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Computation of daily primary production in Icelandic waters; a comparison of two different approaches

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ABSTRACT

Kristinn Gudmundsson, Thórunn Thórdardóttir & Gunnar Pétursson 2003. Computation of daily primary production in Icelandic waters; a comparison of two different approaches. Marine Research Institute. Report Series No. 106.

The daily primary production in Icelandic waters was recalculated, using a set of data originally sampled and calculated according to a modified version of the radiocarbon method proposed by Steemann Nielsen (1952) during 1958–1982. The recalculated production, using a more resent approach, i.e. integrating photosynthetic response of a phytoplankton biomass to variable irradiation, was compared with the original results. Calculated mean of primary production, measured at over five thousand stations was 0.88 $gCm^{-2}d^{-1}$ according to the approach of Steemann Nielsen, **SN-model**, but 0.97 $gCm^{-2}d^{-1}$ according to the integration of equation for biomass related photosynthesis at variable light intensity, **PE-model**. The daily production calculated with these models are highly correlated, r = 0.96. However, due to the difference in account for available light, the results for a distinct station may differ considerably.

A subsequent analyzes of the relative importance of variables, used in calculations of primary production according to the PE-model, highlighted the importance of proper measurements of the attenuation of light with depth. Furthermore, chlorophyll in the surface layer explained 65% of the variance in daily primary production calculated with the PE-model.

ÁGRIP

Kristinn Gudmundsson, Thórunn Thórdardóttir & Gunnar Pétursson 2003. Útreikningar á daglegri frumframleiðni í hafinu við Ísland; samanburður á tveimur mismunandi aðferðum. Hafrannsóknastofnunin. Fjölrit nr. 106.

Dagsframleiðni svifþörunga í hafinu við Ísland, árin 1958–1982, var mæld og reiknuð samkvæmt aðferð Steemann Nielsen (1952), aðlagaðri að íslenskum aðstæðum samkvæmt ráðleggingum hans. Útreikningar á dagsframleiðni samkvæmt jöfnu Steemann Nielsen er mikil einföldun og býður ekki upp á að taka tillit til mismunandi birtuskilyrða. Almennt hefur verið horfið frá notkun aðferðarinnar til útreikninga á frumframleiðni. Í staðinn er notuð heildun yfir dýpi og tíma. Frumframleiðnin er þá reiknuð samkvæmt lýsingu á afkastaferli ljóstillífunar miðað við breytilegan ljósstyrk og lífmassa á mismunandi dýpi og viðkomandi tímabil. Eftirfarandi rannsókn tók mið af að bera saman niðurstöður útreikninga á dagsframleiðni svifþörunga samkvæmt tveimur mismunandi reikniaðferðum. Meðaltal af útkomu reikninga þessarra tveggja aðferða, byggt á mælingum frá meira en fimm þúsund stöðvuum á nefndu árabili, var annars vegar 0,88 $gCm^{-2}d^{-1}$ samkvæmt aðferð Steemann Nielsen, **SN-model**, og hins vegar 0,97 $gCm^{-2}d^{-1}$ samkvæmt aðferð Jassby & Platt (1976), **PE-model**. Fylgnistuðull línulegrar aðfallsgreiningar, r = 0,96, sýnir þess utan að breytileikinn er almennt lítill. Engu að síður getur komið fram talsverður munur á niðurstöðum einstakra stöðva, munur sem vísast má rekja til þess hve frábrugðin nálgunin er varðandi mat á ljósaðstæðum í þessum tveimur reikniaðferðum.

Vægi mismunandi mælinga, skoðað sem áhrif á útkomu reiknaðrar dagsframleiðni samkvæmt PE-modeli, var síðan metið með því að útiloka viðkomandi þátt mælinganna í útreikningunum. Greinilegt var að mælingar á framleiðni í 0 og 10 metra dýpi eru veigameiri en mælingar á 20 og 30 metra dýpi og samanburðurinn undirstrikaði líka hve mælingar á deifingu ljóss með dýpi eru mikilvægar. Að lokum var sýnt fram á að niðurstöður mælinga á magni blaðgrænu á 10 metra dýpi útskýra 65% af breytileika reiknaðrar dagsframleiðni samkvæmt fyrirliggjandi gögnum. Slík niðurstaða er vissulega áhugaverð í ljósi þess að hve auðvelt er að nálgast upplýsingar um magn blaðgrænu í yfirborðslögum sjávar.

INTRODUCTION

The bulk of data gathered on phytoplankton productivity in Icelandic waters since 1958 originates from measurements of ^{14}C uptake at light saturation and ambient temperature, using incubators. The results have mainly been used to study seasonal and annual changes in potential productivity in relation to hydrographic as well as nutrient conditions (Thórdardóttir 1963, 1976a, 1977, 1984, 1986, Stefánsson & Thórdardóttir 1965, Gudmundsson 1998). The data have also been used to calculate daily primary production and the average annual primary production in the waters around Iceland (Thórdardóttir 1976b, 1994). The calculations of daily primary production per square meter have been based on an adapted version of the formula of Steemann Nielsen (1952), **SN**-model. According to that formula the surface irradiation and that of the water column were approximated on the basis of the number of hours from sunrise to sunset, the depth of the euphotic zone and the weighted average of the productivity values from the upper and lower parts of the euphotic zone. In view of the increasing knowledge on the productivity at variable environmental conditions as well as differences at both species and assemblages levels (Talling 1957; Steemann Nielsen & Jörgensen 1968a,b; Vollenweider 1970; Harris 1973; Platt & Jassby 1976, Côté & Platt 1983, 1984, Geider & Osborne 1992, MacIntyre *et al.* 2002) an estimate of daily primary production calls for greater resolution. Most obviously variables like the ambient light and data on the distribution of biomass in the water column need to be considered. Integration of the production over time and depth is best performed on basis of relevant information on the photosynthetic response to the variable light and depth interval (Platt *et al*. 1991; Longhurst *et al.* 1995; Behrenfeld & Falkowski 1997a).

The data, collected for calculations of daily primary production according to the method of Steemann Nielsen (1952), do not include all the information needed for a different approach to calculate the production, as frequently only incubator values on ^{14}C uptake rates at four fixed depths are available. Additional knowledge, however, on the chlorophyll distribution, the surface irradiation, the attenuation with depth, as well as information on the photosynthetic response at different light intensities, *i.e.* $P^B vs.E$ experiments, has been accumulating. Justified by this additional information and the general knowledge of the area, a recalculation of daily primary production per square meter has been attempted from the incubator values and compared with the earlier results. Thus, in addition to the already mentioned **SN** calculation model, another model was adopted, **PE,** based on P^B*vs*.E-equation (Jassby & Platt 1976). As mentioned, some of the variables needed for the calculations according to the **PE**-model were not measured routinely. As an example, the ratio of light saturated ^{14}C uptake and chlorophyll *a* at 10 m depth is used as P^B_{max}, the specific photosynthetic rate at optimal light intensity. The slope of the light-saturation curve, α, is assumed on basis of a number of P^B*vs*.E-experiments. The primary production is integrated on hourly basis as a function of ambient light intensity over the day for the water column of the euphotic layer, given the relevant values. Secchi depth is only taken during the daytime and some measurements are missing. Therefore, both these models include several empirically derived equations for calculations of Secchi depth from biomass of phytoplankton, as well as several other equations for computation of variables needed for the calculations at each station. Furthermore, the choice of an appropriate equation to calculate the daily primary production (McBride 1992, Longhurst *et al*. 1995, Behrenfeld & Falkowski 1997b), and evaluations of the variables needed together with the achieved results, are the aims of this paper. Methods adapted for calculations of the daily primary production in Icelandic waters are described and the results compared with the original calculations. Thus, a link is made between an extensive dataset, collected and utilized during the last 40 years of the last century, and the present methods.

P^B*vs*.E equations, and information on the relevant variables, may be suitable for calculation of the primary production of extensive regions when indirect measurements of the biomass are available, *e.g.* remote sensing (Longhurst *et al.* 1995; Behrenfeld & Falkowski 1997b). Calculation of the daily primary production according to the chosen model from, on the one hand a complete dataset and on the other hand only information on chlorophyll at the surface, reveal how much of the variation in the calculated production can be explained from the chlorophyll variable, given the assumptions made.

MATERIAL AND METHODS

The rate of uptake of radioactive carbon by phytoplankton at four standard depths has been routinely measured in Icelandic waters according to the ^{14}C method (Steemann Nielsen 1952), adjusted to the prevailing conditions in the area as recommended by Steemann Nielsen (pers. comm.). The set of data used is mainly from 1958 to 1982. Additionally, some more recent results of P^B*vs*.E experiments are applied. The investigations have been carried out for different water masses of coastal as well as oceanic character and in all seasons, but mainly during the period March-September. The sampling area is for the most part inside the range of 63°-68°N and 10°-30°W. The ambient temperature of the water samples range from -2° to 12°C and the salinity range from 35.2 in oceanic water south of Iceland to as low as 32 at some coastal stations.

The procedure of sampling and measuring has been similar during these years and the modifications made mostly concern the renewal of apparatus with comparable items. Samples for carbon fixation were collected at four standard depths of 0, 10, 20 and 30 m. Seawater samples in 50 ml borosilicate bottles were inoculated with 148 kBq $NaH^{14}CO_3$ solution (Carbon-14 Centralen, Denmark). Since 1964, the samples have been irradiated for 4 hours in air temperature controlled incubators, as an earlier design of water-cooled incubators caused troubles at very low temperatures. The irradiation at the center of each borosilicate incubation bottle (using 2π-quantum sensor) was 200-250 μmol quanta $m^{-2}s^{-1}$ (PAR), provided by fluorescent tubes (Philips TLF 20W/33). This level of irradiation is, in general, inside the range of the saturation level for photosynthesis for the different phytoplankton communities in Icelandic waters (Table 1). Prior to counting in a Geiger counter the nitrate cellulose filters (Sartorius, 0.2 μm pore size) are fumed in concentrated HCl for 5 minutes. During the period 1958-1982 the filters were counted at the top side only, but since then the filters have been counted at both sides in order to correct for the varying penetration of ^{14}C into the filters (Theodórsson 1975, 1984). The improved method increases the precision, being now comparable with that of scintillation counters. For an averaged number of measurements this may have resulted in slightly higher values, and the results of measurements in Geiger counters are probably underestimated (Gudmundsson & Valsdóttir 2004). However, all the ^{14}C measurements used here were counted the same way, except for the P^B*vs*.E experiments (Table 1), which were counted by the improved method. The results of P^B*vs*.E experiments are used here only to find some relevant parameters in P^B*vs.E* equations for calculation of the daily primary production in Icelandic waters. Handling of the samples for P^B*vs*.E experiments are in other respect the same as for the standard depth samples, except for the light intensity. In order to acquire different light intensities for the P^B*vs*.E experiments the light intensity of the incubators was increased to approximately 400 μmol quanta $m^{-2}s^{-1}$, and series of neutral light screens used to cover some of the bottles.

Measurements of chlorophyll *a* started in 1973, and since then it has been routinely measured in samples from the 10 m depth level whenever the ^{14}C uptake by phytoplankton has been measured. Chlorophyll has been sampled at other depths as well, but not as regularly. One liter seawater sample was filtered through Millepore membrane filter (0.2 µm pore size) the first few years. These types of filters are in agreement with the filters used for productivity measurements, but Whatman GF/C glassfibre filters (approx. 1 µm pore size) have been used later in order to avoid reduced transparency of extracted samples. The filters were subsequently dried over silica gel and stored in a refrigerator. The concentrations of chlorophyll *a* were determined with spectrophotometer in extracts of 90% acetone. The analyses and calculations of chlorophyll *a* (mg m^{-3}) were made according to a standard method (Anon. 1966).

Secchi depth (m), Ds, has been routinely measured at all stations when sampled during the daytime. The calculation of the attenuation coefficient (k) are made according to the equation of Poole & Atkins (1929), *i.e*. the euphotic depth (1% light depth) is 2.7 x Ds.

ESTIMATING AVAILABLE RADIANCE FOR PHOTOSYNTHESIS

As the surface irradiation was generally not measured in the surveys the available radiance for photosynthesis has to be estimated. The only indication of the surface irradiation is the observation of the cloud cover at the time of sampling, when performed in daylight. The coastal waters around Iceland was divided into six sections (climatic zones) according to recommendations from the Icelandic Meteorological Office (Markús Á. Einarsson, pers. comm.) and a similarity analysis of cloud observations for the years 1971–1980. One coastal weather station inside each of the sections was selected. In order to perform the calculations of the daily primary production, according to the PE-model, the surface irradiation was calculated from a model, which simulates the photosynthetic available radiance (PAR) at the surface. This adopted model is based on records of hourly means of μmol quanta $m^{-2}s^{-1}$(PAR), covering more than a year at each of three near shore locations (Fig. 1), Grímsey (66°32.1'N, 18°00.1'W), Ísafjörður (66°04.3'N, 23°07.3'W) and Vestmannaeyjar (63°26.6'N, 20°16.6'W). The following equation is used to calculate μmol quanta $m^{-2}s^{-1}$(PAR) at the surface, when the sky is clear.

$$_{\text{clear sky}}PAR_t = 33.75\ H_{12}\ e^{-½[(t\ -\ 12)/(y\ *\ 0.415)]2} - 52.36 \qquad \text{Eq. (1)}$$

where H_{12} is the altitude of the sun at zenith, t denotes the local time of the day (as 24 hours) and y is half the day length (hours). Negative values are equalized to zero, *i.e.* darkness. Equation (1) gives $_{\text{clear sky}}PAR_t$ and accounts for changes in PAR_t due to different latitudes, and the day of the year, in accordance with the changes in the altitude of the sun. The H_{12} is calculated using an equation given in 'The Smithsonian Meteorological tables' (List 1951, p:497). Furthermore, an empirical relationship found by comparing $_{\text{ratio surf.}}PAR$, the ratio of measured PAR to calculated $_{\text{clear sky}}PAR$, with the local cloud cover observations (Fig. 2) is given by the following equation (N: 535, r: -0.571 for calc. lin. regr. of semi-log transformed data):

$$_{\text{ratio surf.}}PAR = 1 - 0.729\ e^{-0.807\ (8\ -\ \text{cloud cover})} \qquad \text{Eq. (2)}$$

Equation (2) is used to reduce the calculated $_{\text{clear sky}}PAR$ in accordance with available local cloud cover observations (density, judged by the eye on the scale 0-8) obtained from the Icelandic Meteorological Institute. The equation gives an approximation of the reduction of $_{\text{clear sky}}PAR$ due to cloud cover (Fig. 2). A comparison of calculated and measured PAR on daily basis (Fig. 3) for almost 3 years in Vestmannaeyjar, an island off the south coast of Iceland, revealed a highly significant correlation coefficient for a linear regression analysis ($_{\text{calc surf.}}PAR=PAR_{\text{measured}} + 0.3$, r: 0.95, d.f. 960). Information on cloud cover for a given site is obtained from one of the six weather stations selected on the coast, as mentioned above. The weather stations represent the "climatic" zones (Fig. 1), defined according to similarity in records on cloud coverage from weather stations along the coast and consultations with experts at the Meteorological Institute (Markús Á. Einarsson, pers. comm.). The validity, however, of using the cloud cover observations at the coastal stations for the offshore sampling stations has not yet been tested.

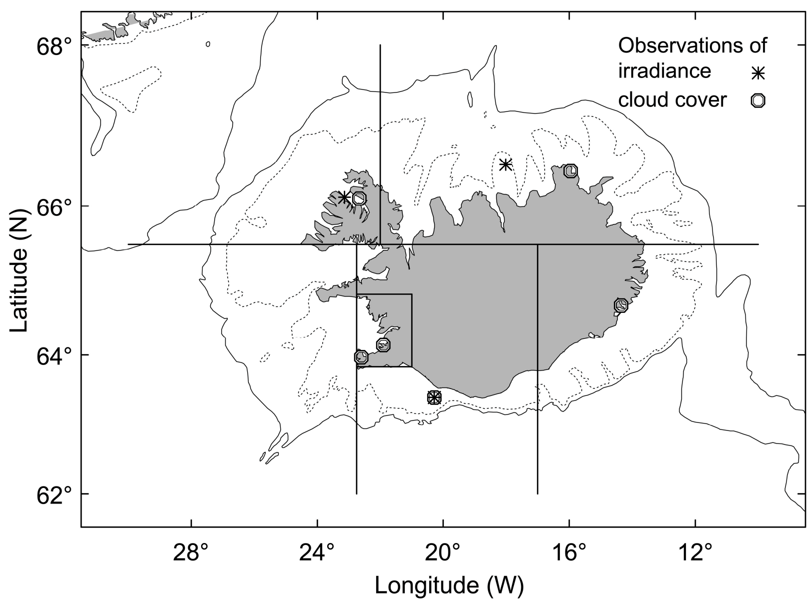

Figure 1. Division of the study area into "climatic zones", based upon similarity analysis. The weather stations (O) and the locations of light recordings (✳) are indicated. The names of the weather stations (O) are, listed clockwise from Reykjavík in the smallest zone: Reykjavík, Æðey, Raufarhöfn, Hólar, Stórhöfði and Keflavík. The places where light was recorded (✳), listed in the same order are Hnífsdalur, Grímsey and Stórhöfði.

1. mynd. Hafsvæðinu skipt í veðursvæði samkvæmt könnun á sambærileika. Veðurathugunarstöðvar (O) og staðsetning ljósmæla (✳) er sýnd. Veðurstöðvarnar (O) taldar frá Reykjavík og réttsælis umhverfis landið eru, Veðurstofa Íslands í Reykjavík, Æðey, Raufarhöfn, Hólar, Stórhöfði og Keflavík. Ljósmælingarnar voru gerðar í Hnífsdal, í Grímsey og á Stórhöfða.

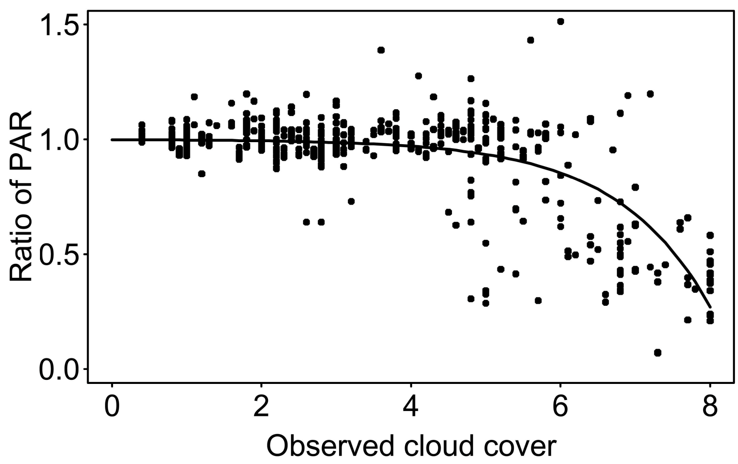

Figure 2. The relationship between the ratio of measured PAR / calculated $PAR_{clear\ sky}$ irradiation at the surface and the density of the local cloud cover (N: 535, r:-0.571 for calc. lin. regr. of semi-log transformed data).

2. mynd. Fylgni annars vegar milli hlufalls af mældu ljósi og reiknuðu ljósi, áfallandi ljós (PAR) við yfirborð sjávar og hins vegar mat á þéttleika skýjahulu á viðkomandi svæði (N: 535, r: -0,571 samkv. reiknaðri jöfnu beinnar línu fyrir semi-logaritmiska vörpun niðurstaðanna).

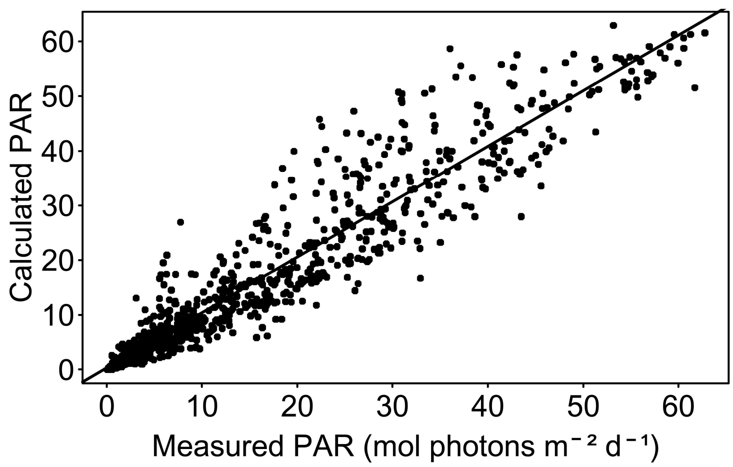

Figure 3. The relationship between calculated and measured irradiation at the surface in Heimaey 1989, the line of 1:1 ratio is shown.

3. mynd. Samband áfallandi ljóss (PAR), annars vegar reiknaðs og hins vegar mælds, við yfirborð sjávar í Heimaey 1989. Lína 1:1 hlutfalls er sýnd.

As previously mentioned, the attenuation of light with depth was estimated from Secchi disk readings. However, as these are restricted to the daytime, a considerable number of the survey stations lack information on the light attenuation. As most of the stations considered are of oceanic character, the attenuation would primarily be caused by varying amount of phytoplankton biomass.

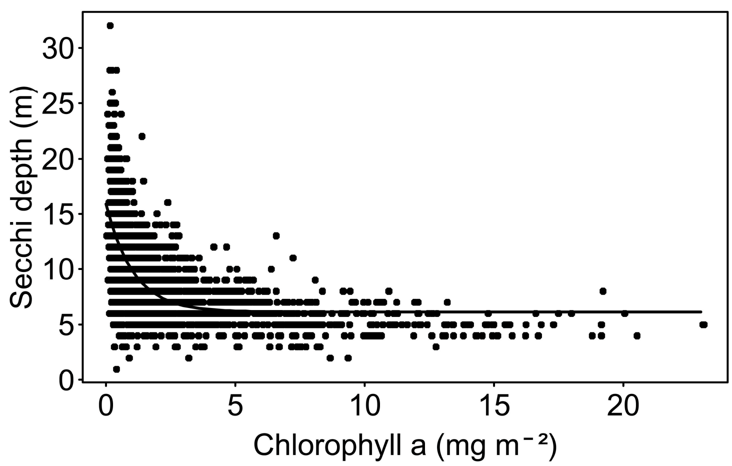

Figure 4. The relationship between Secchi depth and chlorophyll *a* at 10 m depth.

4. mynd. Samband sjóndýpis og a-blaðgrænu á 10 metra dýpi.

Moreover, a general feature of Icelandic waters is the well mixed surface layer down to a depth of at least 20 m (Stefánsson 1962; Gudmundsson 1998). Consequently, a significant relationship (Fig. 4) is found between Secchi depth and chlorophyll *a* measured at 10 m depth (N: 2053, r: 0.68, for calc. lin. reg. of log-log transf. data), given by the following equation:

$$D_S(CHLa) = 9.71\ e^{-0.944 * CHLa} + 6.14 \qquad \text{Eq. (3)}$$

or, alternatively, from the ^{14}C measurements P_{0m} and P_{10m}, at 0 and 10 m depth respectively, $D_S(½(P_{0m} + P_{10m})) = 11.2\ e^{-0.588 * (P0 + P10)/2} + 7.14$ (N: 3476, r: -0.70 for calc. lin. regr. of log-

log transformed data). The compatibility of the two last mentioned equations might be expected as a highly significant correlation was found by linear regression of measured chlorophyll *a* at 10 m on the ^{14}C uptake measurements, the light saturated incubations, from the same depth (P_{10m}(CHL*a*) = 2.26 CHL*a* + 0.11, N: 2734, r: 0.87, for calc. lin. reg), as shown in Figure 5.

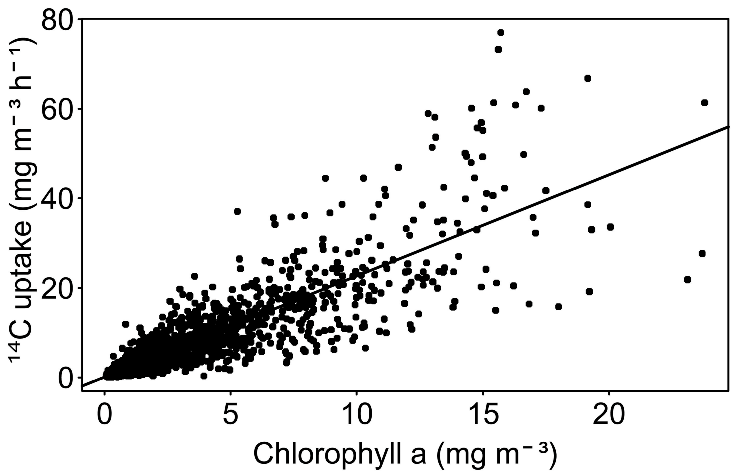

Figure 5. The relationship between ^{14}C uptake rate and chlorophyll *a*, both at 10 m depth, with fitted least-square line: P_{10m} = 2.26 Chl*a* + 0.11, N = 2734, r = 0.87.

5. mynd. Samband mælinga sýna frá 10 m dýpi á upptöku geislakols og a-blaðgrænu og niðurstaða aðfallsgreiningar á jöfnu beinnar línu: P_{10m} = 2,26 Chla + 0,11, N = 2734, r = 0,87.

The photosynthetic available radiance at a given depth, PAR(z), is calculated from the irradiation at the surface according to the equation $I_z = I_0 e^{-kz}$ (Poole & Atkins 1929). As there are no measurements on the spectral distribution of light in the dataset, whatever influence due to color shift there may be on the photosynthesis (Morel 1991), it is not dealt with here.

STANDARD ^{14}C-INCUBATOR MEASUREMENTS AND P_{MAX} VALUES

Data from the P^B*vs.*E experiments, performed occasionally since 1980, have been analyzed to fit equation (4) given by Platt *et al.* (1980),

$$P^B = P^B_{sat}(1-e^{-(\alpha E/PBsat)})e^{(-\beta E/PBsat)} \qquad \text{Eq. (4)}$$

or the equation (5) given by Jassby & Platt (1976), when there is no apparent photoinhibition

$$P^B = P^B_{max} \tanh(\alpha E/ P^B_{max}) \qquad \text{Eq. (5)}$$

where P is the ^{14}C uptake per hour and B is the Chl*a* (biomass), used as denominator. P and B are scaled to mg m^{-3} h^{-1} and mg m^{-3}, respectively, and E, the photosynthetically available radiation, is given in µmol photons $m^{-2}s^{-1}$ (PAR). In addition to the available light intensity, equation (4) includes four Chl*a* normalized variables, the net photosynthesis P^B, mg C (mg Chl*a*)$^{-1}$ h^{-1}, a theoretical maximum photosynthetic rate P^B_{sat}, the slope of light dependent photosynthesis at low light intensities α^B and the slope of inhibited photosynthesis at high light intensities β^B. P^B_{sat} is equivalent to P^B_{max} (equations 4 and 5) when $\beta^B = 0$. P^B_{max} may be calculated from P^B_{sat} when α^B and β^B are known (Harrison & Platt 1986). Among variables derived from fitted curves are E_{opt}, the optimal light intensity for the photosynthesis and E_k, the minimum light intensity required to induce light saturated photosynthesis. Results of the P^B*vs.*E experiments (Table 1) are in accordance with published results from comparable waters (Erga 1989; Rey 1991). The E_{opt} and E_k show that the light intensity used for the incubations is at the level for saturated photosynthesis. Consequently, the ratio of measured ^{14}C uptake rates and chlorophyll *a* at 10 m level may be used as assimilation numbers, AN, *i.e.* C (Chl*a*)$^{-1}$ h^{-1} at light saturation. AN is comparable to the variable P^B_{max} (Jassby & Platt 1976). The AN and P^B_{max} have the same units and in the following text the terms will be assumed to be equivalent, but used to distinguish between the values calculated from the standard incubations and those derived from P^B*vs.*E experiments, respectively. The mean AN for the period 1973-1982 (Fig. 6) is 2.44 C (Chl*a*)$^{-1}$ h^{-1}, with S.D. 1.24, N=2734. The significant difference between the above mean of AN and the mean of P^B_{max} (Table 1), 3.07 C (Chl*a*)$^{-1}$ h^{-1}, may partly be due to the change in the procedure of filter counting, mentioned earlier. But, as the number of the P^B*vs.*E experiments are relatively small, the results may easily be biased by the temporal and/or spatial distribution of the sampling stations. However, in accordance with others (MacCaull & Platt 1977, Harrison & Platt 1986, Rey 1991) a significant correlation, r:0.46, is found by analysis of a linear regression of α^B on P^B_{max} (Table 1), and thus α^B varies according to 0.05 + 0.015*(AN), while the range of AN is between 1 and 5.

Table 1. Variables derived from photosynthetic rate versus light relationships (P^B*vs.*E-curves) and chlorophyll *a*. The data, collected in Icelandic waters 1980-1990, at 10 m level are P: ^{14}C uptake measurements (mgC m^{-3} h^{-1}), B: chlorophyll *a* (mgChl*a* m^{-3}) and E: irradiation (PAR; µmol quanta m^{-2} s^{-1}), E_k is the minimum light level for lightsaturated photosynthesis and E_{opt} the optimum light level for photosynthesis and both α^B and β^B are the slope of biomass related productivity P^B for photosynthetic activity at low- and high light intensities, respectively.

Tafla 1. Breytur, afleiddar af niðurstöðum rannsókna á afkastaferli ljóstillífunar svifþörunga (P^Bvs.E-ferlar) og magn a-blaðgrænu. Rannsóknirnar voru gerðar á hafsvæðinu umhverfis Ísland á árunum 1980–1990. Öll sýnin eru frá 10 m dýpi og breyturnar eru Chla (mg a-blaðgræna m^{-3}), P^B_{max} (hámarks afköst ljóstíllífunar miðað við magn a-blaðgrænu, mg kolefni (mg a-blaðgræna m^{-3})$^{-1}$ m^{-3} klst^{-1}), α^B (hallatala ljóstillífunar, miðað við magn a-blaðgrænu, þegar birtan er takmarkandi lág), E_k (lágmarksbirta fyrir full afköst ljóstillífunar), E_{opt} (kjörmagn birtu fyrir hámarks ljóstillífun), β^B (hallatala ljóstillífunar, miðað við magn a-blaðgrænu, þegar birta er takmarkandi há), P^B_{sat} (skilgreint hámark ljóstillífunar miðað við ástand og umhverfi svifþörunga annars en birtustigs). Birtumagn (I) er gefið upp í einingunni µ mól phótónur m^{-2} s^{-1} og α^B og β^B hafa hvoru tveggja einingarnar (mg kolefni (mg a-blaðgræna m^{-3})$^{-1}$ m^{-3} klst^{-1}) / µ mól phótónur m^{-2} s^{-1}.

N	mean	s.dev.	min	max	
Chl*a*	85	3.95	3.51	0.38	15.2
P^B_{max}	85	3.07	1.08	0.73	5.38
α^B	85	0.060	0.032	0.011	0.165
E_k	85	62.6	37.5	12.9	199
E_{opt}	61	186	65.7	57.9	385
β^B	61	0.0067	0.0137	0.0000	0.1015
P^B_{sat}	61	4.39	2.96	1.50	18.89

The study of the P^B*vs.*E curves (Table 1) reveals derived variables with CV% of around 50, except for the slope of inhibition, β^B, which is much higher. The values of β^B, derived from these P^B*vs.*E-curves, are not considered reliable due to the low number of subsamples incubated at sufficiently high light intensities. Furthermore, in well mixed surface layers, such as those of Icelandic waters (Stefánsson 1962; Gudmundsson 1998), pronounced inhibition is questionable and might be an artifact of the prolonged incubation at high irradiation levels (Harris 1978, Gallegos & Platt 1985). Therefore the more simplistic equation (5) was assumed to be the most appropriate for the integration of daily primary production. It includes P^B_{max} and α as well as available light, but ignore eventual inhibition. And, as earlier stated, AN may be regarded as equivalent to the P^B_{max} and therefore P^B_{max} may be replaced by AN in the PE-model.

$$P^B = AN \tanh(\alpha E/AN) \qquad \text{Eq. (6)}$$

The frequency distribution of the AN (Fig. 6) and the P^B_{max} values (Table 1) show a remarkably narrow peak around the mean, the standard errors being less than 10% of the mean value. This encourages the use of AN as a constant when chlorophyll *a* measurements are lacking. Converting the linear regression of chlorophyll *a* and ^{14}C uptake rates at the 10 m level (Fig. 5) to the geometric mean of regression lines, thus taking into account the error in both the x and the y variables (Ricker 1973), makes the ^{14}C uptake rates and chlorophyll *a* values interchangeable, $P_{10m} = 2.60$ Chl*a* - 0.73.

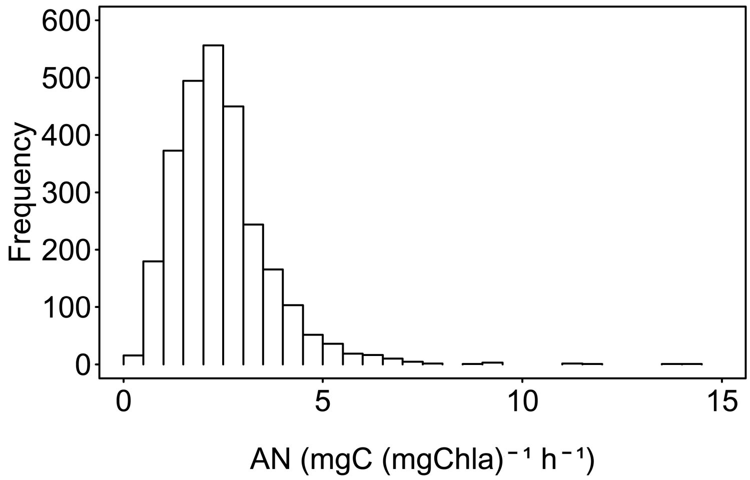

Figure 6. The distribution of assimilation numbers (AN), measured at 10 m.

6. mynd. Dreifing afkastamarka (AN), niðurstöður rannsókna frá 10 metra dýpi.

VERTICAL DISTRIBUTION OF BIOMASS

As stated earlier the surface layers around Iceland are generally well mixed down to about 20 m depth (Stefánsson 1962, Gudmundsson 1998). This is confirmed in quite similar values of ^{14}C uptake at the three standard depths, 0, 10 and 20 m (Fig. 7a,b). The values at 30 m are the least correlated to the values at 10 m (Fig. 7c). However, the scatter of points indicate frequent mixing below 30 m, apparent from the cluster of similar values for 10 and 30 m emphasized by the 1:1 ratio, shown by the broken line in Fig. 7c. This evident heterogeneity of the data will require further analysis. For the time being, the equations found by calculations of the linear regression (Fig. 7) are used in the models to account for variations in biomass with depth. The mean of AN obtained for 10 m depth, is assumed to be equally valid for all the depths considered when transforming ^{14}C data to biomass values in terms of Chl*a* prior to the integration of the productivity over depth. Furthermore, empirical correlation of chlorophyll *a* at 10 m and the ^{14}C uptake at each of the four standard depths, all significant ($p < 0.001$), are used to fill in missing values for the set of data needed for calculations of the daily primary productivity. The geometrical mean of the linear equations of productivity at 0, 20 and 30 m depth to Chl*a* at 10 m are $P_{0m}(\text{Chl}a)_{GM} = 2.51$ Chl*a* - 0.67, P_{20m} $(\text{Chl}a)_{GM} = 2.27$ Chl*a* - 0.62 and P_{30m} $(\text{Chl}a)_{GM} = 1.81$ Chl*a* - 0.45, respectively.

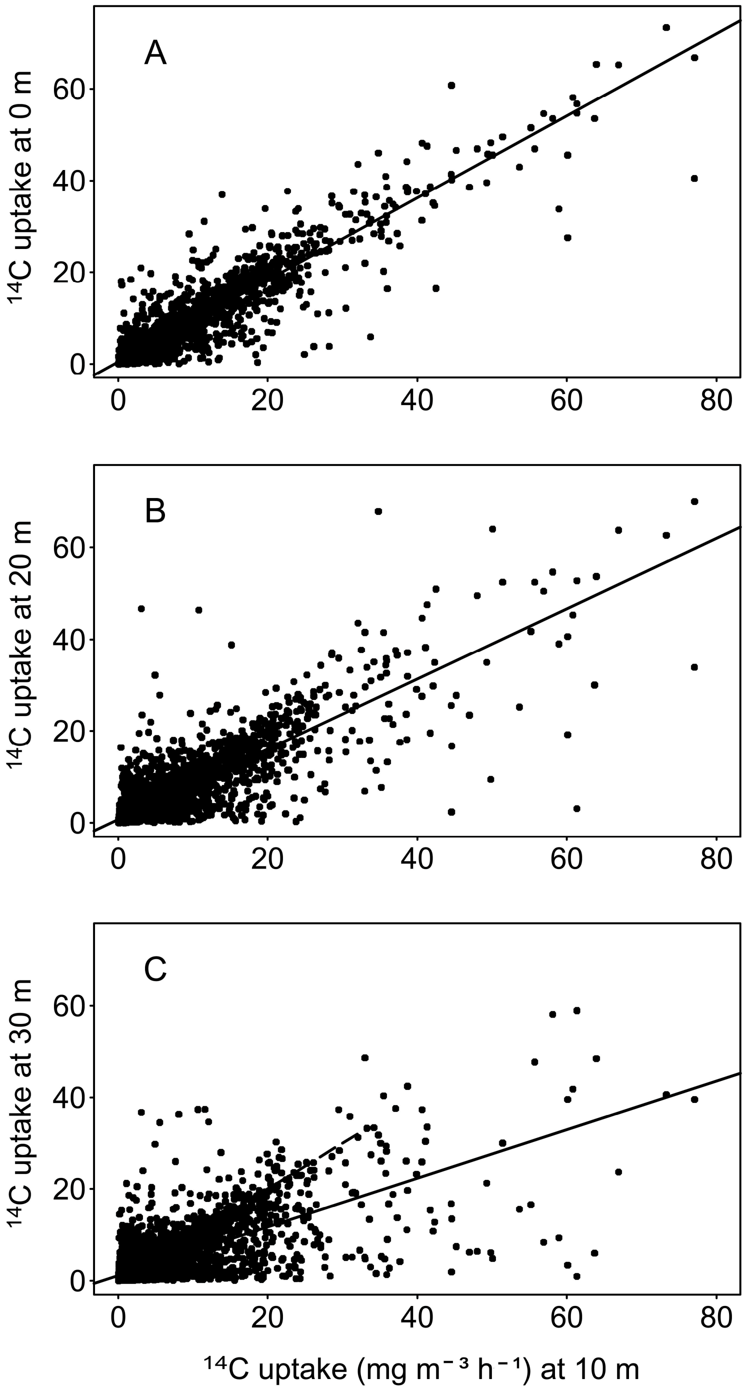

Figure 7. Relationship between the ^{14}C uptake rates at 10 m and that at a) 0 m; $P_{0m} = 0.89\ P_{10m} + 0.39$, N = 5162, r = 0.93, b) 20 m; $P_{20m} = 0.76\ P_{10m} + 0.75$, N = 5105, r = 0.86 and c) 30 m; $P_{30m} = 0.53\ P_{10m} + 1.14$, N = 4870, r = 0.72. Solid lines are the fitted least-square lines and the broken line in Fig. 7c is the 1:1 ratio, indicating occasional vertical mixing down to 30 m depth.

7. mynd. Samband mælinga á upptöku geislakols í sýnum frá annars vegar 10 m dýpi og hins vegar frá a) 0 m dýpi; $P_{0m} = 0,89\ P_{10m} + 0,39$, N = 5162, r = 0,93, b) 20 m; $P_{20m} = 0,76\ P_{10m} + 0,75$, N = 5105, r = 0.86 and c) 30 m; $P_{30m} = 0,53\ P_{10m} + 1.14$, N = 4870, r = 0.72. Heildregnar línur sýna reiknaða bestu línulegu aðfellu og brotalínan á mynd 7c sýnir 1:1 hlutfallið, en dreifing punkta bendir til að það sé ekki óalgengt að blöndun yfirborðslagsins nái niður á að minnsta kosti 30 m dýpi.

MODELS USED TO ESTIMATE THE DAILY PRIMARY PRODUCTION

Assuming that AN is valid in our calculations for the whole euphotic zone (z) and during the time period considered (t), we can define AN as $P_{inc.(t,z)}/B_{(t,z)}$. Thus we can rewrite equation (6) as:

$$P^B_{(t,z)} = AN \tanh (\alpha E_{(t,z)} / AN) \qquad \text{Eq. (7)}$$

When calculating the daily primary production per square meter (gC m^{-2} d^{-1}), the multiple of $P^B_{(t,z)}$, and $B_{(t,z)}$ is integrated over depth and time,

$$g\ C\ m^{-2}\ d^{-1} = \int\int B_{(t,z)}\ P^B_{(t,z)}\ dz\ dt \qquad \text{Eq. (8),}$$

where $P^B_{(t,z)}$ is obtained from equation (7). As AN is the ratio P/B and is assumed valid for the depth and time range indicated by t and z, the term $B_{(t,z)}$ becomes reduced again with respect to the equation (7).

The daily production according to PE-model, which is the results of the integration of equation (8) and based on all available information, is compared to the earlier calculations of the daily primary production (Thórdardóttir 1976b). These earlier calculations were made according to the approach given in Steemann Nielsen (1952), using an equation modified for Icelandic waters (Steemann Nielsen pers. comm.). The equation used to calculate the daily primary production in the SN-model is given by the equation (9):

$$gC\ m^{-2}\ d^{-1} = (2A + 2B + C + D)/6 \times d/2 \times e \qquad \text{Eq. (9)}$$

where A, B, C and D are the ^{14}C uptake at light saturation in the incubator, from the four standard depths of 0, 10, 20 and 30 meters, respectively, *d* is the number of hours from sunrise to sunset and *e* is the depth of the euphotic zone, here defined as 2.7 times the Secchi depth.

RESULTS AND DISCUSSION

A set of comparable data on ^{14}C uptake at light saturation, from standard measurements during 1958-1982, was used to calculate the daily primary production per square meter. Two different models, *i.e.* PE and SN as defined above, were employed. The calculated mean of the daily production per square meter according to PE-model, based on 5271 observations, is 0.97 g C m^{-2} d^{-1}, with a standard deviation of 1.07.

The calculated mean of the daily production per square meter, for the 5271 stations according to the SN-model is 0.88 g C m^{-2} d^{-1}, with a standard deviation of 0.91. The calculated values according to the PE-model are thus approximately 10% higher than that of the SN-model, as an average. The correlation coefficient of a linear regression analysis (r) is nevertheless highly significant, 0.96, for the comparison of the results (Fig. 8). The good correlation observed between these calculations underlines the applicability of the simple method proposed by Steemann Nielsen, for the waters around Iceland. There is, however, some scattering of points around the calculated regression line (Fig. 8), reminding of the different approach in these two models regarding the available light. The SN-model does obviously not account for the variable light conditions from one day to another, but seem to be in line with the light climate in general.

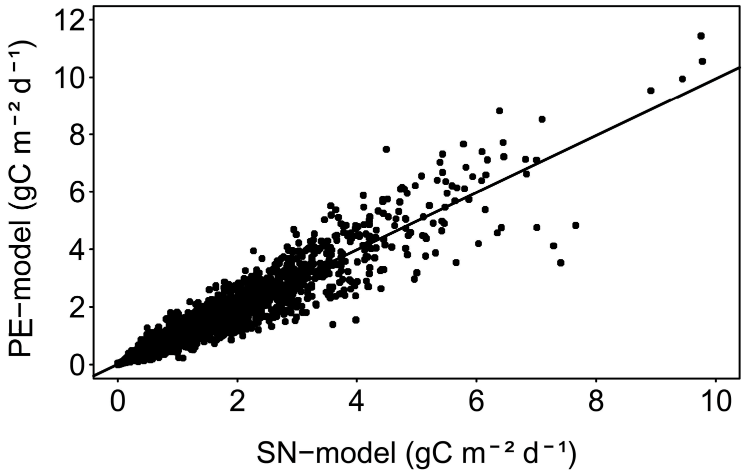

Figure 8. Daily primary production. Comparison of results using the SN-model plotted against result using the PE-model, with the fitted least-square line, $P_{SN} = 0.92\ P_{PE} + 0.08$, N = 5271, r = 0.96.

8. mynd. Dagsframleiðni svifþörunga undir fermetra yfirborðs sjávar. Samanburður á niðurstöðum útreikninga samkvæmt annars vegar SN-aðferð og hins vegar PE-aðferð. Línan sýnir bestu línulega aðfellu, $P_{SN} = 0,92\ P_{PI} + 0,08$*, N = 5271, r = 0,96.*

As mentioned earlier, estimated values are used when some data in the table of measurements are lacking. This was the case for about 65% of the stations applied. As might be expected, that applies most often to lack of the Secchi depth, but including most of the other variables as well. It is therefore worth while to consider what changes in results may appear when measured variables are replaced by estimated ones, one variable at the time. This was accomplished by selecting stations where information on both chlorophyll at 10 m, ^{14}C uptake rates from all 4 standard depths and the Secchi depth were available, *i.e.* a complete dataset for 1770 stations. Beside information on surface irradiance, these variables are necessary for the calculation of daily production by the present approach and the PE-model. One by one, the measured variables were replaced by the estimated ones and the recalculated daily production (PE') plotted against the calculations using all the measured variables (Figs. 9 and 10). The results of recalculations using estimated ^{14}C uptake rates for the four standard depths (Fig. 9) show scatter of points around the regression line which is apparently greater in the plots where the estimated values replace the measurements at 0 and 10 m, the upper levels of the euphotic zone (Fig. 9a,b), compared to those at the 20 and 30 m, the lower levels (Fig. 9c,d). The correlation of the recalculated daily production with that calculated from the complete dataset is, however, highly significant in all cases (Fig. 9). This shows that the results from each of the four depths are predictable from the rest of the data. Furthermore, it indicates greater weighting of the samples from 0 and 10 m for the results of calculated daily primary production, relative to the 20 and 30 m depth. The favorable light conditions in the upper part of the euphotic zone may explain that. This is in accordance with the weighting of the four standard depths in the Steemann Nielsen equation (9). One might conclude that measurement of the biomass at 30 m, and even at 20 m depth, were not as important in general as the shallower ones (Fig. 9), according to this set of data. Nevertheless it is worth noticing that the scatter of the plots increases as the calculated daily production diminishes. This is probably due to relatively better light conditions in the deeper part of the euphotic zone when the biomass is low, stressing the importance of knowing the depth distribution of the phytoplankton biomass in the waters. This is not accounted when the SN model is used for calculations of the daily production of phytoplankton.

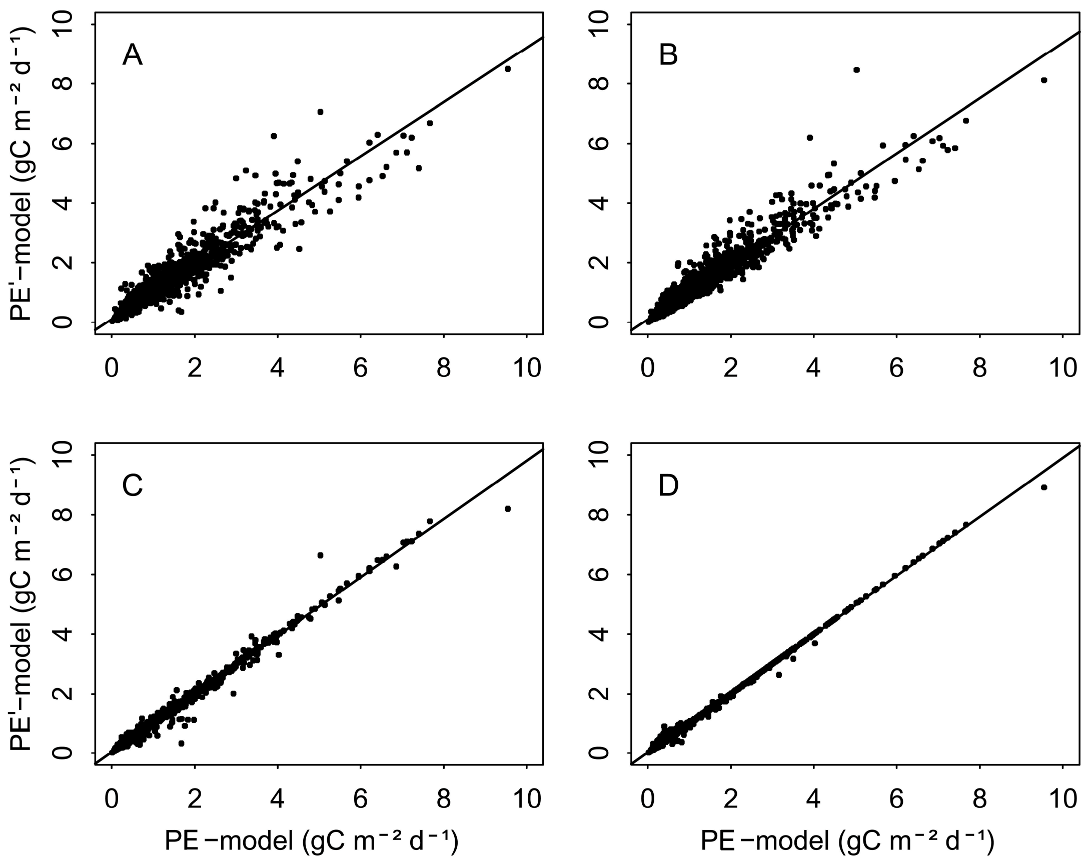

Figure 9. Daily primary production calculated according to the PE-model, using a complete set of measured values (N: 1770), plotted against the recalculated production (PE'-model) where values of ^{14}C uptake were replaced by estimated values for 0m (a), for 10 m (b), for 20 m (c) and for 30 m (d), with fitted least-square lines, all with r > 0.95, slopes > 0.9 and intercepts ≥ 0.1.

9. mynd. Dagsframleiðni svifþörunga undir fermetra yfirborðs sjávar reiknuð samkvæmt PE-aðferðinni, byggt á úrvali gagna þar sem engar mælingar vantar (N: 1770), borin saman við endurreikninga á dagsframleiðni samkvæmt sömu aðferð að öðru leyti en því að í hverri umferð er einum þætti mælinganna sleppt og þess í stað notað mat á viðkomandi þætti byggt á fylgni við aðra mælda þætti. Breyturnar, sem eru þannig endurmetnar, til að meta vægi þeirra í útreiknaðri dagsframleiðni, eru (a) mæld upptaka geislakols í yfirborðssýnum, (b) frá 10 m dýpi, (c) frá 20 m dýpi og (d) frá 30 m dýpi. Lína bestu línulegrar aðfellu er sýnd í hverju tilviki, en allar höfðu þær fylgnistuðul (r) sem er hærri en 0,95, hallatölur hærri en 0,9 og skurðpunkt á x-ásnum þar sem y = 0 sem er minni eða jafnt og 0,1.

When Secchi readings are substituted by estimated Secchi depth as a function of chlorophyll (Fig. 10), the recalculated daily production deviated more from that of the complete dataset than was the case in the previous examples (Fig. 9). The correlation coefficients is, however, highly significant (r = 0.93). The plot shows features worth some consideration. The scatter of the data points form rays, which are the results of measuring the Secchi depth to the nearest meter. This calls into question the reliability of the Secchi disk readings at sea. Apparently an uncertainty of ±2 m is common for a Secchi depth measurement (Fig. 10) in this dataset. Several factors may affect the accuracy of Secchi disk readings (Preisendorfer 1986), *e.g.* weather, waves, solar inclination, uncertainties in the measurements of the length of wire lowered, as well as the touch of different researchers. These results clearly underline the need of good data on the available light, including the light attenuation with depth, for calculations of daily photosynthesis of the euphotic zone.

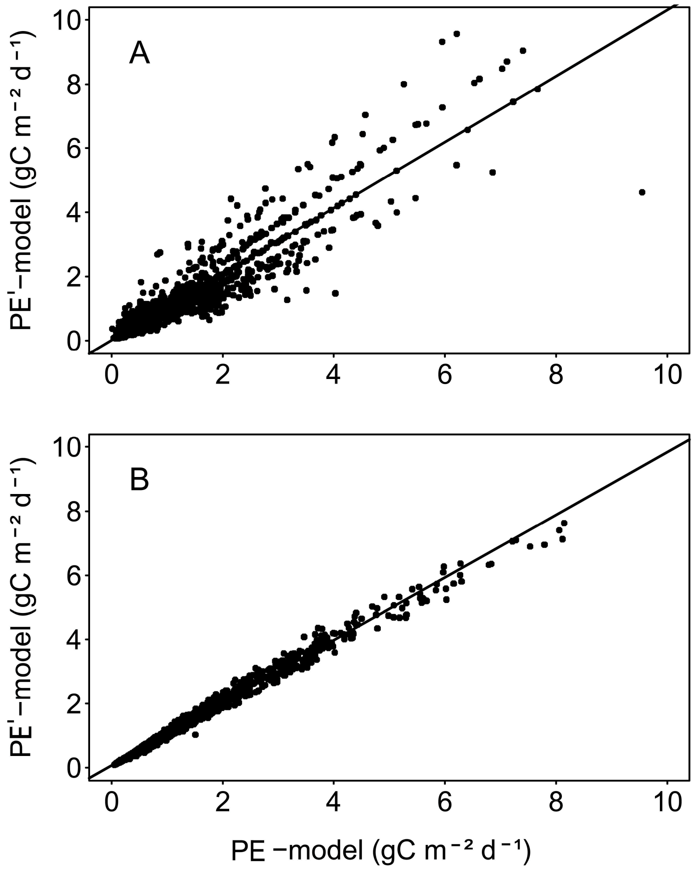

Figure 10. Daily primary production calculated according to the PE-model, using a complete set of measured values (N: 1770), plotted against the production calculated (PE'-model) where the values of measured Secchi depths have been replaced by estimated values from chlorophyll *a* at 10 m depth, with the fitted least-square line P' = 1.03 P + 0.01, r = 0.93 (a), and where the values of measured chlorophyll *a* at 10 m depth have been replaced by estimates using the ^{14}C uptake rate at the same depth, with the fitted least-square line P' = 1.01 P + 0.01, r = 0.99.

10. mynd. Dagsframleiðni svifþörunga undir fermetra yfirborðs sjávar reiknuð samkvæmt PE-aðferðinni, byggt á úrvali gagna þar sem engar mælingar vantar (N: 1770), borin saman við endurreikninga á dagsframleiðni samkvæmt sömu aðferð að öðru leyti en því að í hverri umferð er einum þætti mælinganna sleppt og þess í stað notað mat á viðkomandi þætti byggt á fylgni við aðra mælda þætti. Breyturnar, sem eru þannig endurmetnar, til að meta vægi þeirra í útreiknaðri dagsframleiðni, eru (a) sjóndýpi, sem er endurmetið samkvæmt mælingum á a-blaðgrænu frá 10 m dýpi og jafna bestu línulegrar aðfellu (heildregin lína) er P' = 1,03 P + 0,01, r = 0.93 og (b) a-blaðgræna frá 10 m dýpi endurmetin samkvæmt mælingum á upptöku geislakols í sýnum frá sama dýpi og jafna bestu línulegrar aðfellu (heila línan) er P' = 1,01 P + 0,01, r = 0,99.

Then the PE-model was used to calculate the daily primary production for the same set of data where the chlorophyll values were skipped. As mentioned above, the P^B_{max}, or AN, is found by simply dividing the productivity values by the corresponding Chl*a*, at 10 m depth. But in this case Chl*a* were calculated from the productivity value. Consequently AN is fixed according to the functional regression line Chl*a* = (P_{10m} + 0.73) / 2.60 (see page 14) for all stations and the distribution of biomass with depth is according to the productivity measurements at all the four standard depths, assuming the same AN applies to the whole euphotic zone. The negligible effect of the exclusion of information on the variation in P^B_{max} on the calculated daily primary production (Fig 10b) may reflect the small variation in AN (Fig. 6). It also underlines further the relative importance of the variable on available light for the photosynthesis.

Evidently, all the needed variables for the calculation of daily primary production may be deduced from Chl*a* at 10 m depth, by using the existing empirical relationships, except the irradiation at the surface. Calculations based only on chlorophyll and surface irradiance are of general interest in view of the extensive data becoming available from indirect measurements of phytoplankton biomass in the ocean, *e.g.* remote sensing from satellites, ship of opportunity and moorings. In comparison to the former correlation, this one (Fig. 11), gives the lowest correlation coefficient, r=0.81, but still a highly significant one. According to this the measured chlorophyll alone explains 65% of the variability in daily production values calculated from the complete set of measured variables. In due time this simple model might benefit from studies on the variations in physiological variables of phytoplankton (*cf.* Côté & Platt 1983, 1984; Harrison & Platt 1980, 1986; Behrenfeld & Falkowski 1997a), studies on depth distribution of algae biomass and light (*cf.* Morel & Berthon 1989, Sathyendranath *et al.* 1995), and effects of spectral changes in available light (*cf.* Morel 1991, Kyewalyanga *et al.* 1997, 1998). The model may also improve from an ongoing study of spatial and temporal variability of AN in Icelandic waters.

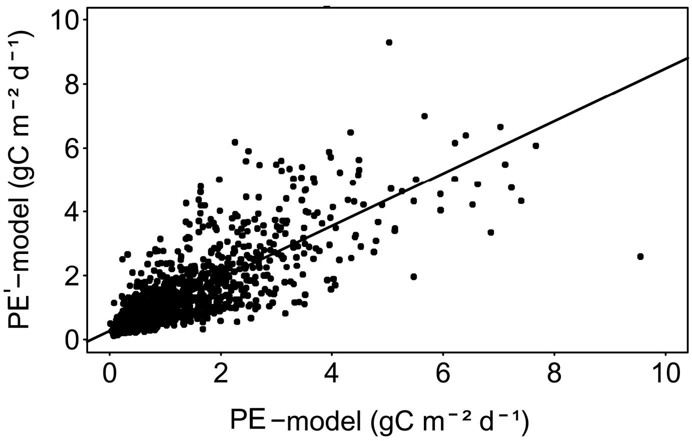

Figure 11. Daily primary production calculated according to the PE-model, using a complete set of measured values (N: 1770) and plotted against that recalculated (PE'-model), using only the chlorophyll *a* values from 10 m depth from the dataset. All the other variables used for the calculations, except the surface irradiance, were replaced by the respective estimates from the chlorophyll *a* values. The fitted least-square line P' = 0.82 P + 0.27, r = 0.81.

11. mynd. Dagsframleiðni svifþörunga undir fermetra yfirborðs sjávar reiknuð samkvæmt PE-aðferðinni, byggt á úrvali gagna þar sem engar mælingar vantar (N: 1770) borin saman við endurreikninga á dagsframleiðni samkvæmt sömu aðferð (PE'-model) og þá aðeins notaðar mælingar á a-blaðgrænu frá 10 m dýpi, en allir aðrar breytur en yfirborðsljósið voru reiknaðar út frá a-blaðgrænumælingunum. Jafna bestu línulegrar aðfellu (heila línan) er P' = 0,82 P + 0,27, r = 0,81.

Measuring the primary productivity *in situ* is generally considered the most realistic method for assessing the production of organic matter in the water column (Marra 2002). It is therefore interesting to see how the calculated daily production based on the incubator measurements agrees with simultaneously measured primary production *in situ*. Some available series of incubations (Thórdardóttir 1973) performed simultaneously both *in situ* and in incubator, *i.e.* successive four hour incubations covering a day, were compared. The daily production summed for the *in situ* experiments revealed highly significant correlation (r = 0.86, N: 45) and a slope of 1.18 for the least-square regression line. The values of daily production (Fig. 12), however, vary considerably when calculated from separate light saturated incubations during a day. This variability, which may be due to diurnal periodicity in the photosynthetic capacity (McCaull & Platt 1977, Harding et al. 1982), or hydrographic fluctuations at the given locality, needs to be studied further.

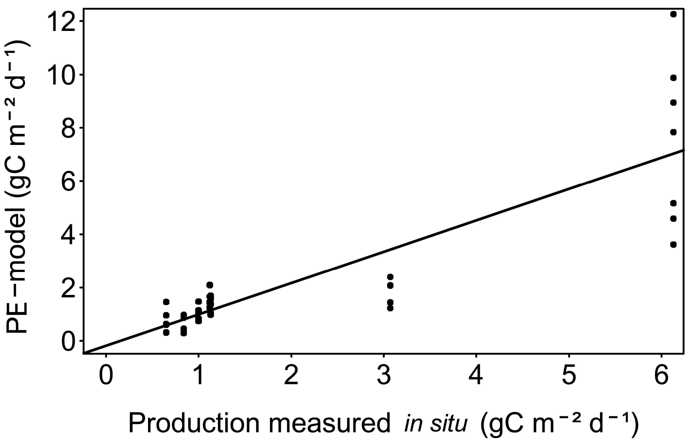

Figure 12. Daily primary production calculated according to the PE-model and plotted against the trapeze integrated production measured simultaneously *in situ*, with the fitted least-square line $P_{PE} = 1.18\ P_{in\ situ} + 0.18$, r=0.86, N = 43.

12. mynd. Dagsframleiðni svifþörunga undir fermetra yfirborðs sjávar reiknuð samkvæmt PI-aðferðinni borin saman við heildaða niðurstöðu framleiðnimælinga í sjó á mismunandi dýpum. Jafna bestu línulegrar aðfellu (heila línan) er $P_{PI} = 1,18\ P_{in\ situ} + 0,18$, *r = 0,86, N = 43.*

CONCLUSIONS

The daily production of phytoplankton calculated according to the recommendations of Steemann Nielsen (pers. comm.) and the results of integrating the productivity at variable light intensity over a day for the euphotic zone are shown to be comparable and highly correlated. Exemptions may be expected at days with unusual light climate. Thus, estimations of the average annual production in the waters around Iceland (Thórdardóttir 1994), as well as other calculated means of productivity measurements based on the Steemann Nielsen approach for these waters, are confirmed.

Comparison of the calculated daily production for successive four hours incubation experiments, made simultaneously both in an incubator and *in situ*, revealed significant correlation.

Secchi depth measurements, used for estimation of the attenuation of light with depth, are the prevalent source for variability in calculated daily production, according to a comparison of the relative importance of measured variables which are used in our model (PE-model). In view of the importance of light on phytoplankton growth in the sea, it is important to improve the estimate of available irradiance. The surface irradiance may be calculated from cloud cover and for stations with negligible influence from rivers or shallow waters, the attenuation may be calculated from the distribution of phytoplankton biomass with depth.

Using only chlorophyll measurements from 10 m depth, along with the surface irradiation, in calculation of daily production with our model explains 65% of the variance when compared to the results on daily production calculated with the same model and all the available measurements.

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