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Identification of ecologically and biologically significant areas (EBSA) in the Estuary and Gulf of St. Lawrence: Primary production

Identification de zones d'importance écologique et biologique (ZIEB) pour l'estuaire et le golfe du Saint-Laurent: production primaire

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ABSTRACT

In this report, we analyse of a large set of chlorophyll *a*, nitrate, and primary production observations gathered from the early 70's as well as results from a 3D coupled physical-biological model to identify ecologically and biologically significant areas (EBSAs) for primary production in the Gulf and Estuary of St. Lawrence. High phytoplankton production and Chl *a* concentration are found successively in all regions of the Gulf and Estuary of St. Lawrence, and thus all regions are important for phytoplankton production at one time or another during the year. However, only a few regions stand out as EBSAs if we consider their importance on an annual basis, based on uniqueness and aggregation criteria as defined in CSAS Ecosystem Status Report 2004/006. The most important zones are the Lower Estuary, the Gaspé Current, and the Northwestern Gulf.

RÉSUMÉ

Ce rapport présente l'analyse d'une importante banque de données de chlorophylle *a*, d'azote et de production primaire récoltées en mer depuis le début des années 70, de même que les résultat d'un modèle 3D couplé physique-biologie, dans le but d'identifier des zones d'importance écologique et biologique (ZIEB) pour la production primaire dans l'estuaire et le golfe du Saint-Laurent. Une production primaire et des concentrations de Chl *a* élevées sont observables successivement dans chaque région du golfe et de l'estuaire du Saint-Laurent. Chaque région est donc importante à un certain moment de l'année en ce qui concerne la production primaire. Toutefois, en considérant les données sur une base annuelle et en se basant sur les critères d'unicité et de concentration tels que définis dans le Rapport sur l'état des écosystèmes 2004/006 du SCCS, seulement quelques régions peuvent être identifiées comme ZIEB. Il s'agit de l'estuaire maritime, du courant de Gaspé, et du nord-ouest du golfe.

INTRODUCTION

Canada's Oceans Act authorizes DFO to provide enhanced protection to areas of the oceans and coasts that are ecologically or biologically significant. As DFO progresses with integrated management approaches to ocean areas, it is necessary to operationalise the term "significant" in this context. Consistent standards are needed to guide selection of areas where protection should be enhanced, while allowing sustainable activities to be pursued where appropriate

Ocean areas can be ecologically or biologically "significant" because of the functions that they serve in the ecosystem and/or because of structural properties. Although structure and function are interdependent, and an area can be "significant" for either reason, many of the functional activities like feeding and spawning of fish occur widely throughout the ocean. Operationalising the term requires establishing whether or not specific areas are particularly important for each function (i.e. "significant"), and thus warrant special attention within an integrated management plan. Criteria and guidance for this operationalisation is provided in DFO (2004). In a previous workshop (DFO, 2006) which focussed on testing the effectiveness of these criteria and guidelines to identify and prioritize a list of significant areas, a Delphic approach was used to determine ecologically and biologically significant areas (EBSA) in the Estuary and Gulf of St. Lawrence. However, this approach was not deemed sufficient to determine EBSA and it was decided to do the exercise again using all the existing data that were rapidly available.

The present document presents an analysis of a large set of chlorophyll *a* (Chl *a*), nitrate (NO3) and primary production (PP) observations gathered from the early 70's (the historical first Gulf wide study of Steven (1974), to the most recent DFO monitoring program (AZMP, e.g., Pepin et al., 2005). Given the poor temporal and spatial coverage of the observations and the complexity of the marine ecosystem, which includes multiple food webs associated with heterogeneous physical regimes, the approach also includes analysis of corresponding simulated fields issued from multiyear (1997-2000) runs made with the 3D coupled physical-biological model developed by Le Fouest et al. (2005). We use observations and model output to determine EBSA for phytoplankton. The resultant list of ecologically significant and representative areas may not be exhaustive, and additional sites may be added as new scientific knowledge becomes available.

LITTERATURE REVIEW

The following review is far from exhaustive but it covers the important aspects. Diatoms and dinoflagellates dominate autotrophic phytoplankton biomass in the Gulf and Estuary of St. Lawrence (Bérard-Therriault et al., 1999). Small phytoplankton (< 5 µm) is present year-round in low concentration, while large phytoplankton (> 5 µm) accounts for seasonal variations in production and biomass (Tremblay et al., 1997; Doyon et al., 2000; Le Fouest et al., 2005). Except for some regions, physical variability is relatively high in the St. Lawrence system and thus large phytoplankton should mainly be under physical control due to the difficulty for grazers to track transient increase in production (e.g., Therriault and Levasseur, 1985; Tremblay et al., 1997).

Nutrients

Nutrients exhibit a nearly conservative behaviour in the well-mixed Upper Estuary, with some uptake of nitrate and phosphate in some parts of the Estuary (Greisman and Ingram, 1977; Yeats, 1988). The Lower Estuary and Gulf are stratified, and thus nutrient profiles show a lower concentration at the surface than at the bottom (e.g. Coote and Yeats, 1979). In general, the concentration of nutrients is higher in the Estuary than in the Gulf, and within the Gulf, it is higher in the Northwest than in the East and South (Starr et al., 2003; Brickman and Petrie, 2003). At depths greater than ~100 m, concentrations of nutrients increase from Cabot Strait towards the head of the main channels (Laurentian, Esquiman and Anticosti) due to a combination of water circulation and nutrient regeneration processes (Coote and Yeats, 1979; Starr et al., 2003).

High concentrations of nutrients at the surface of the Lower Estuary are maintained during most of the year (Levasseur et al., 1984; Therriault and Levasseur, 1985). These high concentrations principally result from tidally-induced mixing between the fresh surface waters with nutrient-rich subsurface layers, and tidally-induced upwelling at the head of the Laurentian Channel (Steven, 1974; Therriault and Lacroix, 1976; Greisman and Ingram, 1977). Rivers, on the other hand, supply between 10 and 25% of the total nutrient input to the surface layer (Steven, 1974; Greisman and Ingram, 1977). The Gaspé Current, and to a lesser extent a vast region west of a north-south line drawn between the eastern tips of Anticosti Island and Prince Edward Island, are also fed by the nutrient pump at the head of the Laurentian Channel, at least at certain times of the year (e.g. Steven, 1974, Sinclair et al., 1976; Brickman and Petrie, 2003). In the rest of the Gulf, surface layer nutrients reach their highest concentrations in winter but get depleted during the spring bloom and afterward in summer (Savenkoff et al., 2000; Yeats, 1988; Lambert, 1982; de Lafontaine et al., 1991 and references therein).

Phytoplankton production

Sea ice melt and the St. Lawrence river runoff control the spatial and seasonal progression of the phytoplankton spring bloom in the Gulf and Estuary. In the Gulf, the spring bloom occurs as sea ice melts in April-May (Steven, 1974; Sevigny et al., 1979; de Lafontaine et al., 1991). The strongest Chl *a* concentrations are initially found East of Anticosti Island and then south, around the tip of the Gaspé Peninsula, and in the Northwestern Gulf (Steven, 1974). In early spring, the lowest concentrations are found in the Southern Gulf due to the later ice melt in that region (de Lafontaine et al., 1991). After the spring bloom, primary production in the Gulf is generally low (Tremblay et al., 2000; Savenkoff et al., 2000) except for the Gaspé Current. High phytoplankton biomass and production have been reported in the Gaspé Current in June, July, and October (Sevigny et al., 1979; Levasseur et al., 1990, 1992; Tremblay et al., 1997).

In the St. Lawrence Estuary, accumulation of phytoplankton biomass is usually delayed until mid-June/beginning of July and lasts until the end of September (Sinclair, 1978; Levasseur et al., 1984; Therriault and Levasseur, 1985). This delay in the spring bloom has been suggested to result from the spring runoff that leads to: (1) high surface water turbidity (Sinclair, 1978), (2) seaward advective transport (Savenkoff et al., 1997; Zakardjian et al., 2000), and (3) decreased eddy exchange between the surface and deeper layers that would prevent seeding of the photic layer by diatom cells (Levasseur et al., 1984). However certain regions of the Estuary are more productive than others. Therriault and Levasseur (1985) defined four regions in the Lower Estuary, based on primary production, that are controlled by different hydrodynamical processes. However, even within these regions, spatial and temporal variability in primary production are very high (e.g. Vézina et al, 1995; Savenkoff et al., 1997). Average production values range between 11 and 179 g-C m^{-2} yr^{-1} (Therriault and Levasseur, 1985). In addition to Therriault and Levasseur's (1985) classification for the Estuary, subdivisions of the Gulf of St. Lawrence into biological production zones have been proposed (see de Lafontaine et al. , 1991 and references therein; Bérard-Therriault et al., 1999, Brickman and Petrie, 2003). A synoptic view of major areas and processes important for biological productivity has also been investigated through modelling (Le Fouest et al., 2005).

METHODS

Observations

Observations relating to primary production in the St. Lawrence Estuary and Gulf, that were readily available, were gathered and converted to the same format and units. The source, type, and date of sampling of each data set are compiled in Table 1. Sampling sites are shown in Figure 1. We use three variables for the analysis (Chl *a* concentration, primary production, and nitrate concentration). Nitrate and Chl *a* concentrations were measured during most cruises, but primary production data are often lacking. Nitrate values usually include nitrite concentration, but on some occasion, only nitrate was available. These variables were measured using conventional methods that sometimes differ from one cruise to the other. The reader is invited to look at references given in Table 1 for more details on the methods.

We present the observations on a grid of 1/8 degree of longitude by 1/12 degree of latitude. Since the temporal coverage is poor, all years were pooled together and the data were grouped by seasons (winter: January to March, spring: April to June, summer: July to September, and fall: October to December) to obtain a spatial coverage sufficient to highlight high concentration/production areas. The data within each grid cell and between depths of 0 and 50 meters were averaged. This method can lead to artificially low primary production and Chl *a* concentrations in areas with shallow euphotic layer depth. Grid cells that do not contain any observation remain blank. The euphotic layer depth was determined from the analysis of data obtained with a multispectral Satlantic profiler (SPMR) in different seasons of the years 1997 to 2001. The 13 spectral bands data were used to calculate photosynthetically available radiation (PAR) according to an integrative spectral approach. The depth of the 1% surface light level was calculated to the closest meter by comparing measurements from the profiler with those from surface reference measurements. These results are compared with the 1% surface light level calculated by the coupled physical-biological model (Figure 2). The model results are smaller than the observations since they are averaged over the day and over the sampling period, but they give a good representation of the spatial variability of water transparency with clearer water in the east and more turbid water in the area under freshwater influence.

Model

The coupled planktonic ecosystem and circulation modelling framework (Le Fouest et al., 2005), which is used to complete our analysis, takes advantages of the high resolution 3D prognostic sea ice-ocean model of Saucier et al. (2003), making use of the mass conservation equations to simulate the most important coupled variables of planktonic ecological interest forming a nearly closed system. It simulates the ecosystems responses, in terms of production and biomass, to the variability of oceanic processes including high frequency (tides, diurnal heat cycles and precipitation), low frequency (atmospheric perturbations, mesoscale variability) and seasonal time scales (seasonal variations of runoff, formation and melting of sea ice, winter convection and summer stratification). Updates for modeling turbulent mixing and sea ice dynamics can be found in Saucier et al. (2004). Comparisons of satellite derived surface Chl *a* (SeaWIFS), and in situ nitrate and Chl *a* concentrations with simulated data for 1997 and 1998, provided a detailed quantitative demonstration of the model's ability to simulate consistent biogeochemical fields (Le Fouest et al., 2005, 2006) for the Gulf of St. Lawrence. The model has also been applied over different years (1997-1999) in the first attempt to reproduce the observed interannual variability, with the latter year (1999) being a special year over which widely spread observations suggested unusually strong planktonic production (Chifflet et al., 2004, 2005). For this study, we averaged four years (1997, 1998, 1999 and 2000) of simulated daily data (Chl *a*, total primary production (new and regenerated) and nitrate). These averaged data were then averaged (Chl *a*, NO3) or integrated (PP) over the upper 50 m of the water column.

Planktonic ecosystem description

The ecosystem model includes both simplified herbivorous and microbial food chains typical of bloom and post-bloom conditions respectively, and can be schematized as follows: the export at depth of the biogenic matter is mediated by the herbivorous food web (nitrate; large phytoplankton (> 5 µm); mesozooplankton (200-2000 µm); particulate organic matter) while the microbial food web (ammonium; small phytoplankton (< 5 µm); microzooplankton (20-200 µm); dissolved organic matter) is mainly responsible for nutrient recycling in the euphotic zone. The tight coupling between small phytoplankton growth and microzooplankton grazing, autochtonous nitrogen release and DON remineralization to NH4 is used to represent the dynamic of the microbial food chain. Biological transfer functions (e.g., phytoplankton growth rate, grazing and remineralization) are derived from bulk formulations using mean parameters found in the literature (see Le Fouest et al., 2005). Biological variables are calculated in Nitrogen units and algal biomass and production converted in Chl *a* and Carbon units using a molar C/N ratio of 106/16 (Redfield et al., 1963) and a C/Chl-a mass ratio of 55 (Sinclair, 1978; Rivkin et al., 1996).

Initial and boundary conditions:

Each simulated year is initialized in November or December of the previous year with observed temperature, salinity, nitrate and Chl *a* data from the corresponding Ice Forecast cruise interpolated in each model layer. Equal concentrations of large and small phytoplankton are assumed to initiate the run. Because of the lack of data for the remaining biological scalars for the same period, idealized profiles are used. Values of 1 mmol-N m^3 for ammonium (e.g., Levasseur et al., 1990; Tremblay et al., 2000; Zakardjian et al., 2000), 0.05 mmol-N m^3 for DON and 0.005 mmol-N m^3 for PON were assigned to each depth interval from the surface to the last active layer. Mesozooplankton and microzooplankton are set to 0.4 mmol-N m^3 (e.g., Sime-Ngando et al., 1995; Roy et al., 2000a; Savenkoff et al., 2000) in the upper 25 m and to 0 below this depth. Horizontal homogenous initial conditions for the biological scalars are assigned to each grid point. Both chemical and biological variables are set to zero in the inflowing rivers while boundary conditions at Cabot Strait and Strait of Belle-Isle are defined as initial conditions and set time invariant, except for nitrate that are prescribed from monthly climatological means of in situ concentration (Chifflet M., unpublished data).

RESULTS

After careful analysis of the observations (Figures 3 to 6) and model results (Figures 7 to 9, and 11 to 13), we divided the area into eight regions (Figure 10). As reported in the literature review, high phytoplankton production and Chl *a* concentration are found successively in all regions of the Gulf and Estuary of St. Lawrence, and thus all regions are important for phytoplankton production at one time or another during the year. The eight regions thus cover most of the Gulf and Estuary (Figure 10), but not all of them were considered as EBSA. Each region was rated according to its importance on an annual basis, based on uniqueness and aggregation criteria as defined in DFO (2004), and the ones with the highest scores were designated as EBSA.

Lower St. Lawrence Estuary (#1 on Figure 10)

This zone could have been divided into areas of important nutrient supply and transport and important primary production and Chl *a* concentrations, but we chose to define it as one region due to its overall importance in the system. Upwelling of nutrient-rich water at the head of the Laurentian Channel and its subsequent mixing with surface water provide an important supply of nutrients year-round (Figures 3 and 7). However, primary production at the head of the Channel and along the south shore is weak due to intense mixing and high turbidity. The initiation of the spring bloom in the Lower Estuary is delayed compared to the Gulf of St. Lawrence, and maximum primary production and high Chl *a* concentration occur in the central part of the area in the summer months (Figures 4, 5, 8, 9). However, despite this delay, the highest annual primary production observed and simulated in the whole St. Lawrence system are found in this area due to the continuous nutrient supply at the head of the Channel. Parts of the nutrients that are not used locally are exported in the Northwestern and Southern Gulf via the Gaspé Current. We rated the uniqueness and aggregation criteria of this zone high.

Gaspé Current (#2 on Figure 10)

The Gaspé Current has a width of about 10-20 km. Its width, intensity and stability are related to freshwater runoff (e.g. Bugden et al., 1992). The importance of the Gaspé Current in terms of primary production and transport of phytoplankton cells and nutrients to adjacent regions is maximal in spring (Figures 4b, 5b, 7c,d, 8c, and 9c,d). However, primary production and Chl *a* concentrations considerably greater than in the rest of the Gulf have been reported in summer and fall (see literature review). In addition to being sustained by a relatively continuous supply of nutrient-rich surface water from the Lower Estuary, upwelling processes associated with the frontal zone also provide nutrients to surface waters of the Gaspé Current (e.g. Tang ,1980). This zone is unique (uniqueness high), has high primary production and Chl *a* concentrations on an extended period of time (aggregation high) and is important for production in the Northwestern and Southern Gulf.

Northwestern Gulf of St. Lawrence (#3 on Figure 10)

The highest nutrient concentrations in the surface waters of this region are found at the end of winter (Figure 3a and 7c). A strong spring bloom cannot be detected with the observations we gathered (e.g. Figure 4b), but it is present in the simulations (Figure 8b,c) and it has been reported in the literature (production values of 5460 mg-C m^{-2} d^{-1} have been measured by Savenkoff et al., 2000; also see de Lafontaine et al., 1991). The cyclonic circulation in this area leads to the retention of phytoplanktonic cells and an abundant biomass is simulated in May (Figure 9c). Instabilities in the Gaspé Current also transport nutrients and phytoplanktonic cells to this region at certain times. We rated its uniqueness high and its aggregation criteria medium.

Southern Gulf of St. Lawrence (#4 on Figure 10)

The Southern Gulf is a vast region under the influence of the Gaspé Current, which splits in two branches past the tip of the Gaspé Peninsula: one fluctuating over the Magdalen Shallows and one following the western edge of the Laurentian Channel (e.g. Sheng, 2001). Simulated primary production is high during the spring bloom (April-May, Figure 8b,c) but low afterwards. However, phytoplankton cells and nutrients transported by the Gaspé Current can produce high biomass accumulation at the tip of the Gaspé Peninsula and at the entrance of Baie des Chaleurs (Figures 5b, 9c,d) and along the western edge of the Laurentian Channel (Figure 9c,d). Upwelling and tidal mixing occurring along the edge of the channel (see Gilbert et al., in preparation) most likely contribute to primary production. Except for the western edge of the Laurentian Channel, the importance of this region is more apparent with the observations than in the simulations (Figures 6, 11, 12 and 13). Uniqueness and aggregation for this zone were both rated medium.

Belle Isle Strait and Mecatina Trough (#5 on Figure 10)

This region is subject to cold Labrador shelf water inflow through the Strait of Belle-Isle and, intense tidal mixing and strong tidal currents near the strait, and upwelling along the north shore (see Koutitonsky and Bugden, 1991 and references therein; Lu et al., 2001; Saucier et al., 2003). There are very few observations in this area but the simulations suggest it is the site of an intense spring bloom (Figure 8b,c), followed by lower but recurrent production during summer (Figure 8, d to g). However, accumulation of Chl *a* is not apparent in the simulations, most likely due to the strong tidal currents that transport phytoplankton cells along the north shore. Due to the lack of information in that area, to its reduced size and to the apparent advection of phytoplankton out of the zone, we rate its uniqueness medium and its aggregation criteria weak.

Lower and middle north shore (#6 on Figure 10)

The north shore is a well–known region of upwelling due to Ekman transport associated with the prevailing winds. The Jacques Cartier Strait, north of Anticosti Island, is also the site of important tidal mixing (see Koutitonsky and Bugden, 1991 and references therein; Lu et al., 2001). These recurrent processes provide nutrients to the surface layer in winter (Figure 7a,b) and during summer after nutrient depletion by the spring phytoplankton bloom. Primary production is detectable throughout spring and summer in the simulations (Figure 8, a to f). Based on the simulated primary production values in Figure 8, it appears that the western part of this area (lower north shore) is subject to more important and more frequent upwelling than the eastern part. Primary production along the north shore during summer is occasional but strong. We thus rate its uniqueness and aggregation medium.

Southern shore of Anticosti Island (#7 on Figure 10)

As for the North shore, this area is subject to recurrent wind-induced upwelling, and to the influence of the Gaspé Current outflow (see Le Fouest et al., 2005 and references therein). High nutrient concentrations in the surface layer can be seen in the simulations in winter (Figure 7a). Primary production is detectable throughout spring and summer in the simulations (Figure 8, a to f). High productivity in this area has also been highlighted by annual and seasonal composites and daily CZCS images of pigment concentration (Fuentes-Yaco et al., 1995, 1996, 1997). As for the north shore, primary production in this area in summer is occasional but strong. We thus rate its uniqueness and aggregation medium.

Northeastern Gulf of St. Lawrence (#8 on Figure 10)

This region has the lowest surface nutrient concentrations in winter (Figure 3). The spring bloom first occurs in this region (Figure 8a) and by the end of April, nutrients are depleted in the surface layer and primary production is weak. The simulations show a slightly higher production in spring than in the observations (Figures 4, 5, 8, and 9). The uniqueness of this vast region and its aggregation criteria were both rated weak.

DISCUSSION

The use of a numerical model was essential in the exercise we made here, as it compensates for the lack of data, but further validation needs to be done. Although the main regions of high phytoplankton production and accumulation are well reproduced by the model, some areas seems to present underestimated values, such as the Gaspé Current and the Southwestern Gulf, while other areas present overestimated values, such as the Northeastern Gulf. Also, the total annual primary production simulated by the model is below the estimates made from observations (see Le Fouest et al., 2005). These differences probably result from an ensemble of factors: (1) an under representation of mixing processes in the estuary (Saucier et al., 2003), (2) a slightly shallow winter mixed layer in the model (e.g. Smith et al., 2006), that lead to a reduction of available nutrients in the mixed layer in spring, (3) an inadequate representation of the Gaspé Current due to its small width (10-20 km) compared to the model resolution (5 km), (4) the representation of the light attenuation factor as a function of salinity is adequate in the Estuary and close to river mouths but might not be adequate further down from the freshwater source as their load of particulate matter decreases. The first factor, i.e., insufficient mixing at the head of the Laurentian Channel due to the low spatial resolution of the model relative to the size of the estuary, was solved by increasing the horizontal eddy viscosity and diffusivity coefficients in the estuary (Sourisseau et al., 2006). Although it might give appropriate primary production and biomass values for the Estuary as a whole, it can blur regional difference within the Estuary, and influence the Gaspé Current “definition”. To help with model validation, more data would be needed, especially south of Anticosti Island, in the Northeastern Gulf, up to Belle-Isle Strait and including the Mecatina Trough. A nutrient sensor could be added to a few CTDs and profiles taken on a regular basis in each DFO cruises. The addition of such sensors would greatly enlarge the spatial and temporal coverage for this biological indicator.

Another model validation tool that might possibly be very useful is the remote sensing of Chl *a* available from a variety of sensors. The main problem presently preventing the use of these images is the large influence of dissolved organic matter (i.e. yellow substances) and suspended sediments on the spectral signature of the ocean, not only in the estuary but also in the much larger area under the influence of the freshwater outflow from the St. Lawrence. There is ongoing research on the characterization of optical properties in the St. Lawrence but more work is required to fully characterize their spatial and temporal variability. Once this problem is solved, we will have a powerful tool to validate models, in addition to ship based sampling.

CONCLUSION

Based on our rating (higher uniqueness and aggregation criterias), the first three regions, Lower Estuary, Gaspé Current, and Northwestern Gulf, can be classified as ecologically and biologically important areas in terms of primary production and phytoplankton biomass accumulation. However, considering the short time delay allotted to do the exercise, the incomplete data base, the lack of data in certain regions or times of the year, and the necessity to further validate the 3D model, the limits of the zones as well as their importance could change in the future. An increased sampling effort would be beneficial along the lower and middle north shore, along the south shore of Anticosti Island and in the Northeast Gulf.

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REFERENCES

Bérard-Therriault, L., M. Poulin, et L. Bossé (1999), Guide d'identification du phytoplancton marin de l'estuaire et du golfe du Saint-Laurent incluant également certains protozoaires. Publ. spéc. can. sci. halieut. aquat. 128. 387 p.

Brickman, D., et B. Petrie (2003), Nitrate, silicate, and phosphate Atlas for the Gulf of St. Lawrence, Can. Tech. Rep. Hydrogr. Ocean Sci., No 231, xi + 152 pp.

Bugden, G. L., B. T. Hargrave, M. M. Sinclair, C. L. Tang, J.-C. Therriault, and P. A. Yeats (1982), Freshwater runoff effects in the marine environment: the Gulf of St. Lawrence example, Can. Tech. Rep. Fish. Aquat. Sci., no 1078, 88 pp.

Bulleid, E., and D. M. Steven (1972), Measurements of primary and secondary production in the Gulf of St. Lawrence, McGill Univ., Mar. Sci. Centre, M.S. Rep. 21, CCIBP contribution, 151, 111 p.

Chifflet, M., V. Le Fouest, M. Starr, F.J. Saucier, and B. Zakardjian (2004). Inter-annual variability of the St. Lawrence productivity: a modelling study. 2004 Joint Assembly of the American Geophysical Union (AGU), the Canadian Geophysical Union (CGU) and the Society of Exploration Geophysicists (SEG). Montréal (Qc), Canada, May 17-21. Book of Abstract.

Chifflet, M., M. Starr M. V. Le Fouest, F. Saucier, and B. Zakardjian (2005). Inter-annual variability of the St. Lawrence productivity: a modelling study. International GLOBEC Symposium : Climate Variability and Sub-Arctic Marine Ecosystems, Victoria, CA, May 16-20. Book of Abstract.

Coote, A. R. , and P. A. Yeats (1979), Distribution of nutrients in the Gulf of St. Lawrence, J. Fish. Res. Board Can., 36, 122-131.

de Lafontaine, Y., S. Demers, and J. Runge (1991), Pelagic food web interactions and productivity in the Gulf of St. Lawrence: a perspective, p. 99-123, In , J.-C. Therriault (ed.) The Gulf of St. Lawrence: small ocean or big estuary? Can. Spec. Publ. Fish. Aquat. Sci. 113.

DFO, 2004. Identification of Ecologically and Biologically Significant Areas. DFO Can. Sci. Advis. Sec. Ecosystem Status Rep. 2004/006.

DFO, 2006. Proceedings of the Zonal Workshop on the Identification of Ecologically and Biologically Significant Areas (EBSA) within the Gulf of St. Lawrence and Estuary. DFO Can. Sci. Advis. Sec. Proceed. Ser. 2006/011.

Devine, L., C. Savenkoff, A. F. Vezina, J.-P. Chanut, S. Roy, L. Comeau, V. Dube, D. Blasco and Y. Gratton (1997), Compilation des données biologiques et chimiques dans l'estuaire maritime du Saint-Laurent : programme COUPPB, 1989, 1990 et 1991, Rapport statistique canadien sur l'hydrographie et les sciences océaniques, 150, 103 pp.

Doyon, P., B. Klein, R. G. Ingram, L. Legendre, J.-É Tremblay, et J.-C. Therriault (2000), Influence of wind mixing and upper-layer stratification on phytoplankton biomass in the Gulf of St. Lawrence, Deep-sea Research II, 47, 415-433.

Fuentes-Yaco, C., P. Larouche, A. Vézina, C. Vigneau and M. Gosselin (1995), atalogue of phytoplankton pigment images from the Gulf of St. Lawrence: Coastal Zone Color Scanner data from 1979 to 1981, Can. Data Rep. Hydrogr. Ocean Sci, 135: 91 p.

Fuentes-Yaco, C., A. F. Vézina, M. Gosselin, Y. Gratton, and P. Larouche (1996), Influence of late-summer storms on the horizontal variabillity of phytoplankton pigment determined by Coastal Zone Color Scanner images in the Gulf of St. Lawrence, Canada. In: Ocean Optics XIII, (S. G. Ackleson, R. Frouin, Eds.) Proc. SPIE, 2963, 678-683.

Fuentes-Yaco, C., A. Vézina, P. Larouche, C. Vigneau, M. Gosselin, and M. Levasseur (1997), Phytoplankton pigment in the Gulf of St. Lawrence, Canada as determined by the Coastal Zone Color Scanner. Part 1. Spatiotemporal variability. Cont. Shelf Res., 17, 1421-1439.

Greisman, P., and G. Ingram (1977), Nutrient distribution in the St. Lawrence estuary, J. Fish. Res. Board Can., 34, 2117-2123.

Koutitonsky, V. G., and G. L. Budgen (1991), The physical oceanography of the Gulf of St Lawrence: a review with emphasis on the synoptic variability of the motion, In: Therriault, J.-C. (ed.) The Gulf of St. Lawrence: small ocean or big estuary? Can. Spec. Publ Fish. Aquat. Sci.,113, p. 57-90.

Lambert, J. D. (1982), Contribution à l'étude des communautés planctoniques de la Baie-des-Chaleurs, M.Sc. Thesis, Univ. Québec Rimouski, Rimouski, 131 pp.

Le Fouest, V., B. Zakardjian, F. J. Saucier, and M. Starr (2005), Seasonal versus synoptic variability in planktonic production in a high-latitude marginal sea : the Gulf of St. Lawrence (Canada), J. Geophys. Res., 110, C09012, doi:10.1029/2004JC002423.

Le Fouest, V., B. Zakardjian, F. J. Saucier, and S. A. Çizmeli (2006), Application of SeaWIFS- and AVHRR-derived data for mesoscale and regional validation of a 3-D high-resolution physical-biological model of the Gulf of St. Lawrence (Canada), J. Mar. Syst., 60, 30-50.

Levasseur, M., J.-C. Therriault, and L. Legendre (1984), Hierarchical control of phytoplankton succession by physical factors, Mar. Ecol. Prog. Ser., 19, 211-222.

Levasseur, M. E, P. J. Harrison, B. R. Heimdal, and J.-C. Therriault (1990), Simultaneous nitrogen and silicate deficiency of a phytoplankton community in a coastal jet-front, Marine Biology, 104, 329-338.

Levasseur, M., L. Fortier, J.-C. Therrieult, and P. J. Harrison (1992), Phytoplankton dynamics in a coastal jet frontal region, Mar. Ecol. Prog. Ser., 86, 283-295.

Lu, Y., K. R. Thompson, and D. G. Wright (2001) Tidal currents and mixing in the Gulf of St. Lawrence: An application of the incremental approach to data assimilation, Can. J. Fish. Aquat. Sci., 58, 723-735.

Pepin, P., B. Petrie, J.-C. Therriault, S. Narayanan, W. G. Harrison, K. T. Frank, J. Chasse, E. B. Colbourne, D. Gilbert, D. Gregory, M. Harvey, G. L. Maillet, M. Mitchel, and M. Starr (2005), The Atlantic Zone Monitoring Program (AZMP) : review of 1998-2003, Can. Tech. Rep. Hydrogr. Ocean Sci., 242, 87 pp.

Petrie, B, and P. Yeats (2000), Annual and interannual variability of nutrients and their estimated fluxes in the Scotian Shelf – Gulf of Maine region, Can. J. Fish. Aquat. Sci., 57, 2536-2546.

Redfield A.C., Ketchum, B.H., Richards, F.A., 1963. The influence of organisms on the composition of sea-water. In: Hill, M.N. (Ed.), The Sea, Wiley-Interscience, New York, pp. 26-77.

Rivkin, R.B, L. Legendre, D. Deibel, J.-E. Tremblay, B. Klein, K. Crocker, S. Roy, N. Silverberg, C. Lovejoy, F. Mesplé, N. Romero, R. Anderson et al. (1996), Vertical Flux of Biogenic Carbon in the Ocean: Is There Food Web Control? Science, 272, 1163-1166.

Roy, S., N. Silverberg, N. Romero, D. Deibel, B. Klein, C. Savenkoff, A. F. Vézina, J.-E. Tremblay, L. Legendre, and R. B. Rivkin (2000a), Importance of mesozooplankton feeding for the downward flux of biogenic carbon in the Gulf of St. Lawrence (Canada), Deep-Sea Res. II, 47, 519– 545.

Roy, S., B. Sundby, A. F. Vézina, and L. Legendre (2000b), A Canadian JGOFS process study in the Gulf of St. Lawrence. Introduction, Deep-Sea Res. II, 47, 377-384.

Saucier, F. J., F. Roy, D. Gilbert, P. Pellerin, and H. Ritchie (2003), Modelling the formation and circulation processes of water masses and sea ice in the Gulf of St. Lawrence, Canada, J. Geophys. Res., 108, 1-20.

Saucier, F. J., S. Senneville, S. Prinsenberg, F. Roy, P. Gachon, D. Caya, and R. Laprise (2004), Modelling the ice-ocean seasonal cycle in Hudson Bay, Foxe Basin and Hudson Strait, Canada, Clim. Dyn., 23, 303-326.

Savenkoff, C., A. F. Vézina, and Y. Gratton (1997), Effect of a freshwater pulse on mesoscale circulation and phytoplankton distribution in the lower St. Lawrence estuary, J. Mar. Res., 55, 353-381.

Savenkoff, C., A. F. Vézina, S. Roy, B. Klein, C. Lovejoy, J.-C. Therriault, L. Legendre, R. Rivkin, C. Bérubé. J.-É. Tremblay, and N. Silverberg (2000), Export of biogenic carbon and structure and dynamics of the pelagic food web in the Gulf of St. Lawrence: Part 1. Seasonal variations, Deep-Sea Research II, 47, 585-607.

Sevigny, J.-M., M. Sinclair, M. I. El-Sabh, S. Poulet, and A. Coote (1979), Summer plankton distributions associated with the physical and nutrient properties of the Northwestern Gulf of St. Lawrence, J. Fish. Res. Board Can., 36, 187-203.

Sheng, J. (2001), Dynamics of a Buoyancy-Driven Coastal Jet: The Gaspé Current, J. Phys. Oceanogr., 31, 3146–3162.

Sime-Ngando, T., M. Gosselin, S. Roy, and J.-P. Chanut (1995), Significance of planktonic ciliated protozoa in the Lower St. Lawrence Estuary: Comparison with bacterial, phytoplankton, and particulate organic carbon, Mar. Ecol. Prog. Ser., 9, 243–258.

Sinclair, M. (1978), Summer phytoplankton variability in the lower St. Lawrence Estuary, J. Fish. Board Can., 35, 1171-1185.

Sinclair, M., M. El-Sabh, and J. R. Brindle (1976), Seaward nutrient transport in the lower St. Lawrence estuary, J. Fish. Res. Board Can., 33, 1171-1185.

Smith, G. C., F. J. Saucier, and D. Straub (2006), Formation and circulation of the cold intermediate layer in the Gulf of Saint Lawrence, J. Geophys. Res., 111, C06011, doi:10.1029/2005JC003017.

Sourisseau, M., Y. Simard, and F. J. Saucier (2006), Krill aggregation in the St. Lawrence system, and supply of krill to the whale feeding grounds in the estuary from the gulf, Mar. Ecol. Prog. Ser., 314, 257–270.

Starr, M., L. St-Amand, L. Devine, and L. Bérard-Therriault (2003), State of phytoplankton in the Estuary and Gulf of St. Lawrence during 2002, Secr. can. de consult. sci. du MPO, Document de recherche 2003/103, 29 p.

Steven, D.M., J. Acreman, F. Axelsen, M. Brennan, and C. Spence (1973a), Measurements of primary and secondary production in the Gulf of St. Lawrence, II, 1970, McGill University, Marine Sciences Centre MS report; 23; CCIBP contribution; 196, 165 pp.

Steven, D.M., J. Acreman, F. Axelsen, M. Brennan, and C. Spence (1973b), Measurements of primary and secondary production in the Gulf of St. Lawrence, III, 1971, McGill University, Marine Sciences Centre MS report; 24; CCIBP contribution; 211, 182 pp.

Steven, D.M., J. Acreman, F. Axelsen, M. Brennan, and C. Spence (1973c), Measurements of primary and secondary production in the Gulf of St. Lawrence, IV, 1971 and 1972, McGill University, Marine Sciences Centre MS report; 25; CCIBP contribution; 212, 99 pp.

Steven, D. M. (1974), Primary and secondary production in the Gulf of St. Lawrence, McGill University Marine Science Center MS Report No. 26, 116 pp.

Tang, C. L. (1980), Mixing and circulation in the northwestern Gulf of St. Lawrence: A study of a buoyancy-driven current system, J. Geophys. Res., 85, 2787– 2796.

Therriault, J.-C., and G. Lacroix (1976), Nutrients, chlorophyll, and internal tides in the St. Lawrence estuary, J. Fish. Res. Board Can., 33: 2747-2757.

Therriault, J.-C., and M. Levasseur (1985), Control of phytoplankton production in the lower St. Lawrence Estuary: light and freshwater runoff. Naturaliste Can. 112:77-96.

Tremblay, J-É. , L. Legendre, and J-C. Therriault (1997), Size-differential effects of vertical stability on the biomass and production of phytoplankton in a large estuarine system, Est. Coast. Shelf Sci., 45, 415-431.

Tremblay, J-É. , L. Legendre, B. Klein, and J-C. Therriault (2000), Size-differential uptake of nitrogen and carbon in a marginal sea (Gulf of St. Lawrence, Canada): significance of diel periodicity and urea uptake, Deep-Sea Res. II, 47, 489-518.

Vézina, A. F., Y. Gratton, and P. Vinet (1995), Mesoscale physical-biological variability during a summer phytoplankton bloom in the lower St. Lawrence Estuary, Est. Coast. Shelf. Sci., 41, 393-411.

Yeats, P. A. (1988), Nutrients, In Chemical Oceanography in the Gulf of St. Lawrence, edited by P. M. Strain, Can. Bull. Fish. Aquat. Sci., 220, Chap 3, pp 29-48.

Zakardjian, B. A., Y. Gratton, and A. F. Vézina (2000), Late spring phytoplankton bloom in the Lower St. Lawrence Estuary: the flushing hypothesis revisited, Mar. Ecol. Prog. Ser., 192, 31-48.

Table 1. Compilation of the sampling time and location for the observations used in our analysis. Sampling stations usually cover a region of the Gulf or Estuary of St. Lawrence, but fixed AZMP stations, visited throughout the year, are also included (CG: Gaspe Current, GA: Anticosti Gyre, Riki: Rimouski, Shediac). Data types include Chl *a* concentration, primary production (PP), nutrient concentrations (nut), which usually includes NO_3, PO_4, $Si(OH)_4$, but sometimes only NO_3, and the depth of the 1% light level (ze01).

Year	Sampling Region	Time of the year	Data type available	Source of data
1969	Gulf	May - Sep.	Chl *a*, PP, nut, ze01	Steven's reports[1,2]
1970	Gulf and Estuary	April - Sep.	Chl *a*, PP, nut, ze01	Steven's reports[2,3]
1971	Gulf and Estuary	April -Sep.	Chl *a*, PP, nut, ze01	Steven's reports[2,4]
1972	Gulf and Estuary	April -Sep.	Chl *a*, PP, nut, ze01	Steven's reports[2,5]
1979	Estuary	June - August	Chl *a*, PP, nut, ze01	SGDO[6]
1979	Estuary	Oct. - Dec.	Chl *a*, PP, nut, ze01	SGDO[6]
1980	Estuary	Feb. - Dec.	Chl *a*, PP, nut, ze01	SGDO[6]
1989	Estuary	June-July	Chl *a*, PP, nut	COUPBB's report[7]
1990	Estuary	June-July	Chl *a*, PP, nut, ze01	COUPBB's report[7]
1991	Estuary	May and July	Chl *a*, PP, nut, ze01	COUPBB's report[7]
1992	Gulf	July - Oct., Dec.	Chl *a*, PP, nut, ze01	JGOFS[8]
1993	Gulf	May-July, Nov.-Dec.	Chl *a*, PP, nut, ze01	JGOFS[8]
1994	Gulf	April, June	Chl *a*, PP, nut, ze01	JGOFS[8]
1996	GA, CG	Feb. - Dec.	Chl *a*, nut	SGDO
1996	Gulf	March	nut	SGDO
1996	Gulf and Estuary	December	Chl *a*, nut	SGDO
1997	GA, CG	Jan. - Dec.	Chl *a*, nut	SGDO
1997	Gulf	June	Chl *a*, nut	SGDO
1997	Gulf and Estuary	August - Sep.	Chl *a*, ze01	SGDO
1997	Gulf and Estuary	November	Chl *a*, nut	SGDO
1998	GA, CG	Jan-March, June, Sep., Nov.	Chl *a*, nut	SGDO
1998	Gulf	March	nut	SGDO
1998	Gulf	June	Chl *a*, nut, ze01	SGDO
1998	Gulf and Estuary	December	Chl *a*, nut	SGDO
1998	Gulf and Estuary	October	Chl *a*, ze01	SGDO
1999	GA, CG	Jan-March, May-Dec.	Chl *a*, nut	SGDO
1999	Riki	May - Nov.	Chl *a*, nut, ze01	SGDO
1999	Shediac	April-June, Aug.-Dec.	Chl *a*, nut	MEDS
1999	IMA transect	September	Chl *a*, nut	MEDS
1999	Cabot Strait	April, October	Chl *a*, nut	MEDS
1999	Gulf	March	nut	SGDO
1999	Gulf	June	Chl *a*, nut	SGDO
1999	Gulf and Estuary	December	Chl *a*, nut	SGDO
1999	Gulf and Estuary	June-July	Chl *a*, nut, ze01	SGDO
2000	GA, CG	Feb, March, May-Dec.	Chl *a*, nut	SGDO
2000	Riki	May-Oct	Chl *a*, nut, ze01	SGDO
2000	Shediac	April-Oct., Dec.	Chl *a*, nut	MEDS
2000	Cabot Strait	April, October	Chl *a*, nut	MEDS
2000	Gulf and Estuary	May	Chl *a*, nut, ze01	SGDO
2000	Gulf	June	Chl *a*, nut, ze01	SGDO

2000	Gulf and Estuary	Nov. – Dec.	Chl *a*, nut, ze01	SGDO
2001	GA, CG	Feb. – Dec.	Chl *a*, nut	SGDO
2001	Gulf	March	nut	SGDO
2001	Riki	May-Sept	Chl *a*, nut, ze01	SGDO
2001	Gulf and Estuary	April-May	Chl *a*, nut, ze01	SGDO
2001	Gulf and Estuary	May - June	Chl *a*, nut	SGDO
2001	Gulf	June	nut	SGDO
2001	Gulf and Estuary	Nov. - Dec.	Chl *a*, nut, ze01	SGDO
2001	Shediac	April - Dec.	Chl *a*, nut	MEDS
2001	Cabot Strait	April, October	Chl *a*, nut	MEDS
2002	GA, CG	Jan., Apr. - Nov.	Chl *a*, nut	SGDO
2002	Gulf and Estuary	March	nut	SGDO
2002	Riki	May - Oct.	Chl *a*, nut, ze01	SGDO
2002	Gulf and Estuary	May - June	Chl *a*, nut, ze01	SGDO
2002	Gulf and Estuary	Oct - Nov.	Chl *a*, nut	SGDO
2002	Shediac	April - Nov.	Chl *a*, nut, ze01	MEDS
2003	GA, CG	Mar, Apr, Jun, Jul, Sep.-Nov.	Chl *a*, nut, ze01	SGDO
2003	Gulf and Estuary	March	nut	SGDO
2003	Gulf and Estuary	April, June	Chl *a*, nut, ze01	SGDO
2003	Riki	May - Oct.	Chl *a*, nut, ZE02	SGDO
2003	Gulf and Estuary	Oct - Nov.	Chl *a*, nut	SGDO
2003	Shediac	April - Dec.	Chl *a*, nut, ze01	MEDS
2004	GA, CG	Feb., Mar., June, Aug., Nov.	Chl *a*, nut	SGDO
2004	Gulf and Estuary	March	nut	SGDO
2004	Riki	May - Oct.	Chl *a*, nut, ze01	SGDO
2004	Gulf and Estuary	June	Chl *a*, nut	SGDO
2004	Gulf and Estuary	November	Chl *a*, nut	SGDO
2004	Shediac	May, June, Sep., Nov.	Chl *a*, nut, ze01	MEDS
2004	Cabot Strait	April - May	Chl *a*, nut	MEDS
2005	GA, CG	Feb., Mar., Jun., Aug., Oct., Nov.	Chl *a*, nut	SGDO
2005	Gulf and Estuary	March	nut	SGDO
2005	Riki	May - Oct.	Chl *a*, nut, ze01	SGDO
2005	Gulf and Estuary	June	Chl *a*, nut	SGDO
2005	Gulf and Estuary	November	Chl *a*, nut	SGDO
2005	Shediac	May, June, Sep.-Nov.	Chl *a*, nut, ze01	MEDS
2005	Cabot Strait	April, August	Chl *a*, nut	MEDS

[1]Bulleid and Steven (1972),
[2]Steven (1974),
[3]Steven et al. (1973a),
[4]Steven et al. (1973b),
[5]Steven et al. (1973c),
[6]Therriault and Levasseur (1985),
[7]Devine et al. (1997),
[8]Roy et al. (2000b).

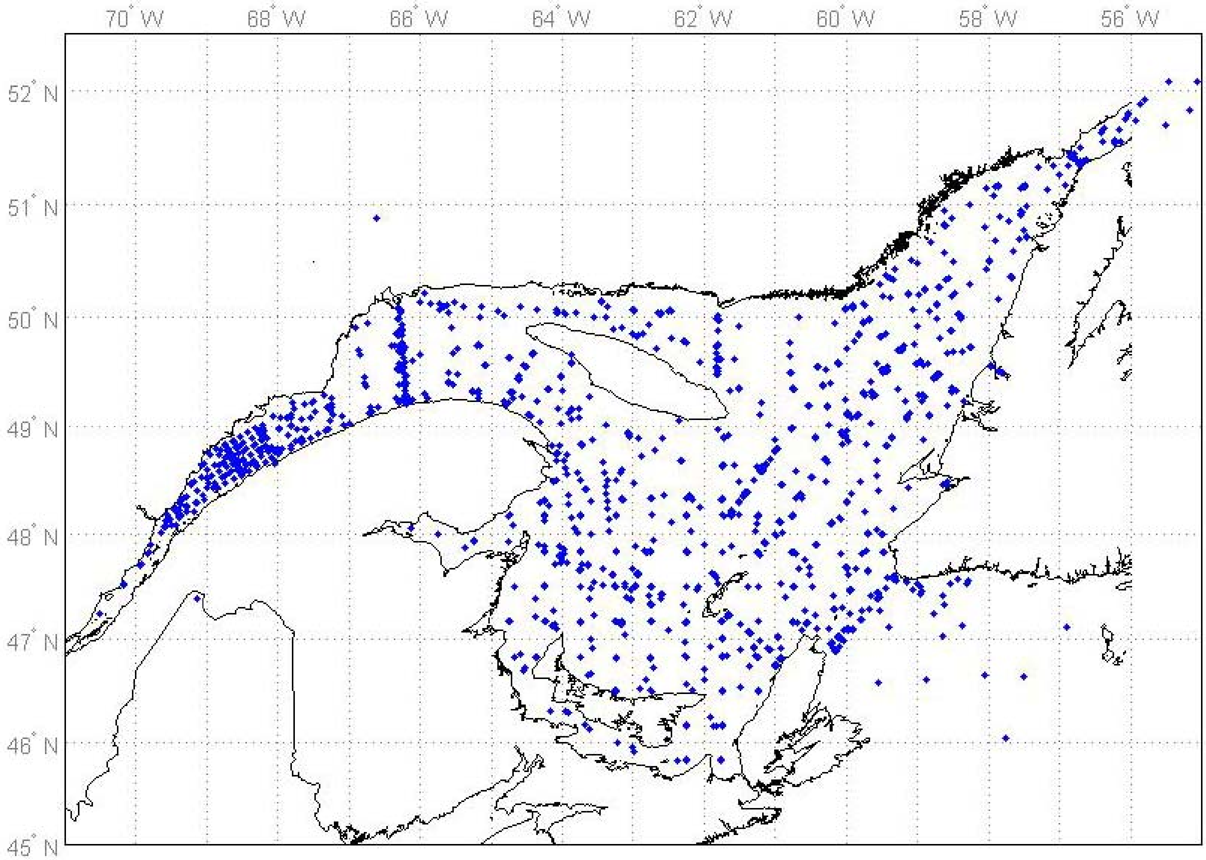

Figure 1. Position of all the sampling sites for the data described in Table 1.

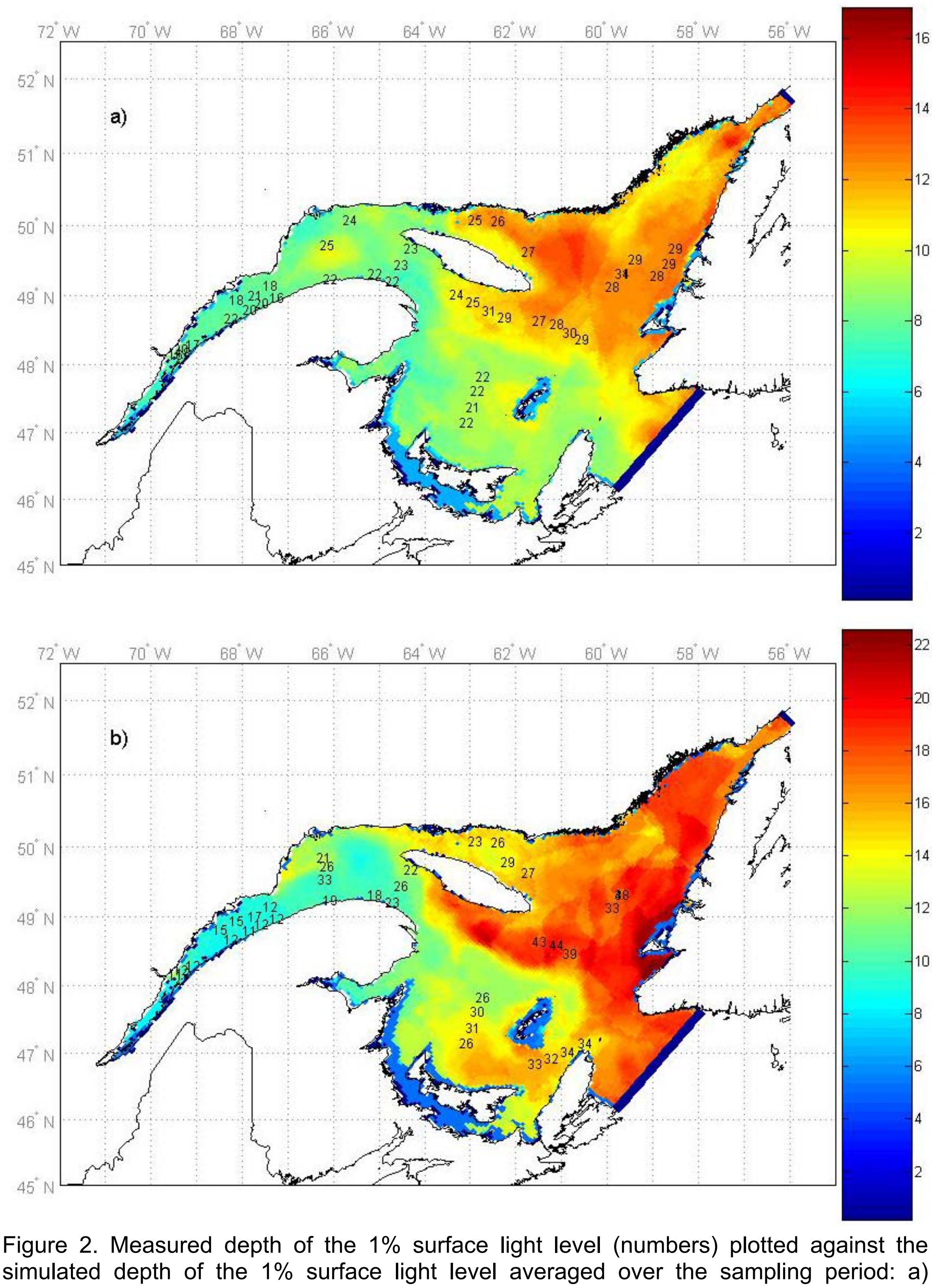

Figure 2. Measured depth of the 1% surface light level (numbers) plotted against the simulated depth of the 1% surface light level averaged over the sampling period: a) August 29 to September 10, 1997, and b) June 26 to July 6, 1999. Units are in m.

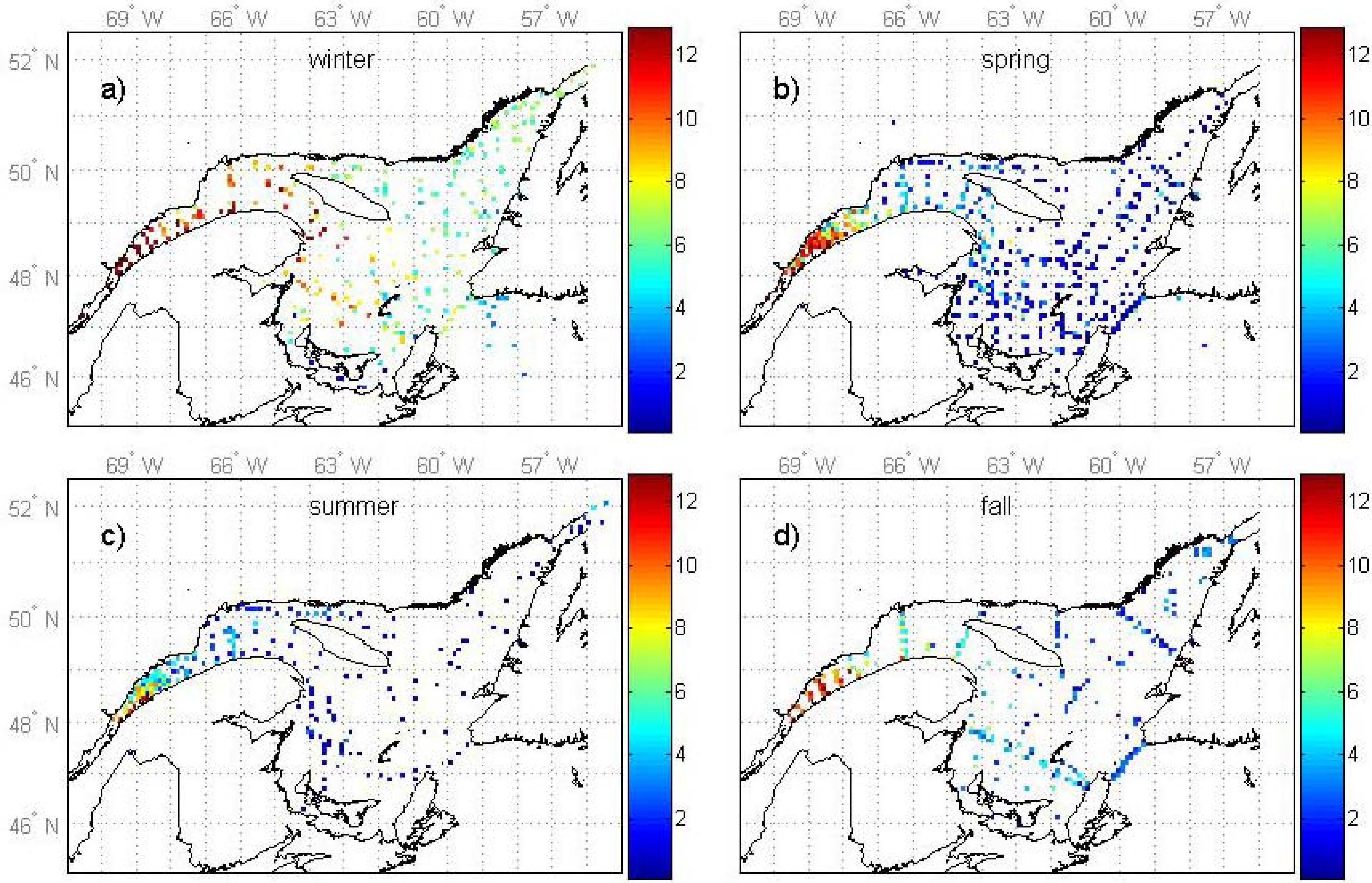

Figure 3. Measured nitrate concentrations averaged over each season and over the top 50 m of the water column within each grid cell. Units are in mmol-N m^{-3}.

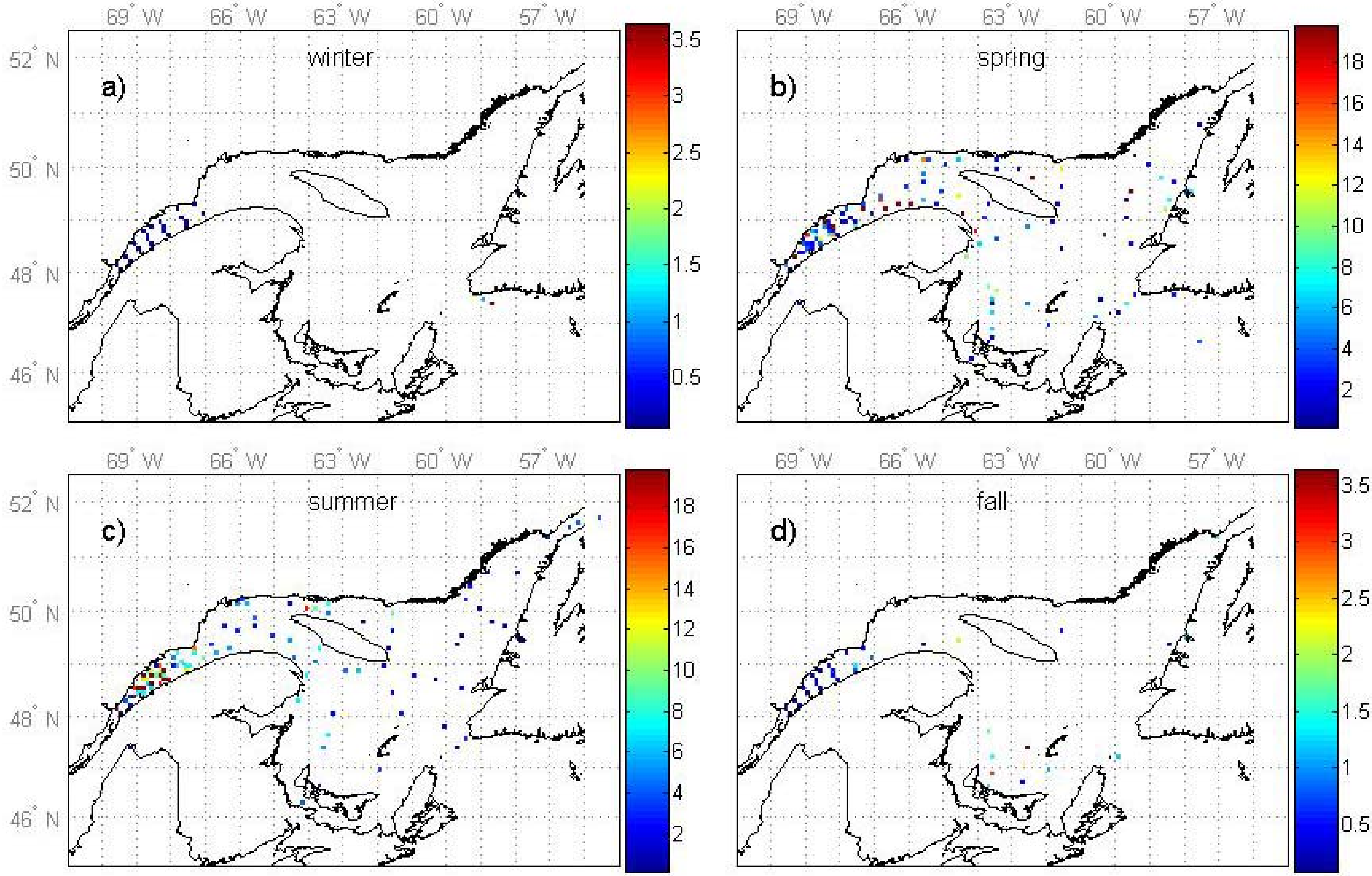

Figure 4. Measured primary production averaged over each season and over the top 50 m of the water column within each grid cell. Units are in mg-C m^{-3} h^{-1}.

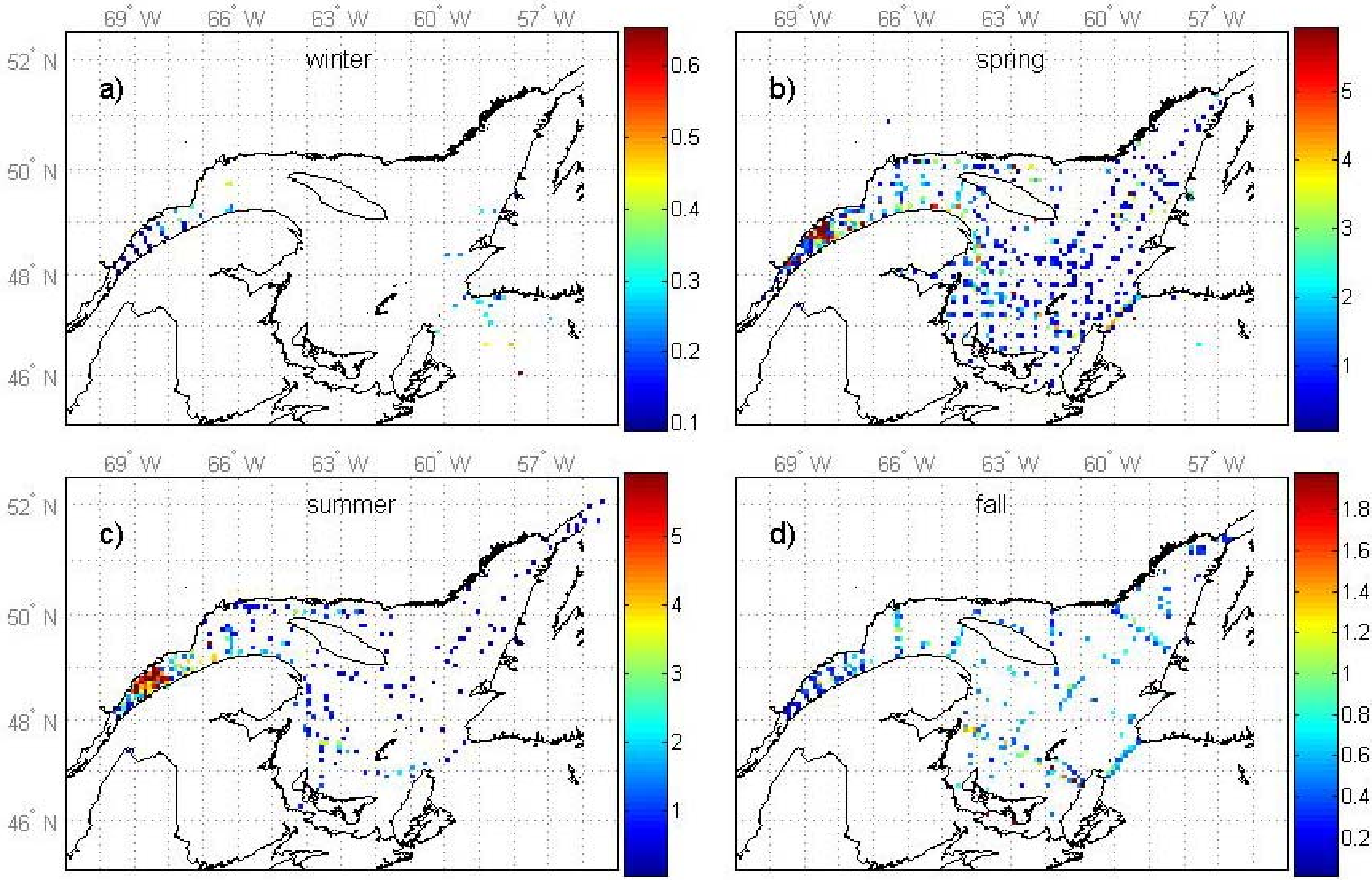

Figure 5. Measured Chl *a* concentrations averaged over each season and over the top 50 m of the water column within each grid cell. Units are in mg-Chl *a* m^{-3}.

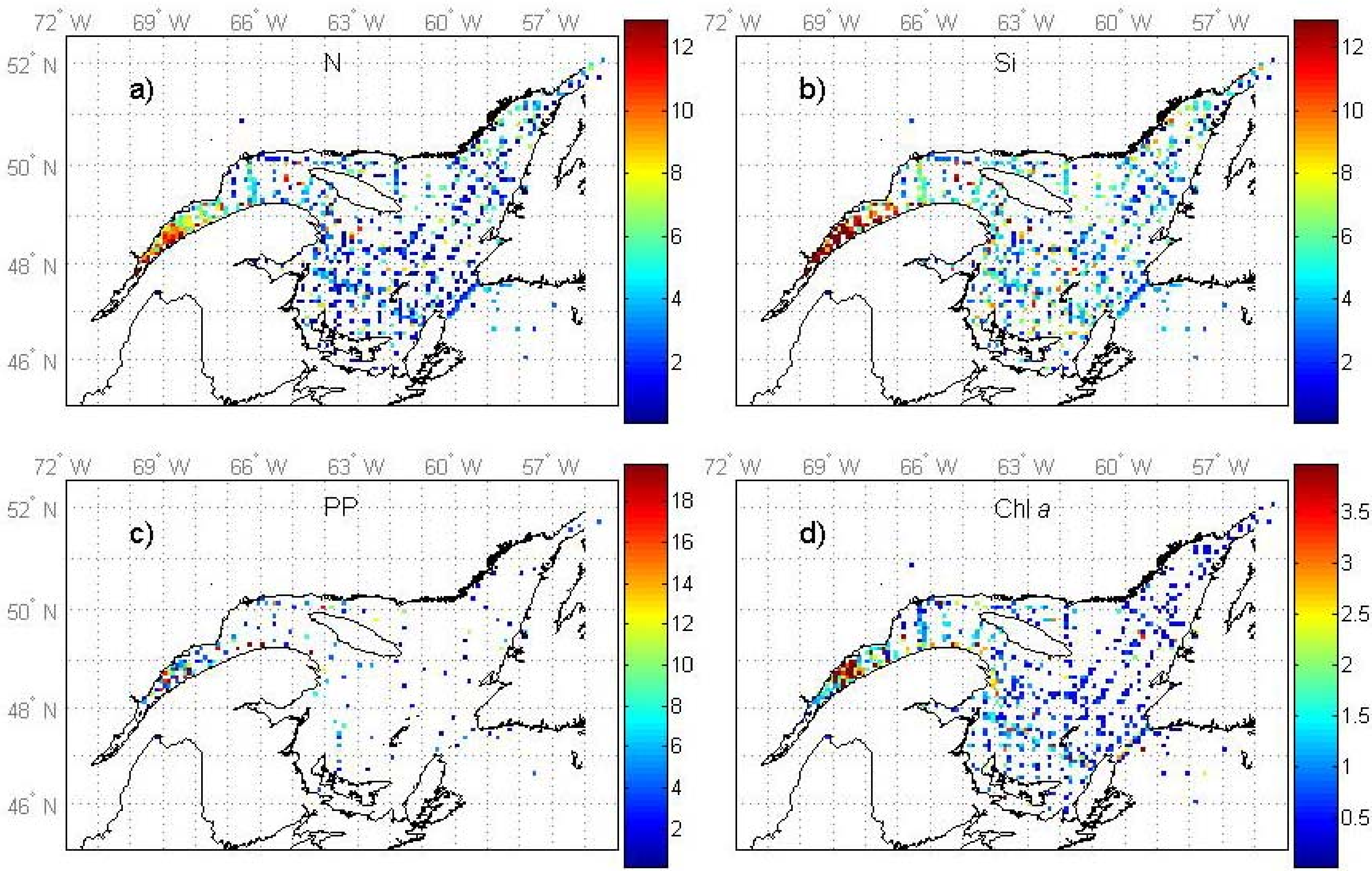

Figure 6. Measured values averaged annually and over the top 50 m of the water column within each grid cell: a) nitrate (mmol-N m^{-3}), b) silicic acid (mmol-Si m^{-3}), c) primary production (mg-C m^{-3} h^{-1}), and d) Chl *a* concentration (mg-Chl *a* m^{-3}).

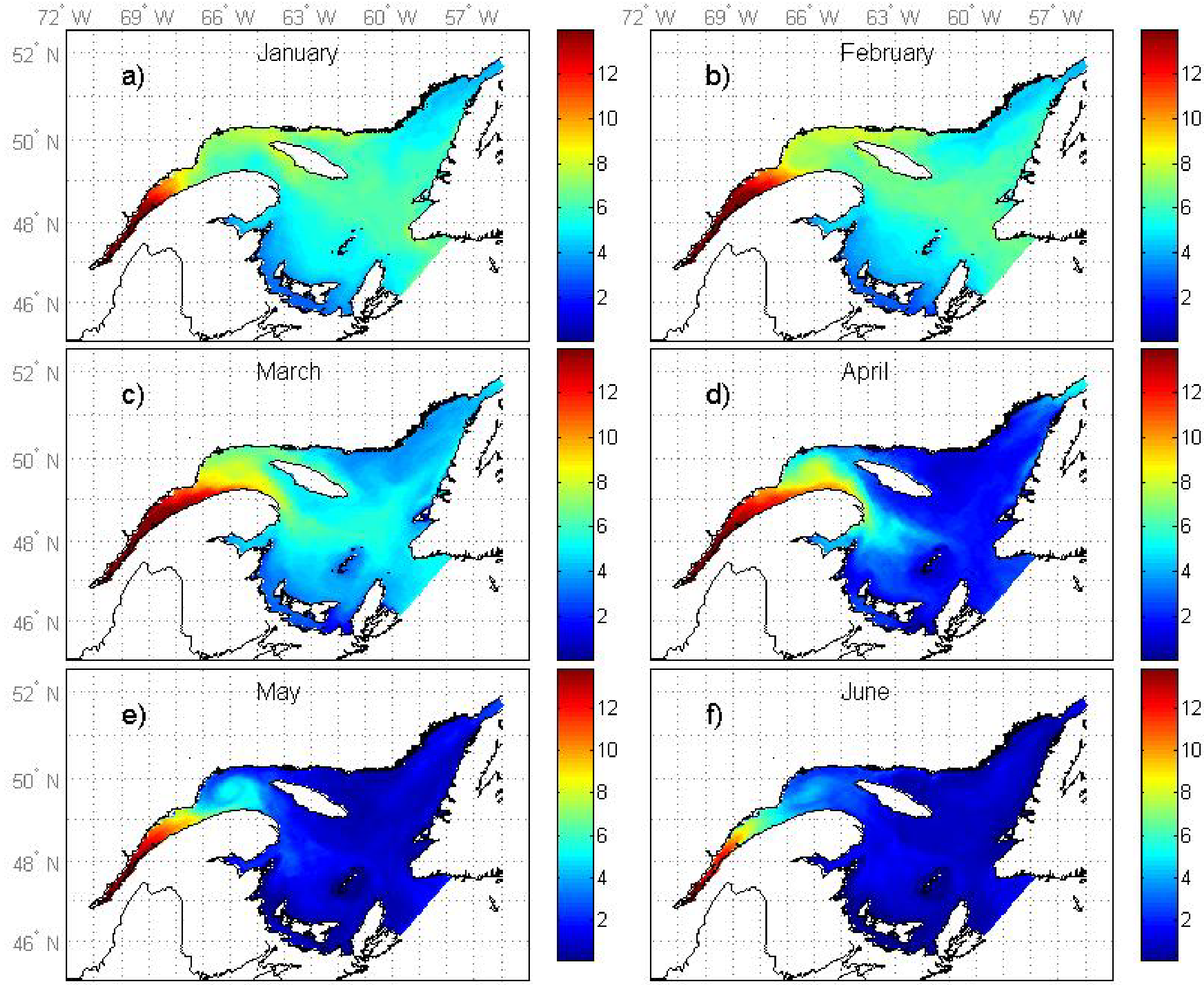

Figure 7. Monthly (January to June) averages of simulated nitrate concentrations (mmol-N m^{-3}) over the top 50 m of the water column.

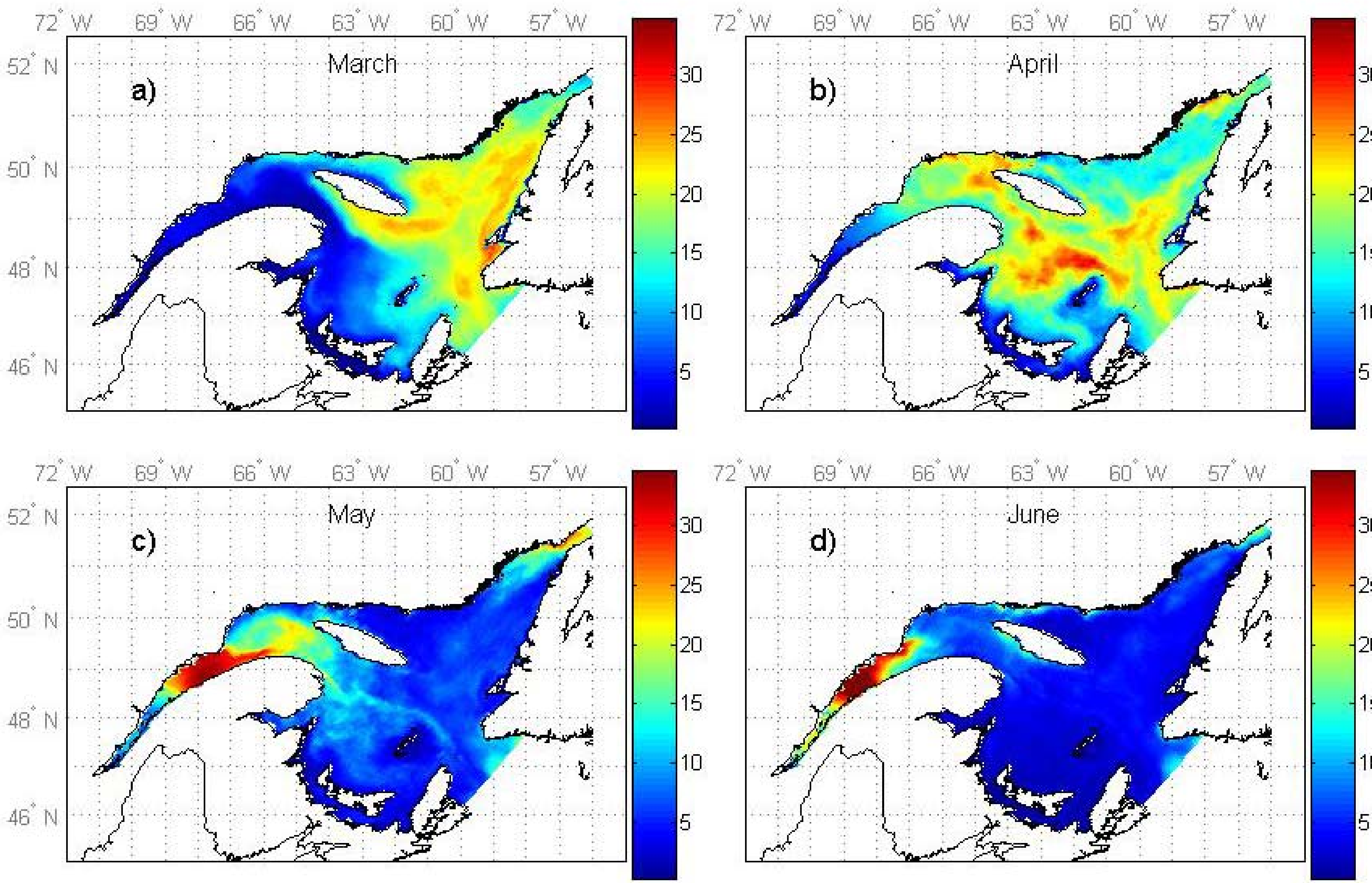

Figure 8. Simulated primary production integrated over each month (March to October) and over the top 50 m of the water column. Units are in g-C m^{-2}.

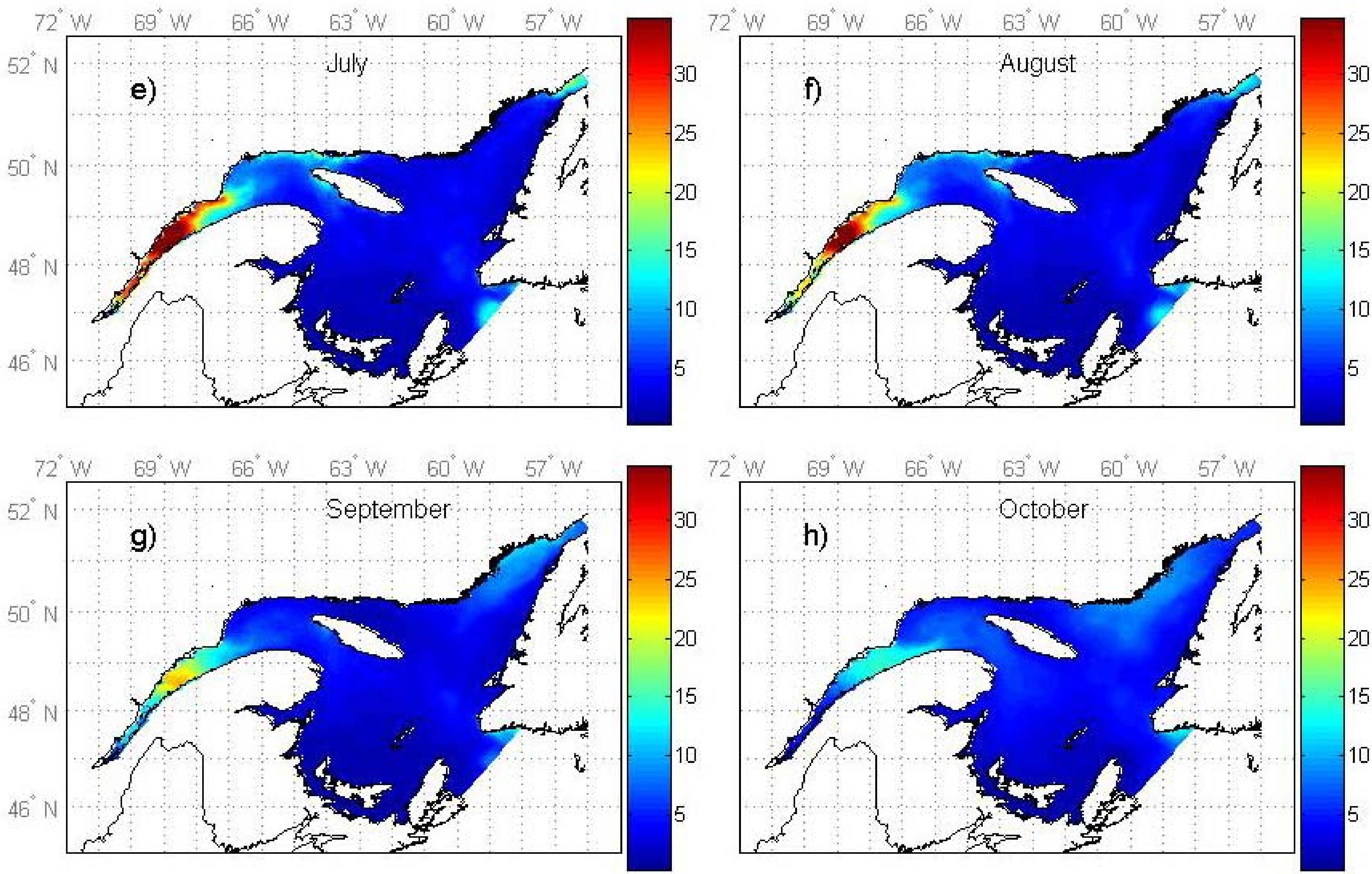

Figure 8. (continued).

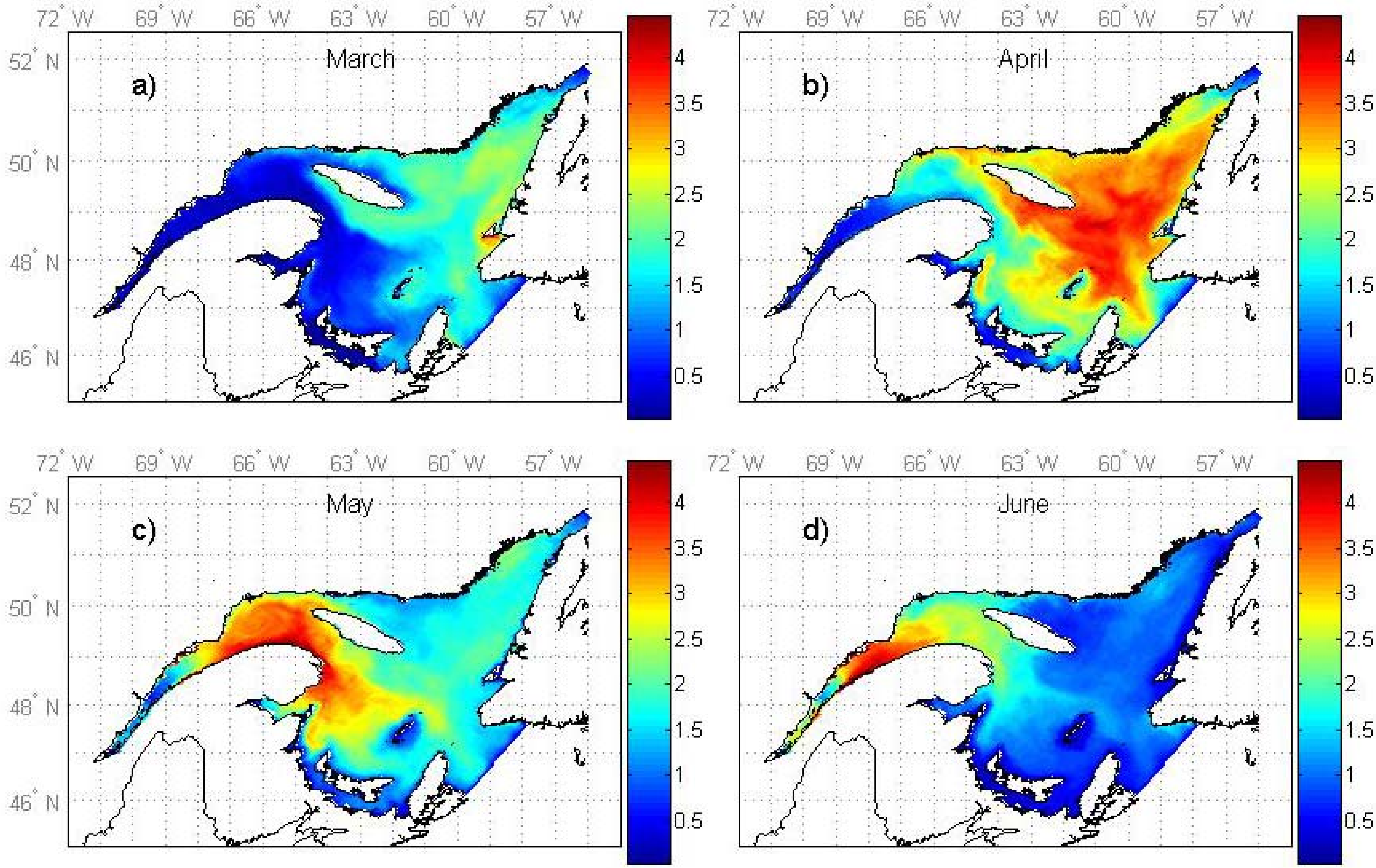

Figure 9. Monthly (March to October) averages of simulated Chl *a* concentrations (mg-Chl *a* m^{-3}) over the top 50 m of the water column.

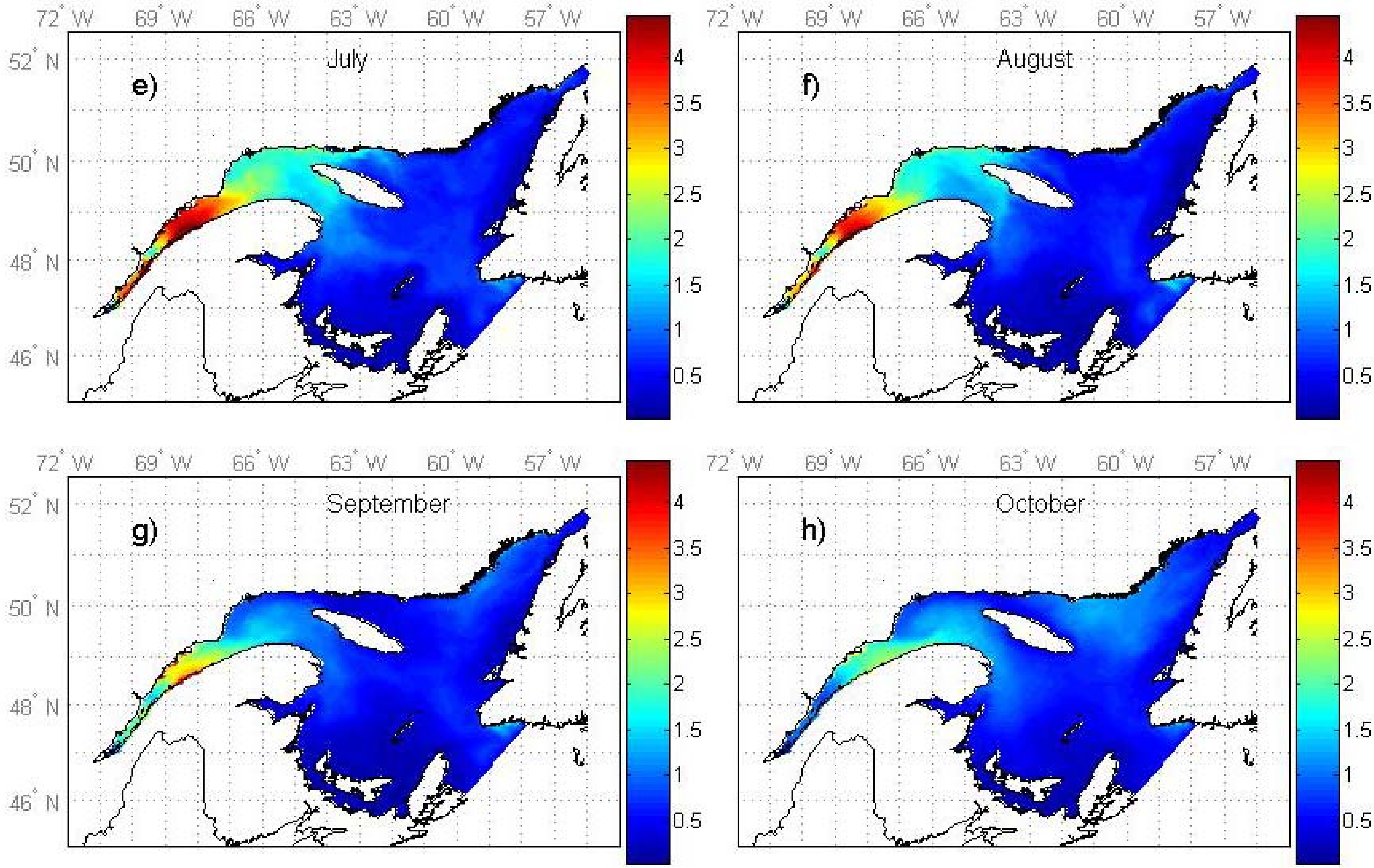

Figure 9. (continued).

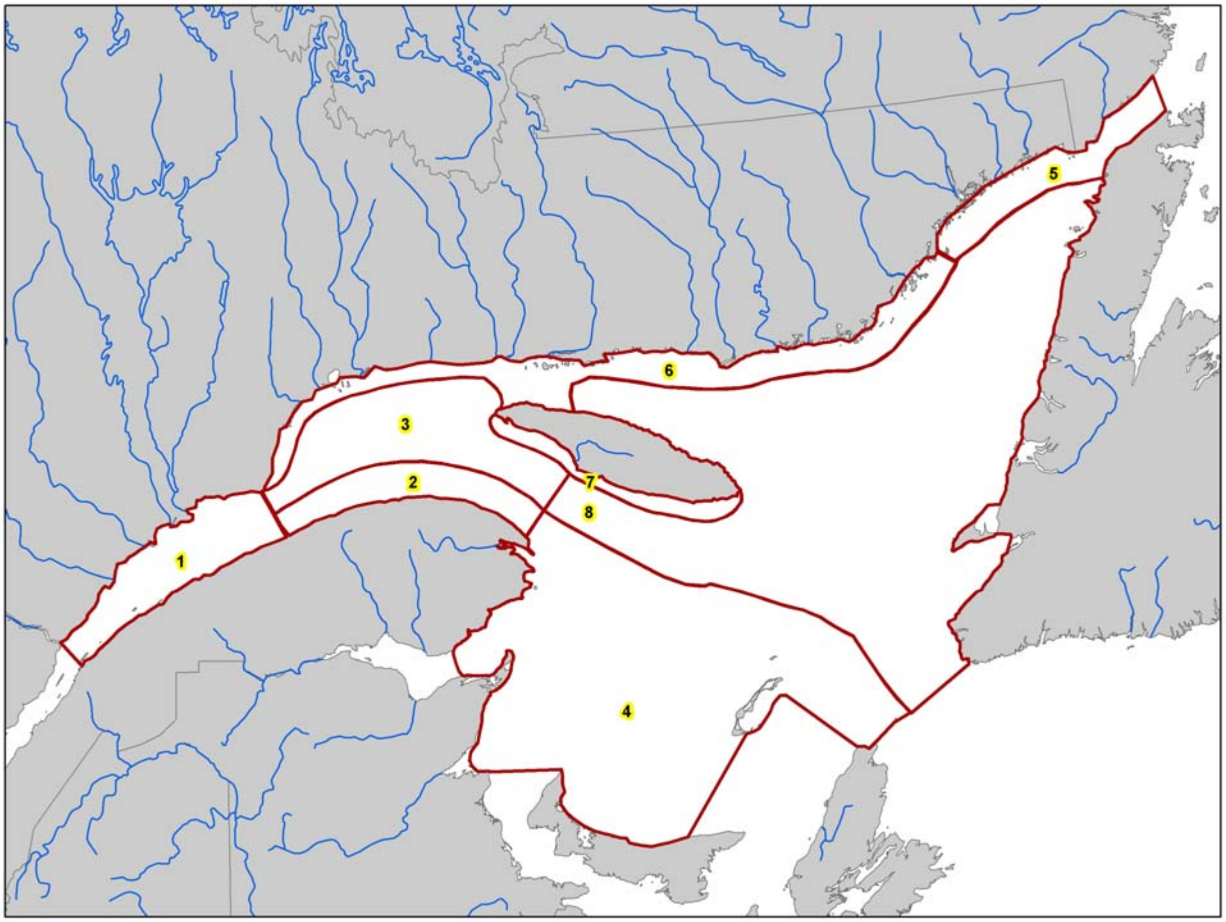

Figure 10. Potential zones of ecologically and biologically significant area (EBSA) for primary production in the Estuary and Gulf of St. Lawrence.

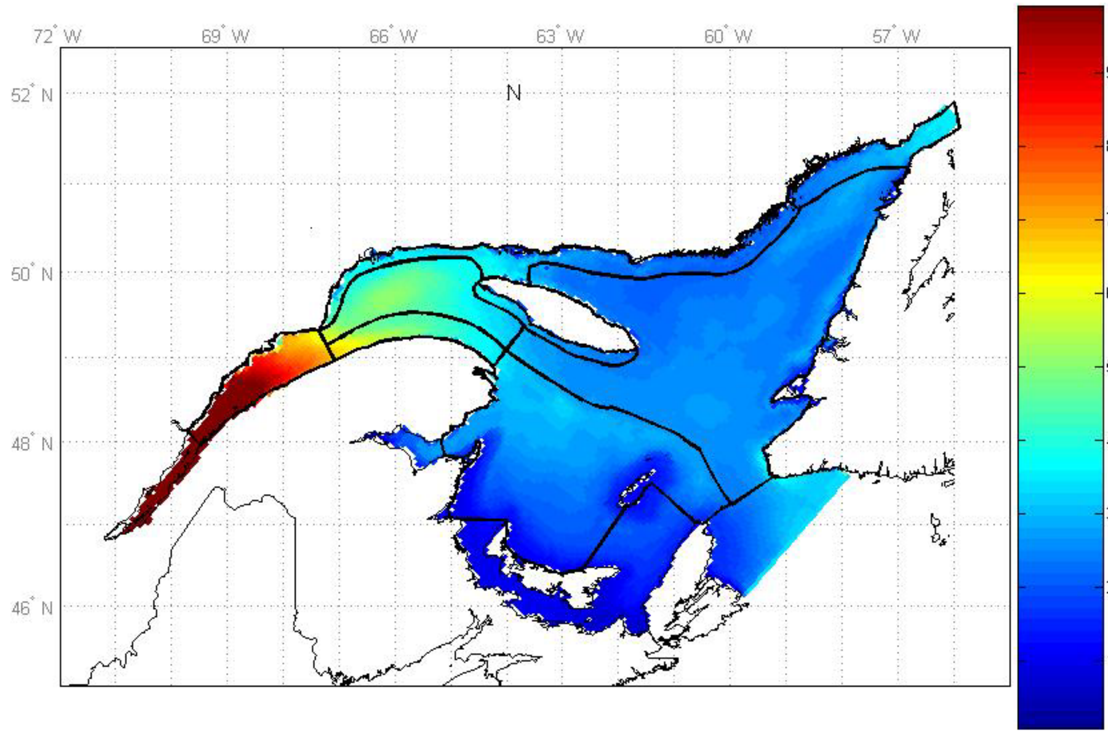

Figure 11. Annual average of simulated nitrate concentrations (mmol-N m^{-3}) over the top 50 m of the water column. The dark lines represent the contours of the zones depicted in Figure 10.

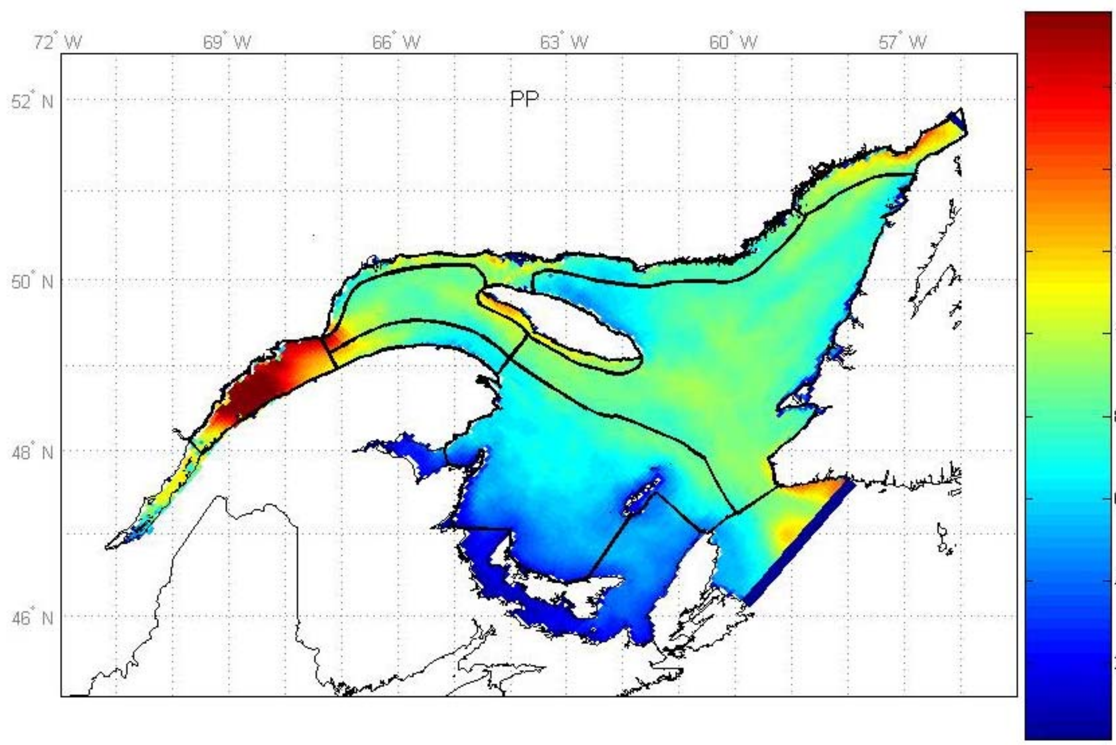

Figure 12. Total primary production (g-C m^{-2} yr^{-1}) over the top 50 m of the water column. The dark lines represent the contours of the zones depicted in Figure 10.

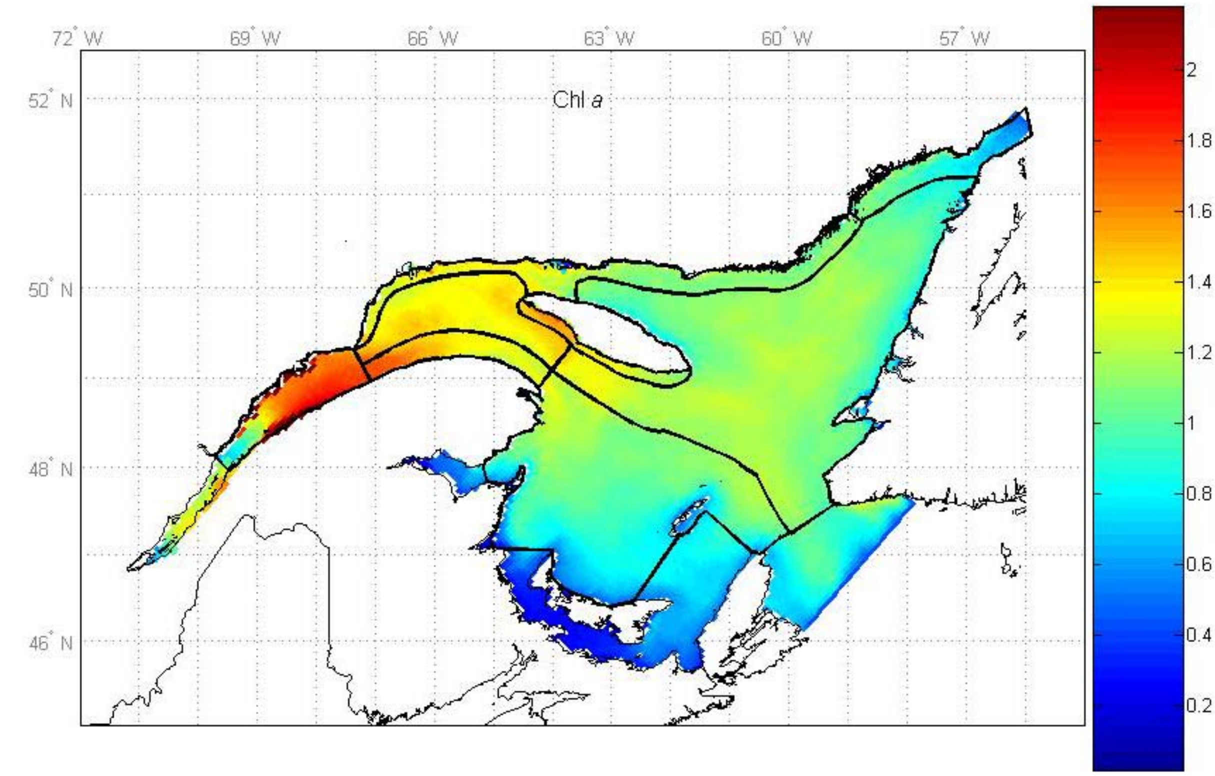

Figure 13. Annual average of simulated Chl *a* concentrations (mg-Chl *a* m^{-3}) over the top 50 m of the water column. The dark lines represent the contours of the zones depicted in Figure 10