000 m) of the Southern Bay of Biscay (Serret et al., 1999). Lacking PO^{14}CP data for the whole series, we have estimated it from GP using a molar ratio of 1.3. This assumes that, given a stoichiometric photosynthetic quotient (PQ) ranging between 1.0 and 1.25 (Laws, 1991; Williams and Robertson, 1991), the percentage of GP allocated to the dissolved fraction ranges from 23% to 5% (Fogg, 1983), which concurs with observations (Teira et al., 2001b).

2.2.2. Comparison of predicted NCP with O_2 saturation

To overcome the paucity of seasonal NCP measurements, especially in the open ocean, an alternative for validation is to use chemical tracers of the plankton GP:R balance, e.g., O_2 saturation (O_2 Sat).

2.2.2.1. Seasonal variability of predicted NCP and O_2 Sat at HOT and BATS. The US JGOFS Hawaii Ocean Time-series (HOT) and Bermuda Atlantic Time-series Study (BATS) are among the most comprehensive physical-biogeochemical long-term studies of the ocean (see programme overviews by Karl and Lukas, 1996; Michaels and Knap, 1996; Steinberg et al., 2001). We have used monthly HOT and BATS PO^{14}CP data from the US JGOFS Data System at http://www1.whoi.edu/jg/dir/jgofs/ to estimate integrated NCP with both the AMT6 and AMT11 models. These results are compared with the variability of the O_2 Sat down to the depth of the winter mixed layer (85 m at HOT -Karl and Lukas, 1996; 200 m at BATS-Bisset et al., 1994; Anderson and Pondaven, 2003) throughout 10 (1989–98) and 9 (1989–97) years, respectively.

2.2.2.2. Mean seasonal cycle of predicted NCP and O_2 Sat in the NADR. One of our final objectives is the global prediction of marine plankton NCP. For this we must rely on satellite-derived estimates of P that can provide both the biogeographically relevant scales for integration and data for model implementation. We have implemented both models with the mean seasonal cycle of Coastal Zone Color Scanner (CZCS)-derived integrated primary production in the North Atlantic Drift Province (NADR, Longhurst et al., 1995; Longhurst, 1998). The derived *mean* seasonal cycle of integrated NCP predicted in the NADR was then compared to the seasonal variation of integrated NCP from 7 published studies and O_2 Sat measured at the most oceanic station in the S Bay of Biscay study (Serret et al., 1999).

2.2.3. Estimation of the mean seasonal cycle of plankton NCP

We have implemented the two NCP predictive models using the seasonal variation of satellite-derived P in the six biogeochemical provinces (Longhurst, 1998) from which the original data were collected (Fig. 1).

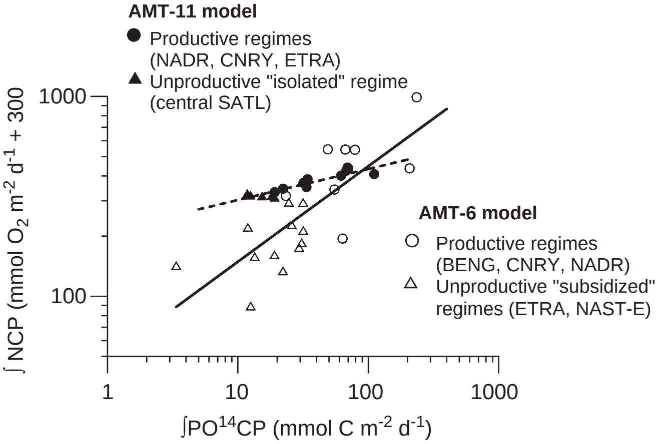

Fig. 2. Relationships between integrated particulate organic ^{14}C-derived primary production (PO^{14}CP) and integrated net community production (NCP) in the AMT6 and AMT11 data bases. The equations giving the best fit to the data are: AMT6 (solid line) $\int NCP = 49.53 \times \int PO^{14}CP^{0.48} - 300$ ($r^2 = 0.61$, $n = 21$, $p < 0.001$); AMT11 (dotted line) $\int NCP = 212.01 \times \int PO^{14}CP^{0.15} - 300$ ($r^2 = 0.85$, $n = 15$, $p < 0.001$). See text for details.

Table 1
Parameters of linear regression models (o.l.s.) of the form $\log\int NCP = a(\log\int PO^{14}CP)+b$.

Model	$a \pm$s.e.	$b \pm$s.e.	r^2	s.e. of the estimate	n	Residuals
AMT-6	1.69 ± 0.14	0.48 ± 0.09	0.61	0.16	21	0.00 ± 0.035
AMT-11	2.33 ± 0.03	0.15 ± 0.02	0.85	0.02	15	0.00 ± 0.005

3. Results and discussion

3.1. A simple statistical model for NCP prediction: basic constraints and description

Fig. 2 presents the relationship observed between euphotic zone integrated NCP ($\int$NCP) and PO^{14}CP ($\int$PO^{14}CP) in the AMT6 and AMT11 data sets. The location of the low production sampling sites in either subsidized (AMT6 model) or isolated (AMT11 model) areas of the ocean is reflected in the different slope of the relationships (Serret et al., 2002). The parameters of the linear regression models (o.l.s.) of the form $\log\int NCP = a(\log\int PO^{14}CP)+b$ are given in Table 1. The power transformations of the best fitted equations are AMT6: $\int NCP = 49.53 \times \int PO^{14}CP^{0.48} - 300$ ($r^2 = 0.61$, $n = 21$, $p < 0.001$) and AMT11: $\int NCP = 212.01 \times \int PO^{14}CP^{0.15} - 300$ ($r^2 = 0.85$, $n = 15$, $p < 0.001$). These equations were subsequently used to predict $\int$NCP from $\int$PO^{14}CP.

To derive a predictive model from the simple empirical relationship between two variables, it is important that the data set incorporates or allows the discrimination of relevant effects of those variables that modulate or constrain the predictive power of the relationship. Food web organization and allochthonous organic matter availability influence community respiration (and hence NCP), which should reflect upon any PO^{14}CP:NCP relationship.

The influence of food web organization on net community metabolism implies that the variation of NCP with PO^{14}CP may be different when analyzed within or between different communities (Serret et al., 2001a). Given that the response of the plankton, in terms of individual growth, to changes in the hydrodynamic regime, nutrients and organic matter availability is very rapid, the bottom-up and top-down connections between turbulence, nutrient concentration, primary production, community structure, grazing and recycling dynamics are usually also rapid. This suggests that plankton community structure and food-web functioning are usually tightly coupled over short to medium scales, which is the basis for the use of phytoplankton size as a proxy for community structure and food web dynamics (e.g., Kiørboe, 1993; Tremblay and Legendre, 1994). Consequently, the influence on NCP of plankton trophic functioning (e.g., Legendre and Rassoulzadegan, 1995) can be incorporated into the $PO^{14}CP$:NCP relationship by utilizing data representative of distinct community structures (Serret et al., 2001a).

The influence of allochthonous organic matter availability on net community metabolism is probably minor when the local primary production is high (e.g., spring bloom, coastal upwelling). However, in low production areas/times, allochthonous DOM may become so relevant as to switch the local balance to net heterotrophy (Robinson et al., 2002 and references therein). Consequently the variation of NCP with $PO^{14}CP$ will be different when low production data come from either isolated (e.g., the central part of mid ocean gyres) or subsidized (e.g., the periphery of the gyres near productive provinces, and the net heterotrophic phase after phytoplankton blooms) habitats. In contrast to community structure, the allochthonous DOM supply may be independent of local GP, thus making subsidized net heterotrophic pelagic ecosystems not only top-down but also donor-controlled. Consequently, the different GP:R relationships obtained with low production data from isolated and subsidized areas of the ocean cannot be combined into a single relationship because they are representative of different controlling mechanisms (Serret et al., 2002, 2006).

Therefore, the most appropriate data set for model construction from empirical $PO^{14}CP$:NCP relationships would be one which covered a range of magnitude of GP, a range of plankton communities, and a single type of low production data, located in either isolated or subsidized areas of the open ocean. These requirements are met by our two models, which differ in the type of low production data. Samples collected during both cruises spanned broad ranges of $PO^{14}CP$ (40–2822 $\text{mg C m}^{-2}\,\text{d}^{-1}$ during AMT6 and 141–1336 $\text{mg C m}^{-2}\,\text{d}^{-1}$ during AMT11) (ca. 3–235 and 12–111 $\text{mmol C m}^{-2}\,\text{d}^{-1}$, respectively). The size distribution of primary production, a proxy for community structure (Kiørboe, 1993), ranged from 73% to 4% by $<2\,\mu$m cells during AMT6 and from 73% to 33% during AMT11 (Serret et al., 2001a, 2002). We suggest that the relationship between GP and R in the World oceans cannot be encapsulated in a single representative model, and so aim to demonstrate inadequacies in both of the empirical models presented here. This approach is strengthened (not weakened) by the fact that both models share most of the same data: since the productive data and the GP range are similar, differences in their predictive ability must come from differences in the GP:R ratio in the different unproductive habitats, whose balance is particularly sensitive to allochthonous inputs of organic matter (see also Serret et al., 2006).

From the constraints defined above, we hypothesize that the AMT6 model should predict, and the AMT11 model should fail to predict, the net metabolism of seasonally or regionally subsidized pelagic ecosystems (e.g., NAST-E, NADR). On the contrary, the AMT11 model should predict, and the AMT6 model should fail to predict the net metabolism in isolated systems where local processes control NCP (e.g., central SATL). This hypothesis has been preliminarily tested in Serret et al. (2002), using only O_2GP:RO_2 models, and will be further explored here.

3.2. *Model validation and implementation*

Similar restrictions to those for model development apply to its validation. The influence of food web structure and DOM dynamics on $PO^{14}CP$:NCP relationships implies that short-term measurements, or studies performed in systems very far from steady-state (e.g., estuaries) would not be of use to validate our empirical models. Data of $PO^{14}CP$ and NCP are required to be photic zone integrated, *representative* of the functional communities and coherent with the origin of the low production data used for the respective model. Unfortunately, there are no published studies in the Atlantic Ocean gyres, apart from those used in our AMT11 model. Hence any validation exercise with independent data must be limited to the AMT6 model. Prediction based on implementing the AMT11 model with $PO^{14}CP$ data from subsidized ecosystems will only be used comparatively. Since both models are based on similar ranges of GP and community structure, the comparison of predictions will be a test of the sensitivity of the models to the hypothesized distinctive functional characteristics of isolated and subsidized oligotrophic pelagic ecosystems.

3.2.1. *Comparison of predicted NCP with measured NCP*

3.2.1.1. General validation. Fig. 3 shows the comparisons between measurements and predictions of $\int$NCP (NCPm and NCPp, respectively) obtained from both the AMT6 and AMT11 models. The 12 suitable studies of plankton metabolism covered a broad range of photosynthesis, community structure, R and NCP, but did not include isolated oligotrophic regions of the ocean such as the central SATL which is included in the AMT11 model. Both relationships between measured and predicted $\int$NCP are statistically significant (AMT6 model: $r^2 = 0.61$, $n = 150$, $p<0.001$; AMT11 model: $r^2 = 0.39$, $n = 151$, $p<0.001$). However, as expected, only the AMT6 model yielded reliable predictions (Fig. 3), as the slope and *x*-intercept of the equation describing the relation between predicted and measured $\int$NCP are not significantly different from 1 and 0, respectively (ANCOVA *F*-test, $p<0.001$), only when the AMT6 model is implemented. This conclusion is sustained when the highest NCPm value (from the wind-driven upwelling off NW Iberia; Teira et al., 2003) is removed from the regression, and when the range of predicted data by the AMT11 model is limited to the range of measurements included in the model (ca. −60 to 125 $\text{mmol O}_2\,\text{m}^{-2}\,\text{d}^{-1}$).

3.2.1.2. Seasonal cycle of NCP in the S Bay of Biscay. Fig. 4 shows the seasonal variation of NCPp and NCPm in the euphotic zone of three stations across the shelf in the S Bay of Biscay (Serret et al., 1999). The AMT6 model produces a remarkably similar trend to NCPm ($r^2 = 0.65$, $n = 42$, $p<0.001$) in both the temporal and spatial (offshore) axes. Both the AMT6-derived NCPp and NCPm show a similar pattern for the first year, characterized at every station by positive values during the spring, followed by a net heterotrophic balance throughout the summer, and a net autotrophic autumn bloom. During the winter, while near-zero values prevailed offshore, net heterotrophy was observed at the coastal station.

Again according to our expectations, the AMT11 model only reproduces the variability of NCP at high rates of primary production, but it always fails to predict the negative NCPm at low primary production rates, hence failing to depict the characteristic net auto-heterotrophic transitions.

Interestingly, both models failed to reproduce NCP measured offshore during spring 1995. At that time, the phytoplankton bloom observed at the coastal station was not related to the seasonal development of stratification but rather to an aged upwelling event (Serret et al., 1999). Such an upwelling also drove the offshore export and sinking of phytoplankton biomass produced near the coast, thus giving rise to high R rates, and NCP measurements close to zero at the shelf-break and off-shelf stations, together with high phytoplankton biomass and P (Serret

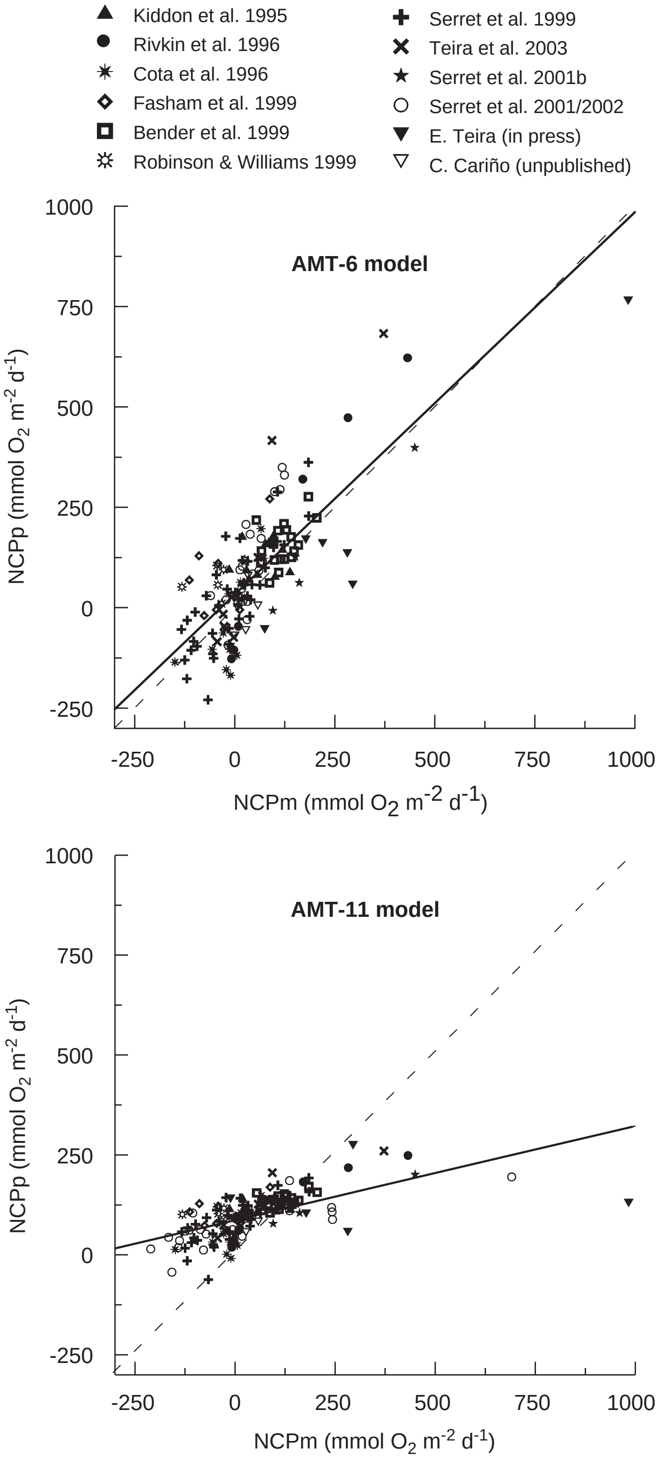

Fig. 3. Comparison of NCP measured (NCPm) and NCP predicted (NCPp) from concurrently measured integrated PO^{14}CP in 12 published studies, by using (A) the AMT6 and (B) the AMT11 empirical models. In (A) data from Serret et al. (2001a) (AMT6) are not included; in (B) data from Serret et al. (2002) (AMT11) are not included. The solid lines are the reduced major axis: AMT6 model: $NCPp = 0.96 \times NCPm + 33.30$ ($r^2 = 0.61$, $n = 150$, $p < 0.001$). AMT11 model: $NCPp = 0.24 \times NCPm + 86.8$ ($r^2 = 0.39$, $n = 151$, $p < 0.001$). The dotted lines are the 1:1 lines. Excluding the highest NCPm value in (A), the equation is: $NCPp = 1.08 \times NCPm + 29.22$ ($r^2 = 0.57$, $n = 149$, $p < 0.001$). Restricting the range of prediction to the range of measurements included in the AMT11 model, the equation (B) is: $NCPp = 0.52 \times NCPm + 81.9$ ($r^2 = 0.40$, $n = 98$, $p < 0.001$) (Rivkin et al., 1996; Cota et al., 1996; Robinson and Williams, 1999).

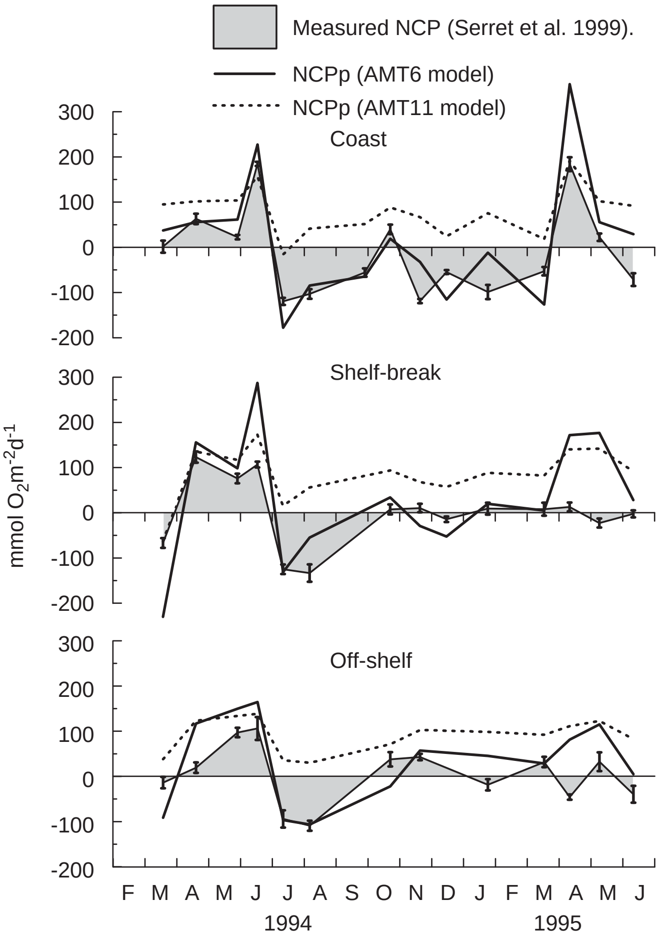

Fig. 4. Seasonal variation in euphotic zone NCP at three stations (ca. 70, 250 and 1000 m depth) across the shelf in the southern Bay of Biscay. The shadowed trend is the measured NCP (Serret et al., 1999) (±s.e.). NCP predicted by the AMT6 and AMT11 models is shown as solid and dotted lines respectively.

et al., 1999). Contrary to the situation observed during the summer, the subsidy of organic matter is mainly in the form of phytoplankton cells rather than DOM. Hence at the offshore stations high primary production data (on which both predictions are based) are not representative of the local plankton community, but rather result from the accumulation of phytoplankton produced inshore.

The failure of the AMT11 model to predict the seasonal net heterotrophy phases and the failure of both models to predict the NCP increase in spring 1995 illustrates the importance of matching the characteristics of the modeled and predicted ecosystems.

3.2.2. *Comparison of predicted NCP with O_2 saturation*

This is not a straightforward comparison. Nevertheless, the percentage of O_2 Sat in the upper ocean will constrain the rates of NCP with a certain time lag (e.g., Najjar and Keeling, 1997). Such a time lag is not constant, which makes direct comparison difficult. For instance, whenever the allochthonous organic matter sustaining a net heterotrophic metabolism is terrigenous, the negative GP:R balance may immediately lead to O_2 undersaturation. However, this is not necessarily the case when such organic matter was produced by aquatic organisms, as its accumulation in a parcel of water is coupled to dissolved O_2 accumulation. Given the dynamic nature of aquatic habitats, such a time lag may translate into a spatial separation of O_2 production by the plankton (in the euphotic zone) and dissolved O_2 accumulation (throughout the upper mixed layer). In addition, the connecting role played by DOM dynamics, which further separates the instantaneous (NCP) and integrative (O_2 Sat) estimates of net ecosystem metabolism, prevents the objective selection of an integration depth.

To validate our empirical NCP models we have not aimed for a quantitative NCP estimation from the O_2 variability, which, beyond the scale difficulties, would require a detailed assessment of the concurrent variability of the physical field (e.g., Emerson et al., 1995; Najjar and Keeling, 1997). However, our comparative goal requires that integrations of both NCP and O_2 Sat will depict the seasonal variation in community metabolism at their respective time-scales. To this end, the euphotic zone appears to be the correct depth for the instantaneous NCP integration because all the production of organic matter should occur within this layer. However, to represent the long-term variation of NCP from the integrative O_2 Sat, neither the euphotic nor the mixed layers are the appropriate depth for integration, as DOM may temporally accumulate below these layers, becoming available throughout the year by vertical mixing. The dynamics of bacterial populations and carbon demand below the euphotic zone (e.g., 100–250 m at Bermuda, Steinberg et al., 2001) is linked to primary production in the euphotic zone, covaries with the introduction and subsequent removal of DOM, and impacts on dissolved O_2 concentration (Steinberg et al., 2001). Assuming a system laterally isolated in terms of organic matter transport (e.g., the central part of a mid ocean gyre), and estimating the lifetime of semi-labile DOM in the upper ocean to be 1–6 months (Yamanaka and Tajika, 1997), the water column where total community R will be entirely sustained by the present plus previous local photosynthesis, will be given by the depth of winter convective mixing. Integrating the O_2 Sat above this depth, for instance to the actual mixed layer, may underestimate both the production of O_2 (e.g., when the euphotic zone is deeper than the seasonal thermocline; Emerson et al., 1995) and the DOM consumption (e.g., during the shoaling of the seasonal thermocline, after a spring phytoplankton bloom). On the other hand, when the convective mixing deepens (e.g., winter), net O_2 consumption in the actual mixed layer cannot be discriminated from intrusion of deep, O_2 undersaturated water. However, such O_2 undersaturation derives from the previous respiration of organic matter below the seasonal thermocline and should therefore be taken into account for the long-term regional balance. Certainly there will be organic matter export out of the winter mixed layer, but neither vertical organic matter import nor mixing with different O_2 saturated water. Hence within such a layer, the long-term variation of O_2 Sat should represent the time-integration of the production and consumption of O_2 by the plankton community. Within this layer, net heterotrophy must be sustained by previous net autotrophy, and the excess GP over R at any given time will be the maximum amount of organic matter available for later net heterotrophy. If these balances do not match over the long term, then the initial premise of lateral isolation for organic matter must be modified.

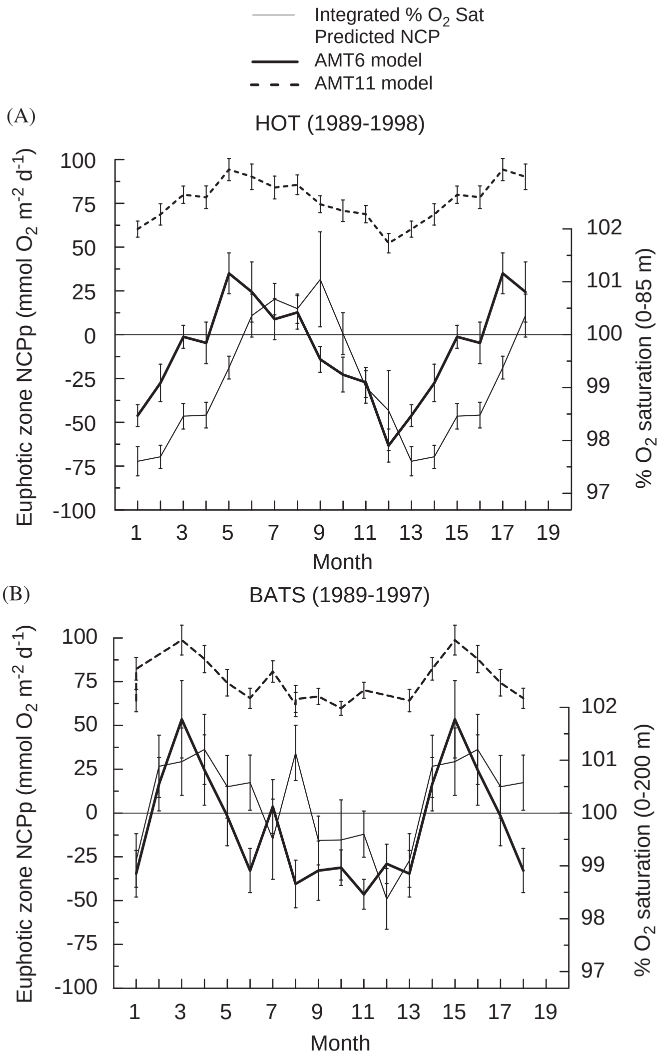

Fig. 5. Seasonal variation of the predicted mean monthly NCP (NCPp) (±s.e.) using the AMT6 (thick solid line) and AMT11 (dotted line) PO^{14}CP:NCP relationships presented in Fig. 2, from euphotic zone integrated PO^{14}CP rates at (A) the US JGOFS Hawaii Ocean Time-series (HOT) Sta. ALOHA (31°50′N, 64°10′W) and (B) the US JGOFS Bermuda Atlantic Time-series Study (BATS) (31°50′N, 64°10′W). The mean monthly percentage of oxygen saturation integrated to the limit of the winter mixing layer is also presented (thin solid line). We thank D.M. Karl, A.H. Knap and A.F. Michaels, and the US JGOFS HOT and BATS programmes for permission to use the data from http://www1.whoi.edu/jg/dir/jgofs/.

3.2.2.1. Seasonal variability of predicted NCP and O_2 Sat at HOT and BATS. Fig. 5 presents the concurrent variation of euphotic zone NCPp and the % O_2 Sat integrated to the depth of the winter mixed layer, averaged for 9 and 8 years at the HOT (Fig. 5A) and BATS (Fig. 5B) stations, respectively. This comparative exercise involves a number of limitations. First, not every productive event (occurring at shorter time-scales) has necessarily been covered by the monthly sampling at the HOT and BATS stations (Bisset et al., 1994; Karl et al., 2003). Second, the depth of winter mixing (WMD) varies from ca. 160 to 300 m at BATS (Michaels and Knap, 1996; Anderson and Pondaven, 2003) and from ca. 70 to 100 at HOT (Karl and Lukas, 1996), an important distinction because the interannual variability of wintertime mixing at BATS is related to the variability in nutrient fluxes, primary production and phytoplankton biomass (Steinberg et al., 2001). Third, the depth of the euphotic zone is ca. 180 m at HOT (i.e. >WMD) and ca. 125 m at BATS (i.e. <WMD). Fourth, excluding physical processes, O_2 Sat integrates the recent history of community metabolism, hence even the direct comparison with measured instantaneous NCP would face difficulties. Given that (a) such a delay is probably smaller than the sampling interval of one month, (b) we use predicted instead of measured NCP, (c) the depths of integration for both variables are different, and (d) physical processes do exist, some inaccuracy in the O_2 Sat to NCPp comparison at the HOT and BATS sites may be expected to occur independently of the ability of any model to predict the actual plankton metabolism.

The variability of the %O_2 Sat integrated to the WMD shows seasonal patterns of alternating oversaturation periods (summer at HOT; late winter to late summer at BATS) with undersaturation phases (winter-spring at HOT; autumn-winter at BATS) (Fig. 5), which is consistent with independent biogeochemical evidence at both the HOT and BATS stations. At the HOT station ALOHA, the dissolved inorganic carbon (DIC) concentration in the upper mixed layer decreases in summer and increases in winter and spring, while the annual cycle of the δ^{13}C of DIC (which increases with the production of organic matter) mirrors the DIC cycle (Quay and Stutsman, 2003). From these budgets, Quay and Stutsman (2003) conclude that positive summertime NCP in the upper mixed layer is approximately balanced by the wintertime upward DIC flux, i.e. by the consumption of organic matter between the seasonal thermocline and the WMD. Vertical mixing is not as important a seasonal DIC source at BATS (Gruber et al., 1998; Quay and Stutsman, 2003). However the DOC dynamics in the upper layers also suggest a clear annual cycle characterized by a spring-summer accumulation in the upper 100 m (reaching 59–70% of the spring bloom NCP; Hansell and Carlson, 1998), followed by a decline during winter mixing. Conversely, the 100–250 m cycle is characterized by the wintertime increase of DOC after mixing with the upper DOC-rich waters, and subsequent reduction to background levels during spring-summer (Steinberg et al., 2001; Anderson and Pondaven, 2003). At this depth range (100–250 m), bacterial biomass increases and O_2 decreases after the introduction of DOC during the spring bloom and deep convective mixing, which suggests the importance of microbial DOC degradation in the O_2 cycle (Steinberg et al., 2001; Hansell and Carlson, 2001). Consequently the depths chosen for the integration of the O_2 Sat (85 m at HOT, 200 m at BATS) represent conservative baselines of the seasonal vertical organic carbon export and remineralization at both HOT and BATS.

Only the AMT6 model produces mean seasonal dynamics of NCPp at both the HOT (1989–1998) and BATS (1989–1997) sites that are consistent with the annual cycles in integrated O_2 Sat (Fig. 5). At HOT, euphotic zone NCPp (AMT6) usually peaks in May–June and is $\geqslant 0$ from ca. March to late August, preceding the O_2 oversaturation period in the upper 85 m (Fig. 5), and the April–September mixed layer DIC drawdown and δ^{13}C increase indicating a net production of organic matter (Quay and Stutsman, 2003). Considering the uncertainties and methodological differences between these approaches, the mean (March–September) NCPp based on the AMT6 model (8.7 ± 6.0 mmol O_2 m^{-2} d^{-1}) agrees very well with the C budget-based estimate of summertime NCP (7.5 ± 3.7 mmol C m^{-2} d^{-1}, Quay and Stutsman, 2003). The AMT11 model produces an implausible mean NCPp of 84.5 ± 3.0 mmol O_2 m^{-2} d^{-1}. At the BATS station, euphotic zone NCPp (AMT6) peaks around March, sometimes with a second peak in July. Again, this pattern precedes the O_2 increases in the upper 200 m (Fig. 5) and the April–October DIC draw down in the mixed layer (Gruber et al., 1998). The mean (February–July) NCPp are 10.6 ± 11.2 mmol O_2 m^{-2} d^{-1} (AMT6) and 81.7 ± 4.6 mmol O_2 m^{-2} d^{-1} (AMT11), while the C budget-based estimate is 6.6 ± 1.0 mmol C m^{-2} d^{-1} (Gruber et al., 1998).

Beyond the consistency in the periods and magnitude of net autotrophy, the most relevant patterns predicted by the AMT6 model are the summer to winter auto-heterotrophy transitions in the euphotic zone, which are followed by positive–negative transitions in the winter mixed layer O_2 Sat (Fig. 5). If our predictions are correct, these transitions would mean that the wintertime increases in DIC and the O_2 decreases in the mixed layer of these oceanic habitats (Quay and Stutsman, 2003; Gruber et al., 1998) are not only caused by intrusion of deep water, but also by the annual cycle of net plankton metabolism within the euphotic zone. The remineralization rates based on the dynamics of O_2, DIC and nitrate at BATS show an annual maximum in the late spring at ca. 120–160 m depth (Ono et al., 2001). However at 20 m, Hansell et al. (1995) measured rates of DOC mineralization amounting to 100–220% of concurrently measured primary production, suggesting periods of net heterotrophy in the surface layer. Assuming that these rates of 0.45 mmol C m^{-2} d^{-1} remain constant throughout the 50–100 m euphotic zone, they would represent ca. 62–125% of the mean NCPp during the August–January net heterotrophic period (-35.8 ± 2.6 mmol O_2 m^{-2} d^{-1}). To our knowledge, the only direct NCP measurements at BATS are three surface estimates in July and August (Williams and Jenkinson, 1982). The average NCP was -0.7 ± 0.1 mmol O_2 m^{-3} d^{-1}, i.e. ca. -35 to -70 mmol O_2 m^{-2} d^{-1} for a euphotic zone 50–100 m depth. This agrees well with the late summer NCPp of -40.5 ± 13.6 mmol O_2 m^{-2} d^{-1} (Fig. 5). Interestingly, bacterial production rates at BATS have been found to exhibit a lag of several weeks to months after primary production peaks, which sometimes leads to bacterial carbon demand exceeding primary production (Steinberg et al., 2001). A larger trophic imbalance is needed to maintain the important protozoan biomass in the area (Steinberg et al., 2001).

At HOT, the variability of dissolved O_2 concentration, based on moored sensors, indicates a temporal decoupling of O_2 production and respiration in the euphotic zone (Emerson et al., 2002; Karl et al., 2003). From these results, Karl et al. (2003) suggested that P is a much more episodic process in the area than R, so that the annual primary production occurs in short and transient pulses. Following Karl et al. (2003), let us assume that HOT represents an oligotrophic region of the open ocean that is regionally isolated. If the short, episodic productive pulses are to support the metabolic demand, not only of the phytoplankton, but also of the community of heterotrophs during the whole year (Karl et al., 2003), then the trophic dynamics of the ecosystem can only be understood as a succession of high-productivity, net-autotrophic (loading) periods followed by low-productivity, net-heterotrophic (subsidized) phases. Consequently, given that during the low-productivity phases the consumption of previously accumulated organic matter (i.e. allochthonous from a temporal perspective) plays a key role in food-web fluxes, the AMT6 model (whose low-production data are all net-heterotrophic) should be a better predictor of the seasonal NCP cycle at HOT than the AMT11 model (whose low-production data are all net-autotrophic). This expectation is confirmed by our results.

Determining whether these seasonal patterns translate into yearly balanced, subsidized or export ecosystems is not possible from the analysis performed here, based on monthly PO^{14}CP data. Nonetheless, our results stress the importance of interpreting food-web processes and budgets in these areas in the context set by the seasonal scale of trophic dynamics.

3.2.2.2. Mean seasonal cycle of predicted NCP and O_2 Sat in the NADR.

Fig. 6 presents the mean seasonal cycles of euphotic zone NCPp derived from the mean variability of CZCS-derived primary production throughout the NADR (Longhurst, 1998) together with the seasonal variation of integrated O_2 saturation measured in 1994–1995 at the off-shelf station by Serret et al. (1999). This station is selected here because the variation of O_2 saturation is less influenced by the advection caused by the upwelling than at the more coastal stations. Predictions based on the AMT6 model generally agree with the ranges of NCP measured across the shelf in the S Bay of Biscay, and with other published studies in the NADR (Fig. 7), which suggests that satellite-derived primary production estimates may be of use to implement our models. Again, only the AMT6 model predicts a mean seasonal net auto-heterotrophy phasing in the entire province, although with some temporal mismatches regarding the local trend observed in the S Bay of Biscay in 1994–1995. Only such a long-term phasing of distinct periods of organic matter accumulation and depletion, would agree with the measured seasonal variation of the integrated O_2 Sat (Fig. 6).

3.2.3. *Estimation of the mean seasonal cycle and annual balance of plankton NCP in six biogeochemical provinces of the E Atlantic Ocean*

Given the considerations above about the functional and scale domains of our models, no reliable prediction can be made in systems not included in the empirical relationship, whose trophic dynamics are unknown and/or, in which previous validation with real data has not been accomplished. This is why we have predicted the temporal variation of NCP from the mean seasonal cycles of CZCS-derived primary production only in the biogeochemical provinces (Longhurst et al., 1995) of the Atlantic Ocean included in the AMT6 and AMT11 models (Fig. 7). Table 2 presents the calculations of the annual NCPp in these provinces, derived from the predicted seasonal cycles. No detailed description of the seasonal cycles of NCPp is intended here as they simply derive from the variability of estimated $PO^{14}CP$, which is described in detail by Longhurst (1998). Despite the data from BENG and CNRY being included in the models, the predictions at these provinces do not concur with the actual NCP values measured during either the AMT6 or AMT11 cruises. In these highly dynamic and spatially heterogeneous upwelling systems neither model is representative of the entire province. Similarly, in the ETRA, where the equatorial upwelling region of high productivity is surrounded by a low productivity and net heterotrophic area (Pérez et al., 2005), different models are necessary (see below). Thus the future use of empirical models based on $PO^{14}CP$:NCP relationships to predict NCP from remote estimates of primary production appears to be viable, but only when models include fully representative data.

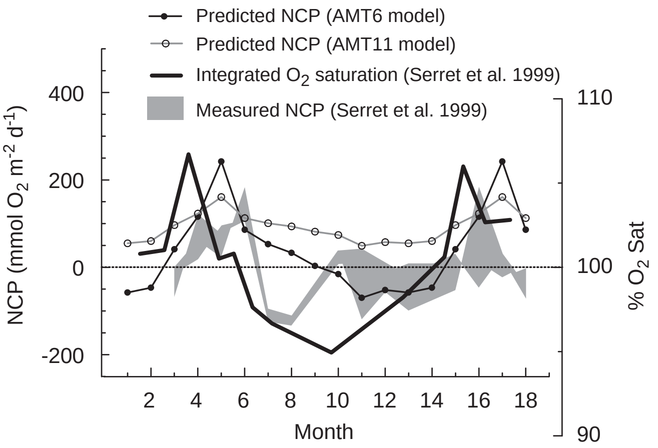

Fig. 6. Mean seasonal cycles of euphotic zone NCP predicted in the NADR (Longhurst, 1998) from the CZCS-derived primary production in this biogeochemical province (Longhurst, 1998), and seasonal variation of the percentage of oxygen saturation integrated to the depth of the winter mixed layer at an off-shelf station (ca. 1000 m depth) in the southern Bay of Biscay (Serret et al., 1999). The range of euphotic zone NCP measurements across the shelf in that study is also presented for comparison (shadowed trend) (see Fig. 4 for individual NCP measurements).

The results presented in Fig. 7 and Table 2 are preliminary and their quantification should be viewed with caution. Firstly, the estimated error on remotely sensed primary production is ca. a factor of two, and different remote estimates (e.g., Falkowski, Behrenfeld, Kolber: http://www.marine.rutgers.edu/opp/index.html; Yoder et al.: http://dixon.gso.uri.edu/yoder3.html) give generally higher values than those used in the present exercise (Longhurst, 1998). We use the CZCS-derived results in Longhurst (1998) since they sustain the biogeographic partition of our data sets on which the different models were built. The differences between primary production estimations may critically affect not only the magnitude, but also the sign of NCPp in low production habitats. Secondly, the results presented here are based on the

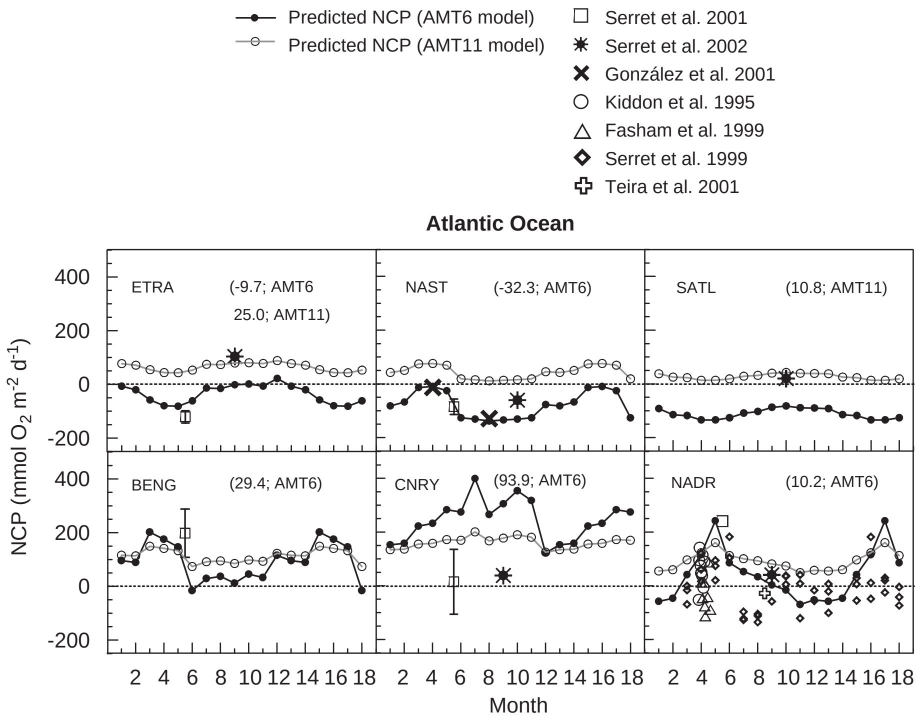

Fig. 7. Seasonal variation of euphotic zone NCP predicted from the CZCS-derived primary production in the six biogeochemical provinces of the Atlantic Ocean (Longhurst, 1998) traversed by the AMT6 and AMT11 cruises, using the empirical $PO^{14}CP$:NCP relationships presented in Fig. 2. Published data, used in Fig. 2, corresponding to any of these provinces, and the average (±s.e.) values of NCP measured in each province during the AMT6 and AMT11 are also presented for comparison. Values in brackets are the more likely annual estimates of NCP for each province in mol $O_2\,m^{-2}\,yr^{-1}$; the respective model utilized for these calculations is indicated.

Table 2
Annual NCPp in the six biogeochemical provinces of the Atlantic Ocean traversed by the AMT6 and AMT11 cruises, estimated from the seasonal variation of NCP predicted by the AMT6 and AMT11 models from CZCS-derived primary production (Longhurst, 1998) (see Fig. 7).

Province	NCPp AMT6 (mol O_2 m^{-2} yr^{-1})	NCPp AMT11 (mol O_2 m^{-2} yr^{-1})	Area (10^6 km^2)	Total AMT6 (Gmol O_2 yr^{-1})	Total AMT11 (Gmol O_2 yr^{-1})
BENG	**29.42**	40.00	1.13	**0.033**	0.045
CNRY	**93.89**	59.84	0.81	**0.076**	0.048
NAST	**−32.27**	13.78	10.25	**−0.33**	0.14
SATL	−38.91	**10.77**	17.8	−0.69	**0.19**
ETRA	−9.72	24.98	5.34	−0.052	0.13
NADR	**10.15**	32.40	3.50	**0.035**	0.11

Bold numbers are the more likely annual estimates for each province in mol O_2 m^{-2} yr^{-1}. See text for details.

mean annual cycles of P, but it is necessary to consider the actual spatial and temporal variability of P within provinces, at both short, medium and long (e.g., ENSO, NAO) scales, and the potential trophic heterogeneity within provinces that are exclusively defined from the variability of photosynthesis.

However this exercise may help in assessing the validity of the trophic–biogeographic partition of the ocean: by comparing predictions with independent local evidence we can decide which model better represents the seasonal dynamics in each province.

3.2.3.1. Net autotrophic biomes. In the productive coastal upwelling provinces of BENG and CNRY where P estimates range from ca. 50 to ca. 250 mmol C m^{-2} d^{-1}, predictions of both models converge (see also Figs. 2 and 3). Although the predictions diverge at the highest P, both provinces appear as net autotrophic, irrespective of the model, with annual balances differing by less than 60%.

3.2.3.2. Oligotrophic provinces: subsidized (net heterotrophic) and locally balanced (isolated) biomes. As expected (Figs. 2 and 3), important differences emerge when P is low ($<$ca. 50 mmol C m^{-2} d^{-1}). In the oligotrophic provinces of the NAST, ETRA and SATL, the AMT6 model always predicts net heterotrophy or a locally balanced metabolism, while the AMT11 model always predicts a net autotrophic balance. This causes substantial differences in both our perception of the trophic functioning and the estimated annual balances for these provinces.

All evidence accumulated in the NAST-E (Duarte et al., 2001; González et al., 2001; Serret et al., 2002, 2006; Gist et al., 2009, this issue) indicates that this province functions as an oligotrophic subsidized biome, where the AMT6 model will correctly predict both the seasonality and hence the net heterotrophic annual balance (Figs. 6 and 7).

In the ETRA we have not found published NCP data apart from the divergent measurements obtained in the AMT6 (-120 ± 22 mmol O_2 m^{-2} d^{-1}) and AMT11 (104 ± 10 mmol O_2 m^{-2} d^{-1}) cruises (see Fig. 7). To understand these differences it is worth remembering the particular location of both sampling stations within the province. During the AMT11, but not during the AMT6, most ETRA stations lie within the influence of the equatorial divergence (Pérez et al., 2005). As in the equatorial Pacific (Bender et al., 1999), such upwelling stations presented a net autotrophic metabolism. On the other hand, net heterotrophy prevailed in the truly oligotrophic ETRA stations that were sampled during the AMT6 cruise at a relatively short distance from Africa (Fig. 1; Serret et al., 2001a, 2002). This could imply that within this province, functionally homogeneous in terms of the phytoplankton response to physical forcing (Longhurst, 1998), different trophic biomes could co-exist (and different P:R relations should apply): a net autotrophic biome at the equatorial upwelling and a subsidized biome through the oligotrophic region influenced by organic inputs from the upwelling and African rivers (see Fig. 1; Robinson et al., 2002). The same would apply to different oligotrophic areas of the World Ocean, where the independent variation of allochthonous subsidies and primary production would impede the choice of a single model to predict the annual P/R balance from the mean annual cycles of P in each region (e.g., compare results at SATL, NAST—Fig. 7—and HOT—Fig. 5) (see also Serret et al., 2006).

3.2.3.3. Seasonally compensated biome. The seasonal variability of NCPm (Fig. 4) and O_2 Sat (Fig. 6) in the S Bay of Biscay suggested that the NADR province, like other temperate pelagic habitats, could be characterized by a seasonal transition of net autotrophic and net heterotrophic phases (Serret et al., 1999). Such a seasonal pattern is correctly predicted only by the AMT6 model (Fig. 4). However even the northernmost station in Serret et al. (1999) was located close to a coastal upwelling, near the southernmost limit of the NADR province (Longhurst, 1998), so that the relevance of our observations for the entire province remains uncertain.

In the absence of other seasonal studies of NCP, comparison with the published open ocean NCP data in the NADR (Fig. 3; Kiddon et al., 1995; Fasham et al., 1999; Teira et al., 2001a; Serret et al., 2002) shows that they are all within the ranges of NCPp estimated by the AMT6 model, but not by the AMT11 model (Fig. 7). Obviously, these disperse local measurements cannot exactly match the averaged seasonality in a province extending ca. 10° of latitude (Longhurst, 1998) and where the timing of the spring bloom appears as a key factor in controlling the seasonality of NCP. For instance, post-bloom net heterotrophy is sometimes measured (Kiddon et al., 1995; Fasham et al., 1999) within the typically productive spring period (Longhurst, 1998). Greater spatial and temporal coverage of measurements is necessary to resolve the mean seasonal cycle of NCP in such a dynamic province, yet with the current information available, prediction based on the AMT6 model appears to be a good estimate. This prediction would give rise to a seasonal compensation of imbalances, with a marginally autotrophic balance on an annual scale (Fig. 7).

3.3. *Testing for trophic-level dynamics in oceanic ecosystems*

The idea that food web fluxes can be predicted in different ecosystems and, in particular by our simple $PO^{14}CP$:NCP empirical models, is based on a very simplistic view of ecological systems (Polis, 1998; Doney, 1999), and derived from the idea that trophic-level dynamics overshadow the enormous taxonomic and functional complexity and diversity of natural communities. This is still a contentious issue (e.g., Polis and Strong, 1996; Hairston and Hairston, 1997), despite some large-scale studies that have shown ecosystem-level patterns of primary production and herbivory in both terrestrial (e.g., McNaughton et al., 1989) and aquatic systems (e.g., Cyr and Pace, 1993).

A critical condition for the empirical approach to understanding ecosystem functioning is that model construction is based on representing functional relations between integrative variables; and that such relations capture some critical processes driving the ecosystem (Pace, 2001). The empirical plankton NCP models presented here were derived to incorporate the influence of GP, community structure and DOM dynamics on net ecosystem metabolism. If these functional requirements are met, the systematic validation of these models becomes a test of the relevance of trophic-level dynamics in marine pelagic ecosystems.

3.3.1. *The problem of equilibrium in empirical marine ecology*

As for mechanistic food web models (Vézina and Pahlow, 2003), a serious difficulty for integrative studies based on empirical relationships derives from the consideration of the degree of equilibrium of the ecosystems. Conclusions obtained from systems in, or close to, equilibrium may not be appropriate for transient systems. Despite the rapid turnover of plankton populations, this is a difficult demand for aquatic systems because of their intrinsic non-equilibrium nature (e.g., Margalef, 1979; Harris, 1986) and the relevant long-term DOM dynamics. This has been recognized as a serious problem in determining the trophic status of aquatic ecosystems from snap-shot measurements of GP and R (Smith and Hollibaugh, 1997), even more so to studying the functioning of ecosystems from simple statistical relationships of spatial variability.

One practical approach to the imprecise, scale-dependent and, to some extent, subjective requirement of equilibrium, is to ensure that the data used to study an ecosystem are *representative* of its functioning, i.e. that they characterize long-term averages (Hairston and Hairston, 1993). However, even this criterion may be difficult to fulfill in marine ecosystems, so that in a previous study (Serret et al., 2001a) we proposed the connection between trophic and population dynamics as a means to address the degree to which a given data set represents a functional plankton community. Only for such representative data sets can we expect that empirical relationships based on short-term measurements of community metabolism may characterize functional relations resulting from the relevant trophic processes. Both the AMT6 and AMT11 data sets meet this prerequisite (Serret et al., 2001a, 2002).

Under these circumstances, the interpretation of the validation exercise presented here (Fig. 3) indicates that the AMT6 model (based on data representative of productive+subsidized communities, Fig. 2) is a credible tool for estimating NCP in different ocean biomes characterized by a relatively high contribution of allochthonous organic matter in low production phases/areas. Most importantly, the concurrent failure of the AMT11 model (based on data representative of productive+isolated communities, Fig. 2) to predict in these distinct ecosystems confirms the system-dependence of our empirical PO^{14}CP:NCP relationships, i.e. their sensitivity to characteristics in the long-term trophic functioning of modeled and predicted ecosystems (Serret et al., 2002).

3.3.2. *The problem of scale*

A further general difficulty for the empirical approach is untangling apparent or actual controls from the complex covariance existing between several variables across large scales (Burke et al., 1997). As such complex covariance may be very different over the spatial and temporal axes, space-for-time substitutions appear to be the most stringent validation exercise.

The relation of NCP to local GP is neither as fast as the response of phytoplankton to hydrodynamics (because of the delayed consumption of DOM, Pomeroy and Wiebe, 1993), nor exclusive (because of the influence on NCP of other independent remote—e.g., allochthonous DOM—or intrinsic—e.g., food web structure—factors apart from GP, Serret et al., 2001a), nor unique (because different biomes produce different relationships influenced in part by the quantity and quality of autochthonous DOM, Serret et al., 2002). Given the system-dependence of our models, space-for-time substitutions performed on ecologically relevant scales provide a robust validation.

Our two models are based on the regional variation of PO^{14}CP and NCP data representative of communities spanning similar ranges of the local controlling factors (photosynthesis and community structure) but differing in the influence of allochthonous (in either space or time) organic matter inputs. The good correspondence between the prediction of NCP based on the AMT6 model and the seasonal cycle of NCP measurements in the S Bay of Biscay (Fig. 4), the coherence with the seasonal variability of O_2 Sat in the winter mixed layer in both the S Bay of Biscay (Fig. 6), and the HOT and BATS stations (Fig. 5), and the agreement of these predictions with independent biogeochemical evidence, and with the published measurement of the seasonal NCP variation in the NAST-E (González et al., 2001) (Fig. 6), all indicate that the trophic processes influencing the dynamics of plankton NCP in these systems are captured by the across-systems AMT6 empirical relationship. Hence that the long-term and large-scale mechanisms connecting GP and R in and between these ocean biomes are similarly governed by the processes of accumulation and consumption of DOM (Hansell and Carlson, 1998), which are ultimately controlled by the interactive effects of hydrodynamics, primary production and food web dynamics (e.g., Teira et al., 2001a). Given the constraints met in this validation, only the existence of common *trophic-level dynamics* may explain this correct prediction of NCP seasonality from GP measurements in areas of the ocean whose location, differences in taxonomic composition and in the hydrodynamic control of the phytoplankton growth has led them to be separated into distinct biogeochemical provinces (Longhurst et al., 1995; Longhurst, 1998). The concurrent failure of the contrasting AMT11 model (Figs. 4–6) gives strength to the validity of this hypothesis.

Karl et al. (2003) have suggested that the annual primary production in the oligotrophic N Pacific is concentrated in short, episodic events, which are difficult to capture with standard sampling protocols. The much lower variability of R throughout the year would explain why short-term measurements in the oligotrophic ocean have tended to depict a net heterotrophic community metabolism. A similar observation led Arístegui and Harrison (2002) to conclude that changes in P but not in R control the net metabolism in the Atlantic Ocean. Karl et al. (2003) concluded that such asynchrony of GP and R rates would impede an assessment of the trophic status of oceanic ecosystems from repeated discrete short-term measurements of net metabolism. In our view, however, the critical difficulty is not the existence of differences in scale between trophic processes, but the scale of their interaction, i.e. the scale of trophic- or ecosystem-level dynamics, which varies geographically. This paper shows that despite the local (even seasonal) untangling of GP and R, short-term measurements of plankton trophic processes can be extrapolated to ecosystem rates only when the spatial and temporal context set by the scale of trophic dynamics is taken into consideration.

3.4. *Integrating local and remote processes in net community metabolism: domains of scale in marine plankton trophic dynamics*

From a biogeochemical perspective, the unsystematic compilation of marine plankton photosynthesis databases has been very useful in constraining seasonal, regional or global C budgets.

However, our results show the difficulties in scaling net community metabolism estimations. The diversity of scales and mechanisms connecting GP and R in different pelagic biomes, and especially the existence of both locally- and donor-controlled oligotrophic communities (Serret et al., 2002, 2006), complicates the estimation of the trophic status of pelagic ecosystems, or the C balance of the World Ocean, by combining independent non-specific GP and R estimates. Basically, if different long-term trophic dynamics characterize diverse provinces of the ocean, and unless a connecting mechanism between provinces is known, local deficits cannot be compensated by remote surpluses of GP. The integration of global databases is only meaningful if both the GP and R data sets include the full ranges of the spatial and temporal variability, including the scales of connection, or if knowledge of such scales allows the integration through functionally weighted means. As DOM dynamics are not always related to the local characteristics of the ecosystem, even organizing such global community metabolism databases by latitude, season, productivity regime or community structure may be biased. The ideal would be to have a variable which concurrently encompasses the magnitude of organic matter locally produced and imported, and its fate at different temporal and spatial scales. However, since such a variable is unknown, we propose a trophic–biogeographic partition of the ocean as a means for the systematic integration of the trophic status of each region.

As an exercise to show the relevance of the proposed trophic–biogeographic context for extrapolation, we can try constraining a representative balance for the SE tropical Atlantic by integrating the annual estimates of NCP at the ETRA, SATL and BENG (see Longhurst, 1998). Using the AMT6 and AMT11 models alone, would produce a regional balance ranging from -0.71 to $0.36\,\mathrm{Gmol\,O_2\,yr^{-1}}$, indicating that the SE tropical Atlantic is either a source or a sink of carbon. Our results suggest that this approach is not correct. The right model for the BENG appears to be the AMT6 model; if we assume that the AMT11 model is correct for the whole SATL, then uncertainty only exists for the ETRA. Implementing the corresponding models at BENG and SATL, and either the AMT6 or AMT11 models only at the ETRA, the results are: 0.17 and $0.35\,\mathrm{Gmol\,O_2\,yr^{-1}}$, respectively. Interpretation of these tentative results would lead us to conclude that the SE tropical Atlantic is a net autotrophic province of the ocean.

Our results have shown the potential of empirical prediction for the estimation of plankton NCP, and that small differences in the type of system where the data are collected may have large effects on the predictive power of the relationships. This impedes the use of generalized relationships, but means that the comparison of the predictive power of functionally distinct empirical relationships is a useful tool for identifying the relevant *domains of scale* where plankton trophic interactions remain invariable (Wiens, 1989), i.e. for defining trophic–biogeographic boundaries in the ocean. Delineating these provinces is necessary in order to include the complex interaction of local and remote processes controlling plankton net community metabolism in ecological and biogeochemical predictions and extrapolations. A comprehensive trophic biogeography of the ocean would be a major step forward in estimating the global impact of the marine biota on the biogeochemical carbon cycle.

Acknowledgements

This work was supported by the NERC AMT programme (NER/O/S/2001/00680; this is contribution number 168. http://www.amt-uk.org) and the CYCIT project CIRCANA (MAR1999-1072-C03-01). P.S. was funded by EU Marie Curie Research Training and Return Grants and a MECD Contrato de Reincorporación, C.R. by a NERC Advanced Research Fellowship, E.T. and E.F. by MECD grants and the EU contract CANIGO (MAS3CT960060), and G.H.T. by an EU MAST fellowship. We thank the Principal Scientists, J. Aiken and E. M. S. Woodward, and all personnel on board RRS JCR during the AMT6 and AMT11 cruises for their support, and P.J.leB. Williams (University of Wales; Bangor) and A. Isla (University of Oviedo) for the generous loan of analytical equipment. SeaWiFS data was provided by the SeaWiFS Project, NASA/Goddard Space Flight Center and ORBIMAGE. We sincerely thank D. M. Karl, A. H. Knap and A. F. Michaels, and the US JGOFS HOT and BATS programmes for the use of their valuable databases, openly available through the World Wide Web. Thanks are also due to B.G. Castro for helpful advice on statistics, and to the anonymous referees whose comments improved the quality of this work.

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