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Importance du Réseau Trophique Microbien dans l'Océan Antarctique; Rôle du Protozooplancton

Sylvie Becquevort

Année Académique 1998-1999

Thèse présentée pour l'obtention du grade de Docteur en Sciences

Sous la direction de Christiane Lancelot

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« L'accumulation de carbone organique dissous dans les milieux aquatiques peut être expliquée par une limitation des bactéries par le phosphore ».

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Directeur de thèse : ME LANCELOT.

THESE ANNEXE:

L'accumulation de carbone organique dissous dans les milieux aquatiques peut être expliquée par une limitation des bactéries par le phosphore.

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la consultation de ma thèse de doctorat intitulée :

Importance du Réseau Trophique Pélagique dans l'Ocean ANTARTIQUE ; Rôle du Protozooplancton

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RESUME

RESUME - Les biomasses et les activités du bactérioplancton, du phytoplancton et du protozooplancton ont été étudiées lors de quatre campagnes océanographiques dans l'océan Antarctique: EPOS leg 2 dans la mer de Weddell à la fin du printemps et en été 1988, ANT X/6 dans le secteur atlantique au printemps 1992, ANTARES 2 à la fin de l'été 1994 et ANTARES 3 au début du printemps 1995 dans le secteur indien. L'ensemble des résultats obtenus a permis d'étudier la structure et le fonctionnement du réseau microbien et particulièrement le rôle du protozooplancton dans l'océan Antarctique.

Le réseau trophique microbien incluant les bactéries, le pico- et nanophytoplancton et le protozooplancton était ubiquiste, généralement caractérisé par des biomasses faibles. Des efflorescences de diatomées de grande taille étaient des phénomènes transitoires et localisés au front polaire, à la confluence des mers de Weddell et d'Ecosse et à la zone marginale de fonte de la banquise.

Au sein du réseau trophique microbien, le protozooplancton constituait une biomasse significative (16 - 30 % de la biomasse microbienne totale) principalement dominé par des espèces nanoplanctoniques. Les distributions spatio-temporelles très semblables du protozooplancton et de sa nourriture potentielle (bactéries et pico- et nanophytoplancton) suggèrent d'une manière indirecte le rôle du protozooplancton dans le contrôle des développements des bactéries et du pico- et nanophytoplancton. Des corrélations significatives entre la biomasse du protozooplancton et la biomasse de sa nourriture potentiel étaient reportées. D'autre part des mesures directes d'ingestion des bactéries et du nanophytoplancton, montraient que le protozooplancton contrôlait entre 32 et > 100 % de la production bactérienne et entre 28 et 54 % de la production phytoplanctonique.

L'analyse exhaustive des données disponibles de la littérature combinée aux simulations mathématiques générées par le modèle mécanistique SWAMCO décrivant le cycle du carbone et des éléments biogéniques associés (N, P, Si, Fe), démontraient que la dominance d'espèces phytoplanctoniques de petite taille dans les eaux antarctiques résulterait de l'avantage compétitif des espèces de petite taille dans un environnement pauvre en fer et souvent limité par la lumière. Ces petites espèces rapidement et efficacement contrôlées par le protozooplancton seraient maintenues à des niveaux faibles en biomasse. Des efflorescences d'espèces phytoplanctoniques de grande taille tel que des diatomées seraient co-gouvernées par la disponibilité de la lumière et du fer dissous. Lesquelles sont en effet observées dans les eaux côtières et continentales enrichies en fer originaire des sédiments côtiers et du continent Antarctique (mer de Ross, baie de Prydz), dans les eaux du "Polar Frontal Jet " qui mémorise un signal significatif en fer provenant des sources côtières et dans les régions influencées par la retraite de la banquise ayant accumulé des apports éoliens en fer.

D'autre part l'estimation de budgets annuels en carbone dans les différentes provinces biogéochimiques de l'océan Antarctique a montré premièrement qu'entre 52 et 65 % de la production phytoplanctonique annuel est assimilée directement ou indirectement par le réseau trophique microbien. Deuxièmement, que malgré qu'une grande partie de ce carbone incorporé soit respirée lors de son transfert vers les microprotozoaires via le réseau trophique microbien, la production secondaire du réseau trophique microbien représente approximativement 50 % de la demande en carbone annuelle du krill. Ceci suggère que le protozooplancton joue un rôle clef dans le transfert d'énergie et de matière du réseau trophique microbien vers la chaîne trophique classique.

ABSTRACT- The biomasses and activities of bacterioplankton, phytoplankton and protozooplankton have been investigated during 4 oceanographic cruises in the Antarctic Ocean: EPOS leg 2 in the Weddell Sea in spring-summer 1988, ANT X/6 in the Atlantic sector in spring 1992, ANTARES 2 in the Indian sector in late summer 1994 and ANTARES 3 in the Indian sector in early spring 1995. Altogether, the results obtained allowed to characterize the structure and the functioning of the microbial food web, and particularly the role of protozooplankton in the Antarctic Ocean.

The microbial food web including bacterioplankton, pico- and nanophytoplankton and protozooplankton was ubiquist and generally characterized by low biomasses. Blooms of large phytoplankton such as diatoms was sporadic and located in the Polar Frontal region, in the Weddell-Scotia Confluence and in the marginal Ice zone in the Weddell Sea in early spring.

In the microbial food web, the protozooplankton dominated by nanosized species constituted a significant biomass (16- 30 %) in the total microbial biomass. The very similar spatio-temporal distribution of the protozooplankton and its potential food (bacteria and pico- and nanophytoplankton) indirectly suggested the protozooplankton role as control factor of bacterioplankton and pico- and nanophytoplankton developments. A significant correlation between the protozooplankton and the potential food biomasses was reported. Direct measurements of the protozoan ingestion rates directly demonstrated that the protozooplankton controlled between 32 and > 100 % of the daily bacterial production and between 28 and 54 % of the daily primary production.

The comprehensive analysis of existing data on phytoplankton, bacterioplankton and protozooplankton biomass and activity combined with the SWAMCO biogeochemical model scenarios performed under contrasting meteorological, chemical and biological conditions conclude that the HNLC (High Nutrient-Low Chlorophyll) prevailing in the Antarctic Ocean are resulting from the successful development of protozooplankton-controlled pico- and nanophytoplankton communities in an iron and light-limited environment. Episodic diatoms blooms are well developing in iron-rich areas provided light conditions are reached and maintained. Such areas are the near-shore neritic areas supplied with iron from shelf sediments and the Antarctic continent (Ross Sea, Prydz Bay), the rapidly eastward flowing Polar Frontal Jet which retains a significant iron signal from shelf sources and to a lesser extent some sea-ice covered areas having accumulated minor aerosol inputs.

On the other hand, annual carbon budget estimations in the different biogeochemical provinces in the Antarctic ocean reported first that between 52 and 65 % of the annual primary production was channeled directly or indirectly through the microbial food web. Secondly, despite a large part of incorporated carbon is respired, the microbial food web via the protozooplankton constituted around 50 % of the annual krill carbon demand. This suggest that protozoa can play a key role in the transfer of energy and material to large metazooplankton and krill in the Antarctic Ocean.

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Chapitre 1

Introduction Générale

1. Objectifs généraux

L'océan Mondial couvre approximativement 70 % de la surface du globe terrestre. De ces 70 %, 10 % sont couverts par l'océan Antarctique. L'intérêt pour l'Océan Mondial s'est tout d'abord porté sur l'exploitation de ses ressources biologiques sans souci de préservation des écosystèmes marins. C'est ainsi que les ressources biologiques de l'océan Antarctique ont été intensément surexploitées. Premièrement, les phoques furent chassés principalement pour leur huile et en l'espace de 50 ans leurs populations ont diminué de manière drastique et disparu quasiment des sites accessibles facilement par l'homme. Au 19èmes siècle, le développement rapide de l'industrialisation de la pêche à la baleine fut un désastre pour les effectifs des grands cétacés. Plus récemment, le krill, crustacé servant de nourriture aux mammifères marins, a été intensément pêché par les bateaux russes et japonais à des fins agro-alimentaires. Craignant que la pêche industrielle ne déséquilibre le milieu marin, différents programmes aussi bien nationaux qu'internationaux (BIOMASS, GLOBEC) ont été entrepris dans les années 80 afin de quantifier les ressources biologiques de l'océan Antarctique et de déterminer les facteurs physiques, chimiques et biologiques qui les contrôlent.

D'autre part ces dernières années, se sont développés de nombreux programmes nationaux et internationaux (JGOFS) dont la problématique est d'étudier le rôle des océans dans le cycle globale du carbone et leurs influences sur la régulation du climat. En effet depuis le début de l'ère industrielle, la teneur en dioxyde de carbone (CO_2) dans l'atmosphère augmente de manière exponentielle. En moyenne la combustion des carburants fossiles et de la biomasse issue de la déforestation rejette 7, 1 GT de carbone par an depuis ces 10 dernières années (IPPC, 1996) sous forme de gaz carbonique. A long terme, cette augmentation de CO_2 d'origine anthropogène pourrait conduire à un réchauffement global de l'atmosphère engendrant de profondes modifications climatiques. Les océans peuvent agir comme un énorme tampon absorbant les excès de CO_2 d'origine anthropogène produits lors de ces dernières décades (Mitchell 1989). Si l'Océan Mondial contient 50 fois plus de carbone inorganique qu'il n'y a de CO_2 dans l'atmosphère, les réservoirs en carbone que constituent l'atmosphère et l'océan sont en relation étroite via les échanges à l'interface mer-atmosphère. Des changements dans le cycle biogéochimique des océans ainsi que des modifications dans la circulation océanique globale affectant respectivement la quantité de carbone inorganique contenu dans l'eau et le temps de résidence du CO_2 dans l'océan, pourraient ainsi affecter la quantité de CO_2 atmosphérique. De manière similaire, les processus continentaux qui produisent du CO_2 dans l'atmosphère affecte le contenu en carbone inorganique des océans. Lors des dix dernières années, l'océan mondial a

pompé de 33 % du CO_2 résultant de la déforestation et la combustion de carburants fossiles (Siegenthaler et Sarmiento 1993). La capacité des océans à absorber du CO_2 atmosphérique dépend de la combinaison de processus physiques, chimiques et biologiques interagissant entre eux.

L'océan Antarctique non seulement par son volume mais aussi par ses caractéristique hydrographiques et biologiques pourrait donc jouer un rôle significatif dans la régulation du climat. Son rôle de source ou de puits vis à vis du CO2 atmosphérique fait aujourd'hui encore l'objet de débats animés. C'est ainsi que des mesures in situ de delta-pCO_2 suggère que l'océan Antarctique est un puits net de CO_2 atmosphérique (Takahashi *et al.* 1993). Par contre les modèles mathématiques couplé océan/atmosphère (par exemple Tans *et al.* 1990) supporte l'idée que l'océan Antarctique est neutre par rapport à l'assimilation et l'émission de CO_2. Ces contradictions s'expliquent par la complexité des mécanismes physico-chimiques et biologiques en jeu et par le fait que l'océan Antarctique n'est pas une entité homogène. Sa capacité d'adsorption du CO_2 atmosphérique pourrait donc varier selon la saison et géographiquement.

2. Rôle de la production primaire dans le contrôle des ressources biologiques et de l'exportation de carbone

Via la photosynthèse, le phytoplancton converti la lumière en énergie chimique. Cette énergie chimique est utilisée pour fixer du carbone inorganique et le transformer en carbone organique (Fig. 1). Une partie du carbone organique formé lors du processus de photosynthèse transite par le réseau trophique pélagique et suivant son efficience trophique produit des ressources biologiques éventuellement exploitables par l'homme. Une autre partie de ce carbone organique formé quitte la couche d'eau de surface et est exporté vers l'océan profond sous forme de carbone organique particulaire et dissous. Ce transfert de CO_2 de l'atmosphère via l'assimilation phytoplanctonique vers le fond de l'océan est appelé la pompe biologique. Une grande partie de ce carbone organique est cependant dégradée et respirée lors de son transfert vers le fond de l'océan ainsi qu'au niveau des sédiments. En moyenne 10 % seulement de ce flux organique particulaire atteint les sédiments superficiels et moins de 1 % est enfoui dans les sédiments profonds pour y subir le processus de diagénèse. L'océan agit donc comme un puits temporaire en CO_2, une majeur partie retourne vers l'atmosphère à des échelles de temps plus ou moins longues via des processus biogéochimiques et la circulation océanique globale.

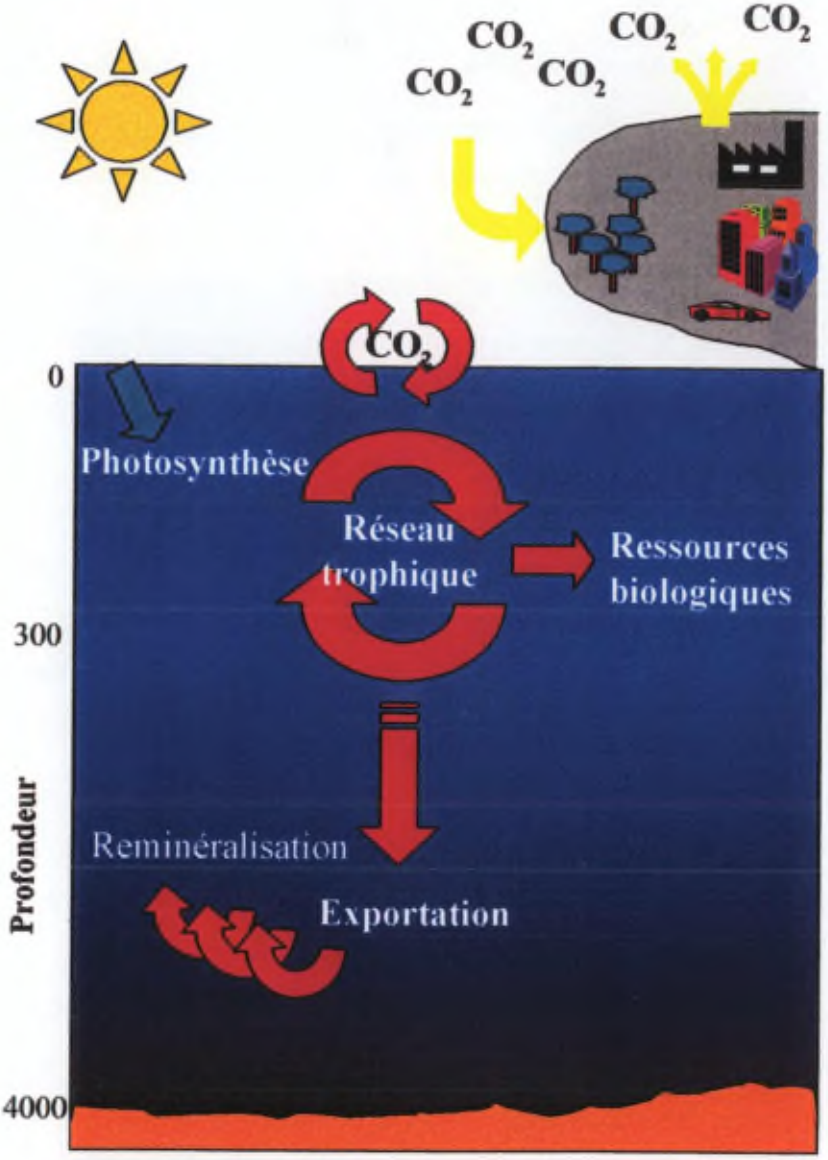

Figure 1. *Rôle de la production primaire dans le contrôle des ressources biologiques et de l'exportation de carbone.*

3. Rôle de la structure du réseau trophique pélagique dans le contrôle des ressources biologiques marines et de l'efficacité de la pompe biologique.

La quantité de ressources biologiques marines disponibles ainsi que l'efficience de la pompe biologique sont liés non seulement à la quantité de production primaire mais aux groupes phytoplanctoniques prédominants dans l'écosystème pélagique. Ces derniers étant caractérisés par des taux différents de sédimentation, de broutage par le zooplancton et de biodégradabilité, ont un effet déterminant sur la structure du réseau trophique pélagique.

La communauté phytoplanctonique peut être classée en deux grands groupes majeurs: le microphytoplancton (principalement des diatomées) et le pico- et nanophytoplancton (principalement des flagellés).

Les deux grands groupes de phytoplancton ne sont pas distribués de manière homogène dans les océans. Leurs productions varient suivant la localité mais aussi la saison et sont contrôlées à la source par la disponibilité en lumière et en nutriments inorganiques (Thingstad et Sakshaug 1990, Riegman *et al.* 1993), les espèces de petite taille étant plus compétitives que les espèces de grande taille à faible lumière et/ou faible concentration en nutriments.

En effet, le taux de photosynthèse spécifique diminue avec une augmentation de la taille de la cellule (Morel et Bricaud 1981, Geider *et al.* 1986). Ceci s'explique par la dépendance du coefficient d'absorption quantique spécifique à l'aire de la surface cellulaire. Les cellules de petite taille sont dès lors favorisées en raison de leur rapport surface/volume plus élevé.

A de faibles concentrations en nutriments, le taux de diffusion des molécules vers la surface cellulaire peut limiter l'apport de nutriments à la cellule (Morel *et al.* 1991). Si le taux d'assimilation potentielle excède le taux de diffusion, une région limitée en nutriments peut exister autour de la cellule et dès lors le taux d'assimilation devient limité non pas par le nombre de site d'assimilation mais par la diffusion des nutriments vers la surface cellulaire. Dans ce cas-là, les cellules de petite taille sont avantagées dans des écosystèmes oligotrophes.
D'autres facteurs tel que la mobilité, la sédimentation des cellules ainsi que la turbulence du milieu sont des facteurs pouvant bien sur influencer la disponibilité en lumière et en nutriments pour les cellules phytoplanctoniques (Kiorboe 1993).

Donc dans un écosystème limité par la disponibilité en lumière et en nutriments, seulement les petites cellules phytoplanctoniques seront responsables de la production primaire car elles sont des meilleurs compétiteurs pour la lumière et les nutriments (Fig. 2). Dans un tel écosystème, le taux de sédimentation du matériel organique est faible du à la petite taille des particules (Smayda 1970). Egalement du à la taille (pico et nanoplancton) de ces particules, ils sont consommés principalement par le protozooplancton (Sherr *et al.* 1986). Ceux-ci ayant des temps de génération similaire à ceux de leurs particules alimentaires, sont capables de répondre rapidement à un développement de pico- et nanophytoplancton et d'empêcher ainsi l'accumulation de biomasse au sein du réseau microbien (Sherr et Sherr 1988). Au sein du réseau microbien, la plupart du carbone assimilé via la photosynthèse est rapidement recyclé par la respiration et est retenu dans les eaux de surface. De plus, le protozooplancton ainsi que les

bactéries régénèrent rapidement des nutriments inorganiques tel que l'ammonium et le phosphate dans les eaux de surface (Williams 1981, Azam *et al.* 1983, Sherr et Sherr 1984, Capriulo 1990) qui sont utilisés préférentiellement par le pico- et le nanophytoplancton. On parle dans ce cas- là de production régénérée (Eppley et Peterson 1979) en référence à la régénération constante d'ammonium dans les eaux de surface et son utilisation préférentielle par rapport au nitrate par le pico- et nanophytoplancton. On utilise également le terme de chaîne de rétention par le fait qu'elle retient la matière biogénique en suspension dans les eaux de surface.

Par contre dans des écosystèmes non limités par les nutriments et la lumière, le microphytoplancton tel que des diatomées forme des efflorescences importantes. Les diatomées de grande taille sont associées à de la production nouvelle basée sur un nouvel apport de nitrate dans la couche photique d'une origine naturelle (remontée d'eau profonde) ou anthropogène (zones côtière enrichies par les apports des rivières).

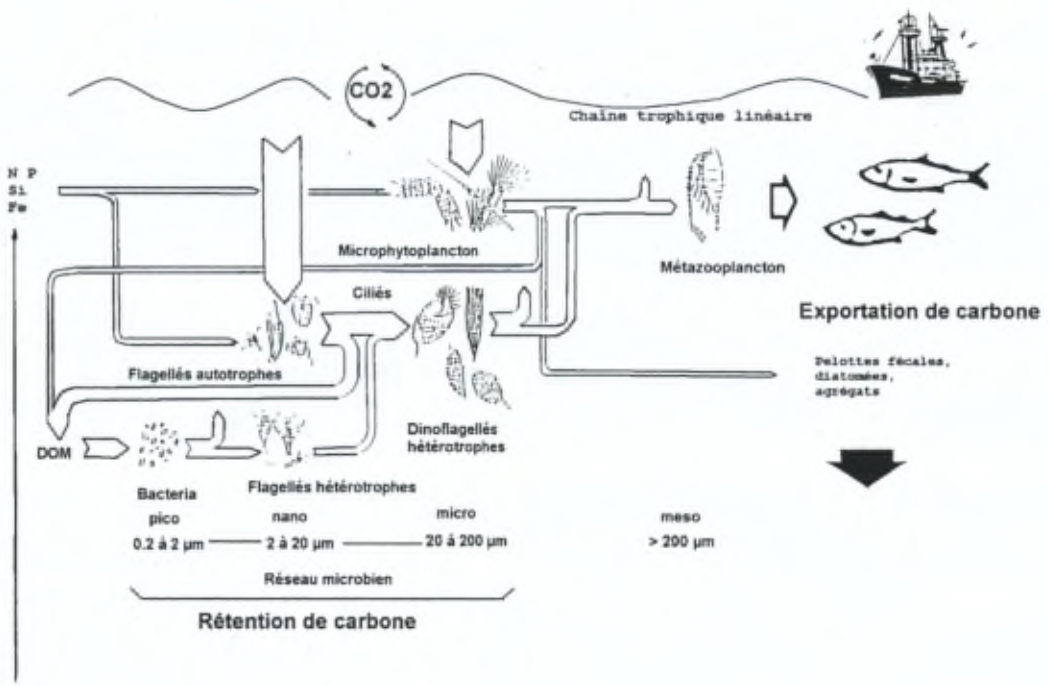

Figure 2. *Rôle de la structure du réseau trophique pélagique (chaîne trophique linéaire versus réseau trophique microbien) dans le contrôle des ressources biologiques marines et de l'efficacité de la pompe biologique (exportation de carbone versus rétention de carbone).*

Les diatomées d'une part initient la chaîne trophique linéaire caractérisée par une efficience trophique très importante (Odum 1959) et d'autre part sont largement exportés vers les fonds de l'océan (chaîne d'exportation, Peinert *et al.* 1989). Cette exportation est soit directe par sédimentation du phytoplancton ou des agrégats formés à partir du phytoplancton, soit indirecte par l'intermédiaire du broutage de ces algues par le métazooplancton qui produit des pelotes fécales pouvant avoir des taux de sédimentation élevés. La proportion relative du carbone qui est exporté directement sans être incorporé dans le réseau trophique dépend essentiellement de la présence ou non de mesozooplankton au moment de l'efflorescence phytoplanctonique capable de consommer cette production (Kiorboe 1993).

En conclusion, le réseau trophique pélagique est toujours composé du réseau trophique microbien caractérisé par des biomasses faibles et relativement constantes sur lequel se surimpose des efflorescences de microphytoplancton quand les disponibilités en nutriments et/ou en lumière ne sont pas limitantes.

4. Réseau trophique pélagique dans l'océan Antarctique

L'océan Antarctique apparaît comme un système paradoxal: dans la plupart des écosystèmes marins, les nutriments inorganiques sont épuisés par l'assimilation phytoplanctonique durant la période de croissance. Cependant quelques vastes régions océaniques (océan Pacifique équatoriale, océan Pacifique Sub-Arctique et L'océan Antarctique) où les nitrates, phosphates et silicates restent à des concentrations importantes tout au long de l'année sont caractérisées par des biomasses phytoplanctoniques (dominées par du pico- et du nanophytoplancton) et des productions primaires faibles par rapport à la disponibilité des nutriments. Ces régions sont appelées régions "HNLC" (High Nutrients, Low Chlorophyll) dans le jargon des océanographes. Parmi ces régions, l'océan Antarctique est caractérisé par des concentrations élevées en nutriments majeurs (nitrate: 32.5 $mM.m^{-3}$; phosphate: 2.5 $mM.m^{-3}$; silicate: 100 $mM.m^{-3}$) dans ses eaux de surface (Bainbridge, 1980). Cependant, en dépit des hautes concentrations en nutriments, la production primaire dans les eaux antarctiques est généralement faible (voir la revue Mathot *et al.* 1992, Mathot 1993) et dominée par des espèces pico- et nanophytoplanctoniques (Smetacek *et al.* 1990). La production primaire net annuelle dans l'océan Antarctique (Smith *et al.* 1988; Lancelot *et al.* 1993b, Mathot *et al.* soumis) a été approximativement estimée à 120 tera moles-C (1.4 - 1.85 gigatonnes de carbone) c'est à dire pas plus de 3 à 9 % de la production mondiale marine (entre 20 et 40 Gt-C selon Longhurst 1991).

D'autre part à cette faible production primaire annuelle, caractéristique d'un système oligotrophe, l'océan Antarctique associe un niveau de production secondaire élevé dont témoigne l'abondance du krill (euphausiacae) et d'importants dépôts sédimentaires biogéniques dans les fonds océaniques, principalement de la silice (Tréguer *et al.* 1995).

Des productions élevées de microphytoplancton très localisés dans l'espace et dans le temps sont cependant observées (i) dans la zone du front polaire entre les latitudes 45° et 50° sud (Bathmann *et al.* 1994) (ii) dans les eaux côtières peu profondes (Hom-Hansen et Mitchell 1991) et (iii) à proximité de la retraite de la glace de mer (Smith et Nelson 1985; Lancelot *et al.* 1993b). Mais là encore la biomasse phytoplanctonique n'atteint pas 25 mg Chla.m^{-3}, ce qui pourrait être attendu d'après les quantités disponibles en nutriments (Mitchell et Holm-Hansen 1991).

Selon les connaissances actuelles, la production phytoplanctonique des eaux antarctiques serait contrôlée par différents facteurs tel que (i) la disponibilité en lumière résultant de l'importance de la radiation solaire, de l'étendue de la couverture de glace de mer et de la profondeur de la couche de mélange (par exemple Veth *et al.* 1992), (ii) la disponibilité en fer (de Baar *et al.* 1995, de Baar et Boyd 1998, Lancelot *et al.* 1997) et par (iii) le broutage par le zooplancton (Smetacek *et al.* 1990).

Le cycle annuel du rayonnement solaire incident contrôle bien évidemment la croissance phytoplanctonique en Antarctique (Smith et Sakshaug 1990) . En hiver et à la fin de l'automne, le rayonnement incident est très faible voir inexistant et limite la productivité. De plus durant l'hiver, l'étendue de la glace de mer augmente. Dépendant de la couverture de neige, la glace peut reémettre 1 - 99.9 % du rayonnement atteignant la surface de l'eau. Durant le reste de l'année, même si le rayonnement solaire est du même ordre de grandeur que celle mesurée sous les tropiques (Holm-Hansen *et al.* 1977, Campbell et Aarup 1989) le rayonnement atteignant la surface de l'eau est affecté par la couverture nuageuse (Bishop et Rossow 1991). D'autre part, due aux vents importants, la couche supérieur de la colonne d'eau est souvent profonde (plus de 100 m) et excède la profondeur critique comme définie par Sverdrup (1953). Il est maintenant admis que les zones libres de glace avec des couches de mélange profondes de la colonne d'eau ne sont pas hautement productives et sont dominées par des communautés nanoplanctoniques (El-Sayed 1984, Smetacek *et al.* 1990). D'autre part, beaucoup d'observations (Smith et Nelson 1985, Sakshaug et Holm-Hansen 1984, Nelson *et al.* 1987, Sullivan *et al.* 1988, Lancelot *et al.* 1991) indiquent que la zone marginale de fonte de glace est une région de haute production phytoplanctonique due à la formation au moment de la fonte de glace d'une couche de mélange stable peu profonde et de l'ensemencement de la colonne d'eau par des organismes séquestrés

dans la glace (Garrison *et al.* 1987, Mathot *et al.* 1991). Cependant la biomasse phytoplanctonique dominée soit par du nanophytoplancton (Hewes *et al.* 1990, Lancelot *et al.* 1993b) soit par des diatomées (Bianchi *et al.* 1992) atteinte dans ces zones reste modeste (< 10 mg Chl a m^{-3}) et significativement inférieure à ce que l'on pourrait s'attendre du stocks de nutriments disponibles (Hayes *et al.* 1984) .

Les teneurs élevées en nutriments majeurs des eaux Antarctiques excluent à priori toute limitation de la production primaire par ceux-ci. Par contre les très faibles teneurs en nutriments mineurs tel que le fer seraient susceptibles d'être un facteur limitant pour le développement phytoplanctonique. La limitation en éléments en trace sur la croissance phytoplanctonique, en particulier en fer, a été étudiée depuis 1988 dans plusieurs régions de l'océan Antarctique: Les mers de Weddell et d'Ecosse (de Baar *et al.* 1990), le passage de Drake (Hebling *et al.* 1991, Martin *et al.* 1990), la mer de Ross (Martin *et al.* 1990) et les secteurs atlantiques et pacifiques du courant circumpolaire antarctique (de Baar *et al.* 1995). Ces résultats indiquent que la faible disponibilité en fer pourrait bien limiter la croissance phytoplanctonique et ainsi justifier la dominance de espèces phytoplanctoniques de petite taille dans les eaux antarctiques. En effet de faibles concentrations en fer limite la croissance des diatomées de grande taille mais n'affecte pas la croissance d'algues pico- et nanoplanctoniques, plus compétitives à de faible concentration en nutriments (Morel *et al.* 1991). D'autre part la demande cellulaire apparaît plus faible pour les petites espèces. En effet, le nanoplancton est observé comme étant le consommateur majeur d'ammonium pendant que les plus grandes espèces phytoplanctoniques utilise le nitrate comme source d'azote. L'assimilation de nitrate est cependant de loin plus "coûteuse" en fer, dû à la nécessité d'être réduite en ammonium avant d'être incorporée en molécules organiques.

Cependant, les diatomées de grande taille ne sont pas systématiquement présente et dominante dans les régions non limitées en fer et en lumière.

La distribution des silicates composants majeurs des diatomées montre un important gradient positif nord - sud, avec des valeurs aussi faibles que 5 µM dans la zone du front polaire. A partir de culture de diatomées antarctiques, Jacques (1983) et Sommer (1991) ont démontré la faible affinité de ces diatomées pour le silicate, ce qui pourrait dés lors appuyer l'hypothèse de la limitation en silicate dans certaines régions de l'océan Antarctique. Nelson and Tréguer (1992) ont détecté des faibles mais significatives limitation en silicate en mer de Ross durant l'été.

D'autre part selon la présence ou l'absence de krill hivernant sous la glace lors de l'initiation de l'efflorescence phytoplanctonique, différents scenarios peuvent exister (Fig.3).

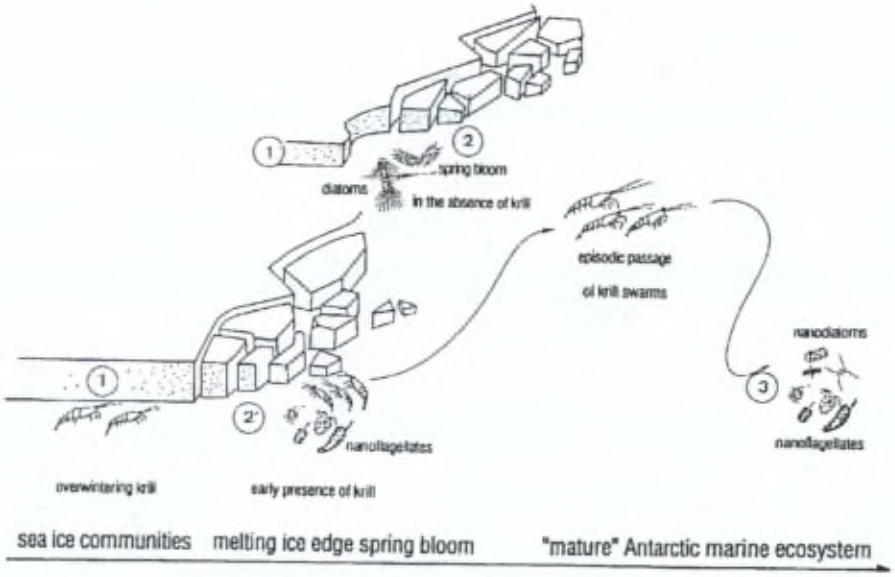

Figure 3. *Scenario représentant l'évolution du phytoplancton au printemps et en été selon la présence ou non de krill sous la banquise (Lancelot et al. 1993).*

La présence de krill lors de la retraite de la glace pouvant consommer préférentiellement les cellules de grande taille peut limiter l'ensemencement de la colonne d'eau par des diatomées. Le nanophytoplancton dès lors domine (Fig. 4).

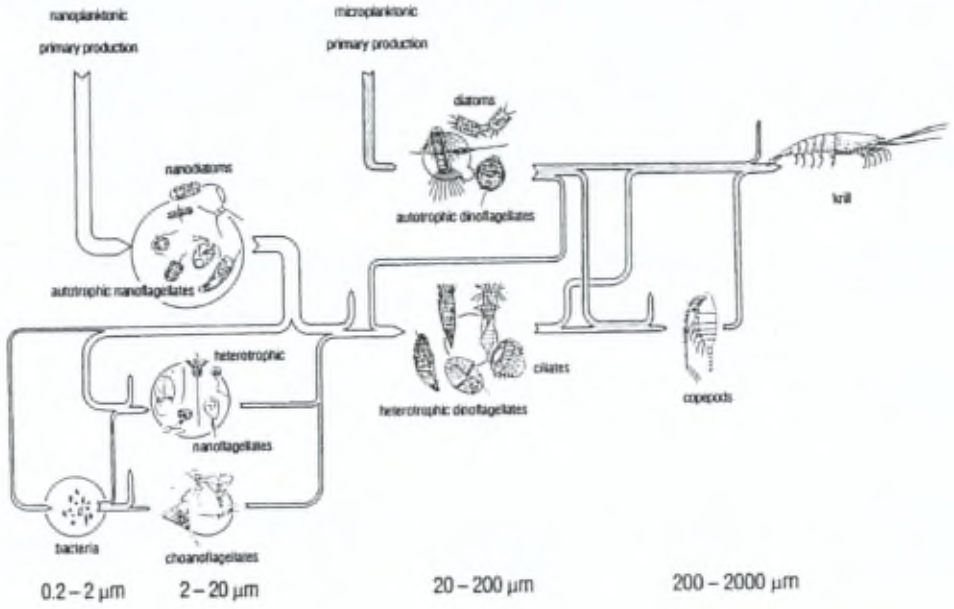

Figure 4. *Structure du réseau trophique pélagique en présence de krill (Lancelot et al. 1993).*

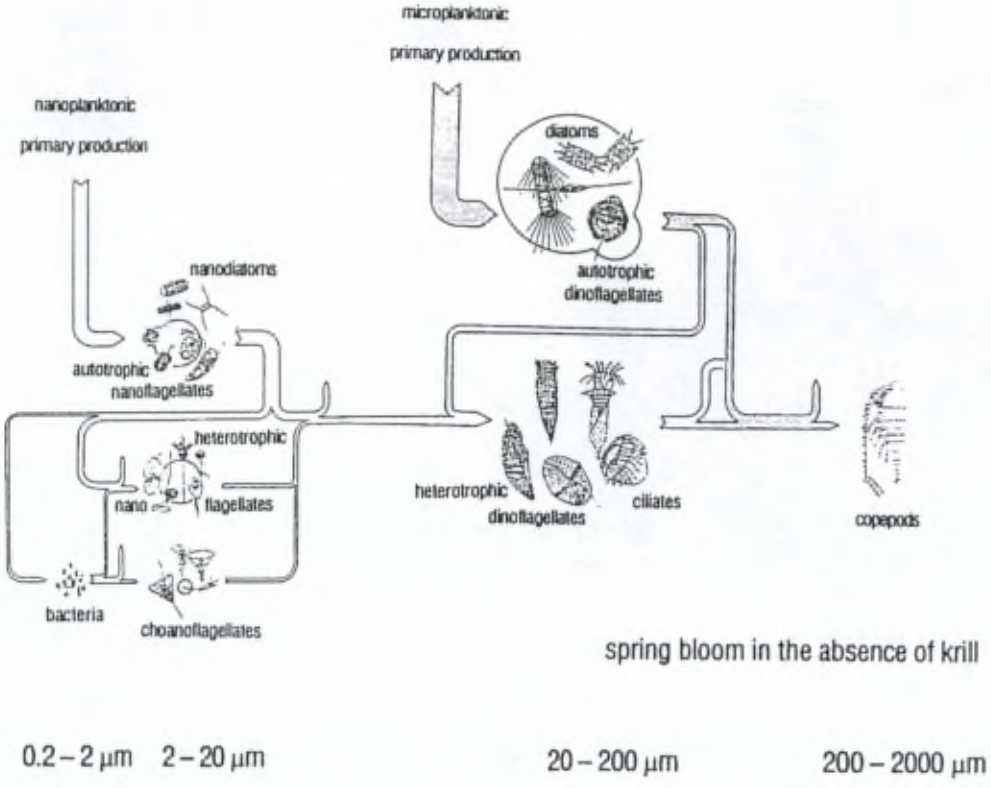

Figure 5. *Structure du réseau trophique pélagique en absence de krill (Lancelot et al. 1993).*

Par contre en absence de krill (Fig. 5), des diatomées de grande taille ensemencent la colonne d'eau et constituent des efflorescences importantes de phytoplancton (mer de Ross, Smith et Nelson 1985, Nelson et Smith 1986). Dans les eaux du large, krill et seiches (Dubischar et Bathmann 1997) se déplacent en essaim dépassant parfois le milliard d'individus. Episodiquement, ces essaims, capables de repérer les floraisons phytoplanctoniques, "nettoient " littéralement les eaux de surface en se nourrissant préférentiellement des organismes micro- et mesoplanctoniques. Par exemple, lors d'un passage d'un essaim de krill dans la confluence des mers d'Ecosse et de Weddell au printemps 1988, la concentration en chlorophylle a était réduite de 2.5 à 0.3 mg m^{-3} en moins de 10 heures et la composition phytoplanctonique passait d'une dominance microplanctonique (diatomées) vers une dominance nanoplanctonique (flagellés) (Jacques et Panouse 1991).

5. Importance du protozooplancton dans un écosystème dominé par des producteurs pico- et nanoplanctoniques

Les protozoaires sont ubiquistes (Sieburth 1979, Sherr et Sherr 1984, Fenchel 1987, Reid *et al.* 1991) et si ils sont reconnus depuis longtemps comme un compartiment important de la communauté pélagique dans les océans tempérés et tropicaux, le protozooplancton a été peu étudié dans les eaux antarctiques pour une raison historique. En effet pendant longtemps on a considéré l'écosystème Antarctique comme l'exemple type d'écosystème dominé par la chaîne trophique classique (diatomées - krill) en raison de son apparente richesse en mammifères marins. A présent qu'il est évident que le réseau trophique pélagique de l'océan Antarctique est le plus souvent dominé par du pico- et nanophytoplancton, l'étude du rôle du protozooplancton dans le contrôle de la production phytoplanctonique et bactérienne ainsi que dans le transfert d'énergie et de matière vers les niveaux supérieurs de la chaîne alimentaire devient une recherche prioritaire. Cependant infiniment peu de données sur les biomasses et particulièrement sur les activités biologiques du protozooplancton sont disponibles dans l'océan Antarctique, notamment en comparaison aux connaissances sur les autres compartiments trophiques. L'état des connaissances sur le rôle du protozooplancton dans l'océan Antarctique lors du commencement de ce travail est repri dans les chapitres qui suivent.

5.1. Composition taxonomique

Les protozoaires constituent un des sous-règnes des protistes (Lee *et al.* 1985). Ce sont des organismes unicellulaires dont la taille varie de 2 à 20000 µm. Le sous-règne des protozoaires est composé de 6 phylums qui comptent environ 50000 espèces connues. L'identification taxonomique des protozoaires reste difficile, de ce fait les océanographes les classent le plus souvent par classe de taille selon une échelle logarithmique (Sheldon *et al.* 1972): le nanoplancton (2 à 20 µm) où sont essentiellement présents des flagellés (choanoflagellés, dinoflagellés et flagellés nus) et plus minoritairement des ciliés, le microplancton (20 à 200 µm) qui comprend des dinoflagellés et des ciliés et enfin le mésoplancton où les protozoaires ont des tailles supérieures à 200 µm. Une revue exhaustive de la taxonomie des protozoaires dans les écosystèmes marins a été réalisée par Sleigh (1991).

Des études récentes (Nöthig 1988, Garrison et Buck 1989a-b-c, Garrison *et al.* 1991, 1993, Becquevort *et al.* 1992, Scharek *et al.* 1994, Burkill *et al.* 1995, Becquevort 1997, Klaas 1997)

ont montré que la biomasse protozooplanctonique dans les eaux de surface antarctiques est dominée par des flagellés hétérotrophes et des ciliés.

Parmi les flagellés hétérotrophes, les choanoflagellés ont été les mieux étudiés (Takahashi 1981, Buck et Garrison 1988, Marchant et Perrin 1990, Thomsen *et al.* 1990, Thomsen & Larsen 1992). Trois familles de cet ordre sont représentées; les Codonosigidae, les Salpingoecidae et les Acanthoecidae. La plupart des choanoflagellés dans les eaux antarctiques appartiennent à la famille des Acanthoecidae (Thomsen *et al.* 1990). Les choanoflagellés consomment principalement des bactéries, mais ils sont capables aussi de consommer du nanoplancton autotrophe et des débris cellulaires de phytoplancton (Marchant 1985), de la matière organique de haut poids moléculaire (Sherr 1988) et des particules de la taille de virus (Gonzales et Suttle 1993). Les choanoflagellés individuellement sont de la taille du nanoplancton mais certains se trouvent en colonies et peuvent alors atteindre la taille du microplancton et être consommés par le metazooplancton tel que le krill (Tanoue et Hara 1984, Marchant et Nash 1986). De nombreux autres nanoflagellés hétérotrophes ont été répertoriés de manière épisodique mais leur diversité et leur abondance sont peu documentés (Buma *et al.* 1989, Thomsen *et al.* 1991). Les dinoflagellés hétérotrophes semblent cependant dominer la biomasse des nanoflagellés hétérotrophes. Au moins 25 espèces du genre *Protoperidinium* ont été trouvés dans les eaux antarctiques (Garrison et Mathot, 1996). Les formes athecates appartenant aux genres *Amphidinium*, *Gymnodinium*, *Gyrodinium*, *Katodinium*, *Nematodinium* sont considérablement plus abondantes. Les dinoflagellés incluent des formes qui sont hétérotrophes et quelques autres qui apparemment retiennent des chloroplastes fonctionnels de leurs proies et sont mixotrophes (Elbrächter et Zölffel 1993). Les dinoflagellés peuvent ingérer des proies de la taille de bactéries jusqu'à des cellules qui approchent ou excèdent leur taille (Nöthig 1988, Gaines et Elbrächter 1987).

La plupart des ciliés pélagiques sont de l'ordre des Oligotrichida. Les tintinnides sont les plus facilement reconnaissables et par conséquence beaucoup d'espèces ont été répertoriées dans les eaux antarctiques. Les tintinnides antarctiques consomment des bactéries (Lessard et Rivkin 1986) mais aussi des diatomées et des dinoflagellés (Gowing 1989, Gowing et Garrison 1991). Cependant les ciliés les plus abondants sont les autres oligotriches. Peu d'espèces ont été identifiées et on les regroupent souvent sous l'appellation ciliés nus ou sans lorica. Quelques espèces de ciliés sont des phototrophes obligatoires ou des mixotrophes. Parmi ceux-ci, le cilié *Mesodinium rubrum* est présent dans la glace et dans l'eau environnante (Garrison et Buck 1989, Satoh et Watanabe 1991).

D'autres taxons sont présent dans les eaux antarctiques tels que les Sarcodines, les Radiolaires et les Foraminifaires (voir revue Garrison et Gowing 1993). Ils sont cependant moins abondants et contribuent moins a la biomasse carbonée totale protozooplanctonique que les protozoaires présentés ci-dessus, mais peuvent constituer un rôle significatif dans l'exportation de carbone (Wefer *et al.* 1988) ou de silice (Fisher *et al.* 1988) vers les eaux profondes.

5.2. Distribution spatio-temporelle de la biomasse du protozooplancton

Le protozooplancton est ubiquiste dans l'océan Antarctique et constitue une fraction significative de la biomasse microbienne (nano- et microplancton) totale. Cette fraction variait entre 6 et 76 % (Garrison 1991) suivant les régions et la saison. La seule étude qui rapportait des mesures de biomasse protozooplanctonique le long d'un cycle saisonnier dans une même région de l'océan Antarctique était l'étude (AMERIEZ, Antarctic Marine Ecosystem Research in the Ice Edge Zone) réalisée dans la zone marginale de fonte de glace de mer de la mer de Weddell (Garrison et Buck 1989, Garrison *et al.* 1991, 1993). Cette étude montrait notamment que la biomasse des protozoaires varie en étroite corrélation avec les productions phytoplanctoniques et bactériennes le long d'un transect à travers la zone adjacente à la banquise au printemps et en automne

5.3. Rôle du protozooplancton dans le contrôle de la production bactérienne et phytoplanctonique

Des corrélations significatives entre la biomasse des protozoaires et celle de la biomasse combinée des bactéries et du phytoplancton ont suggéré un contrôle directe par le protozooplancton sur la production bactérienne et phytoplanctonique. D'autres auteurs (Garrison et Buck 1989, Garrison et Mathot 1996) ont à partir de l'abondance des protozoaires et de leur nourriture et des taux de filtration rapportés dans la littérature, estimé qu'entre 10 et 85 % de la production primaire journalière et qu'entre 10 à 53 % de la biomasse bactérienne étaient consommés par les dinoflagellés hétérotrophes et les ciliés dans la zone marginale de fonte de la banquise de la mer de Weddell.

Deuxièmement, des mesures directes préliminaires de l'ingestion du protozooplancton dans l'Océan Antartique ont été obtenues par la technique de dilution proposée par Landry et Hasset (1982) (Taylor et Haberstroh 1988). Cette étude montre que le prozooplancton consomme entre 0 et 76 % de la biomasse phytoplanctonique. Cette technique fut également utilisé par la suite par de nombreux autres auteurs (Burkill *et al.* 1995, Fronemann et Perissinotto 1996a, b, Froneman *et al.* 1997, Klaas 1997) et selon ces études entre 4 à 271 % de la production primaire journalière était contrôlée par le protozooplancton.

5.4. Rôle du protozooplancton dans la régénération de nutriments et le transfert d'énergie et de matière vers les hauts niveaux trophiques

Par leurs activités métaboliques, les protozoaires constituent d'importants reminéralisateurs de nutriments (Caron 1991) permettant de soutenir la production primaire d'un écosystème. Le niveau de régénération des nutriments est lié au métabolisme des protozoaires ainsi que la qualité nutritive de ces particules alimentaires, ainsi les protozoaires régénèrent les nutriments ingérés selon leur rendement de croissance. Nutriments qui sont contenus dans leurs particules alimentaires ne seront clairement pas disponibles pour la régénération s'ils sont utilisés pour former de la biomasse. Donc les rendements de croissance placent la limite supérieure de la quantité de nutriments qui sera régénéré directement par les protozoaires. Des rendements de croissance élevés, supérieur à 50 %, ont été déterminés expérimentalement pour les protozoaires (Stoecker et Evans 1985, Fenchel 1982, Sherr *et al.* 1983, Caron *et al.* 1985). Björnsen et Kuparinen (1991) estimaient un rendement de croissance de 40 % pour une population naturelle de dinoflagellés hétérotrophes consommant des flagellés autotrophes dans l'océan Antarctique. Donc si les protozoaires sont des remineralisateurs importants de matériel organique, une fraction substantielle des nutriments ingérés est retenue dans la biomasse des protozoaires, qui est potentiellement disponible pour les hauts niveaux trophiques (Azam *et al.* 1983). Dû a la difficulté de mesurer l'ingestion du protozooplancton par le zooplancton, très peu de mesures directes sont disponibles dans la littérature. Néanmoins, il y a de plus en plus d'évidences démontrant leur importance comme nourriture pour métazooplancton dans l'océan Antarctique. Premièrement, la présence de protozooplancton dans l'estomac de zooplancton a été très souvent observée (Hopkins 1985, Hopkins et Torres 1989). D'autre part Tanoue et Hara (1984) rapportait la présence de lorica de choanoflagellés dans les pelotes fécales de krill et Marchant et Nash (1986) observaient que le krill était en effet capable de consommer des choanoflagellés. Deuxièmement, la contribution relative des protozoaires à la biomasse planctonique totale et leur taille similaire au phytoplancton suggèrent qu'ils peuvent être des proies importantes pour le métazooplankton particulièrement durant l'hiver austral et dans les régions couvertes de glace où la production phytoplanctonique est limitée (Garrison et Buck 1989, Garrison *et al.* 1990a&b).

5. Cadre de ce travail

Cette thèse s'intègre dans un travail d'équipe du Groupe de Microbiologie des Milieux Aquatiques. Ce groupe de recherche a développé une approche méthodologique conceptuelle intégrée combinant les études de processus biologiques ainsi que l'expérimentation numérique conduisant à l'élaboration de modèles biogéochimiques mécanistiques décrivant les écosystèmes planctoniques. Ces modèles constituent d'un part un outil de recherche par sa possibilité d'intégrer un grand nombre de mécanismes, d'autre part il peut servir d'aide à la gestion rationnelle des écosystèmes aquatiques. Dans le cadre du programme national d'étude de l'océan Antarctique, l'objectif de notre groupe de recherche fut d'établir un modèle mécanistique décrivant la circulation du carbone, de l'azote, de la silice et du fer au sein du réseau trophique microbien planctonique de l'océan Antarctique afin d'estimer d'une part le potentiel nutritif de ce réseau pour les organismes supérieurs, d'autre part le rôle de l'océan Antarctique dans la régulation des changements climatiques.

6. Objectifs du travail

L'objectif général de ce travail était de déterminer l'importance du réseau trophique microbien et le rôle du protozooplancton dans l'océan Antarctique. Dans ce cadre-là, les questions adressées étaient les suivantes:

- **Qu'elles sont les facteurs physiques, chimiques et biologiques contrôlant la structure du réseau trophique pélagique et la dominance d'un type de réseau trophique par rapport à un autre?**
- **Est-ce que le protozooplancton peut contrôler la production pico- et nanoplanctonique (bactéries et phytoplancton)?**
- **Le réseau trophique microbien via le protozooplancton peut-il constituer un apport significatif en nourriture pour le métazooplancton?**

7. Plan du travail

Le support expérimental à ce travail acquis lors de campagnes océanographiques occupant des régions différentes de l'océan Antarctique à différentes périodes de la saison végétative est décrit dans le **chapitre 2**.

Etant donné le peu d'informations disponibles sur les protozoaires dans l'océan Antarctique, nous nous sommes tout d'abord attachés à étudier sa distribution spatio-temporelle aussi bien dans la glace de mer que dans l'eau libre de l'océan Antarctique. La distribution du protozooplancton a été analysée et discutée en relation avec la distribution de sa nourriture potentielle (bactéries, et pico- et nanophytoplancton). D'autre part, l'ingestion des bactéries et du phytoplancton par le protozooplancton a été directement estimée.

Beaucoup d'évidences ont indiqué que la zone marginale de glace est une région de haute productivité dû à la formation au moment de la fonte des glaces d'une couche d'eau peu profonde ainsi que l'ensemencement de la colonne d'eau par des micro-organismes vivant dans la glace de mer. Leurs contributions relatives à l'ensemencement du réseau trophique planctonique a été étudié dans la zone marginale de glace de la mer de Weddell au printemps (**Chapitre 3**).

La structure du réseau trophique microbien planctonique incluant les interactions trophiques entre phytoplancton et bactéries, ainsi que celles entre phytoplancton, bactéries et protozooplancton, a été étudié dans différentes régions de l'océan Antarctique (mer de Weddell, secteur atlantique et secteur indien) et à différentes périodes de l'année d'octobre à mars (**Chapitre 4**).

L'ensemble de ces résultats nous ont permis de caractériser la dynamique du protozooplancton dans l'océan Antarctique et d'intégrer un sous-modèle décrivant la dynamique du protozooplancton dans le modèle biogéochimique SWAMCO-Sea Water Microbial Communities (Lancelot *et al.* 1991, Lancelot *et al.* 1993a) décrivant les cycles du carbone, de l'azote, de la silice et du fer dans les systèmes planctoniques de l'écosystème Antarctique (**Chapitre 5**).

L'ensemble de ce travail a été synthétisé et intégré dans l'ensemble des connaissances actuelles sur la dynamique du réseau trophique pélagique de l'océan Antarctique (**Chapitre 6**).

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Chapitre 2

Biotope

1. Caractéristiques physico-chimiques de l'océan Antarctique.

L'océan Antarctique est défini comme les masses d'eau entourant le continent Antarctique et limité au nord par un front quasi-stationnaire la convergence antarctique (ou front polaire), dont la position varie suivant les secteurs entre les latitudes de 50° et 60° sud, qui défini la frontière entre les eaux de surface antarctiques froides et les eaux sub-antarctiques chaudes au nord (Fig.1).

Figure 1. *Carte de l'océan Antarctique avec localisation du front polaire. Les flèches indiquent la circulation du courant circumpolaire antarctique. En ligne hachurée est indiqué la divergence antarctique. Les croix indiquent la position approximative de la confluence Weddell-Ecosse.*

Sa surface est de 38.5 10^6 km^2, représentant approximativement 10 % de la surface totale des océans (Deacon 1982). L'écosystème antarctique inclut une large diversité d'habitats depuis la glace de mer (hyper-saline et super froide) jusqu'au monde océanique pélagique du courant circumpolaire antarctique. De plus à cette diversité spatiale s'ajoute la variabilité saisonnière extrême incluant le cycle annuelle de formation de la glace et du rayonnement solaire.

Le moyenne d'extension de la banquise varie typiquement entre 4 10^6 km^2 en été (février) à 21 10^6 km^2 en hiver (août) (Zwally *et al.* 1983). Durant cette période, 55 % de l'océan Antarctique est couvert de glace. D'autre part la photopériode varie par exemple à 55°S en latitude de 16 heures en décembre à 7 heures en juin et à 70°S en latitude de 24 heures à la mi-décembre à 0 heure à la mi-juin (Sakshaug & Holm-Hansen 1984).

La circulation des masses d'eau (Fig.1) est dominée par le courant circumpolaire antarctique approximativement 130-190 millions de m^3 par seconde (Sverdrup 1953). Sous l'action des vents dominants (les quatrièmes rugissants et les cinquièmes hurlants) et de la force de Coriolis, il circule d'ouest en est sur une distance d'environ 24000 km et une largeur de 200 et 1000 km; Aux abords des côtes littorales antarctiques, le sens giratoire est inversé et les eaux côtières antarctiques circulent d'est en ouest. Ces deux zones de circulation hydrologique sont séparées par la divergence antarctique.

Au sud, les eaux du courant circumpolaire antarctique deviennent plus denses car elles se refroidissent et deviennent plus salées dû au rejet d'eau salée lors de la formation de glace de mer. Cette eau s'écoule alors le long des bords du plateau continental et se répand sur les fonds jusqu'à l'hémisphère nord, sa production étant particulièrement intense sous les "ice-shelfs" de Weddell et de Ross et le long de la côte Adélie. La présence de ce courant profond (eaux antarctiques de fond) pouvant atteindre mille mètres d'épaisseur est une des caractéristiques majeure de la circulation générale des océans.

D'autre part, au nord, au niveau de la zone du front polaire, ces eaux de surface froides rencontrent les eaux plus chaudes sub-antarctiques et donc plongent sous elles, formant les eaux antarctiques intermédiaires. Les eaux antarctiques de fond et les eaux antarctiques intermédiaires exportent d'énorme quantité en nutriments vers le reste de l'océan mondial et contribuent indirectement à la fertilisation de zones côtières très productives tel que les upwelling du Pérou et du Chili.

Ensuite, la circulation thermohaline transporte les eaux profondes enrichies en nutriments par la reminéralisation des détritus biogéniques. La remontée de ces eaux circumpolaires de fond au niveau de la divergence antarctique provoque une fertilisation des eaux de surface de l'océan Antarctique. La gamme des concentrations en nutriments dans les eaux de surface de l'océan Antarctique sont typiquement de l'ordre de 22 - 28 µM pour les nitrates, 1.4 - 1.8 µM pour les phosphates et 5-30 µM pour les silicates (Le Corre et Minas 1983).

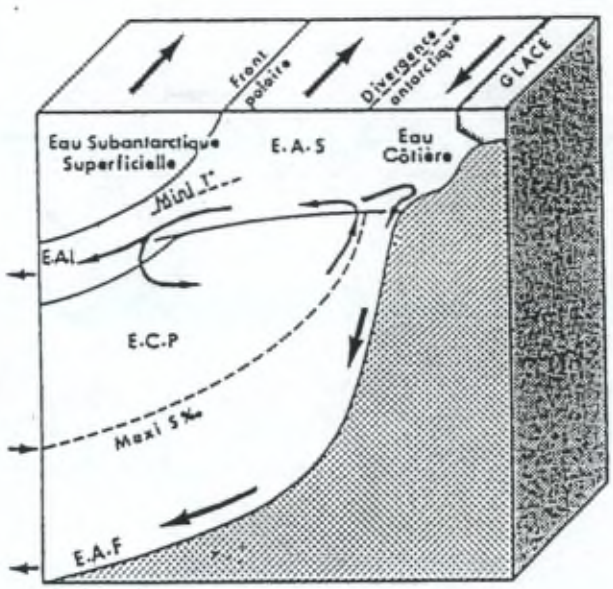

Figure 2. *Représentation schématique de la circulation des masses d'eau principales dans l'océan Antarctique (E.A.S, Eaux Antarctiques de Surface; E.C.P., Eaux Circumpolaires Profondes; E.A.F, Eaux Antarctiques de Fond; E.A.I., Eaux Antarctiques Intermédiaires).*

2. Provinces biogéochimiques de l'océan Antarctique

Comme il a été reporté par de nombreux auteurs, l'océan Antarctique ne peut être considéré comme un système homogène mais plutôt comme une mosaïque de provinces biogéochimiques (Tréguer et Jacques 1992). En effet un large spectre de conditions climatiques, et hydrographiques existant dans l'océan Antarctique produit des environnements très variables pour les organismes particulièrement pour les producteurs primaires dont la croissance peut être contrôlée par un ou une combinaison de facteurs physiques, chimiques et biologiques, variable d'une province à une autre (Mathot 1993, Mathot *et al.* soumis).

L'écosystème pélagique antarctique est actuellement considéré comme formé d'au moins 5 provinces biogéochimiques différentes mais interdépendantes, c'est à dire 1) les zones frontales (Frontal Zone, FZ), 2) la région océanique ouverte (Open Ocean Zone, OOZ), 3) la région marginale de fonte de glace (Marginal Ice Zone, MIZ), 4) la région couverte de manière permanente par la glace (Closed Pack Ice Zone, CPIZ) et 5) le plateau continental et côtier (Coastal and Continental Shelf Zone, CCSZ) (Fig. 3). Les frontières géographiques de ces différentes régions varient selon un cycle saisonnier dynamisé par la retraite et la formation de la banquise.

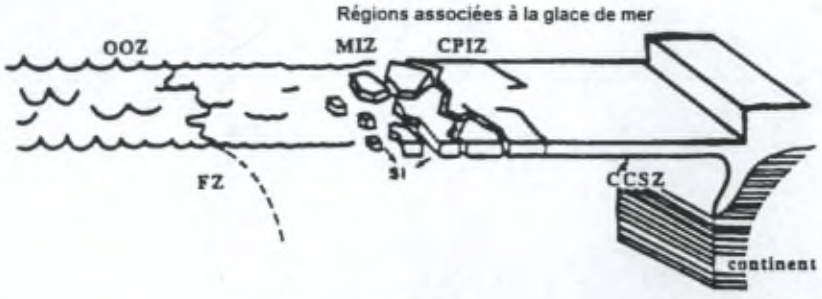

Figure 3. *Représentation schématique des 5 provinces biogéochimiques. OOZ (Open Ocean Zone); FZ (Frontal Zone); MIZ (Marginal Ice Zone); CPIZ (Closed Pack Ice Zone); CCSZ (Coastal and Continental Shelf Zone) (Mathot 1993).*

2.1. Zones frontales

Ces régions (le front polaire, la divergence antarctique, ou la confluence Weddell-Ecosse) marquent les transitions entre différentes masses d'eau et présentent des structures complexes incluant des méandres et des tourbillons (Gordon *et al.* 1977; Veth *et al.* 1997), accompagnés par des fluctuations spatio-temporelles dans les deux directions aussi bien verticales qu'horizontales. Dans ces zones, la couche océanique de surface est généralement stabilisée et le phytoplancton peut y être concentré et maintenu dans les eaux de surface, avec un apport continuel en nutriments (majeurs et mineurs) par les remontées d'eau profonde et avec des conditions lumineuses favorables permettant une croissance phytoplanctonique importante. Ces zones sont généralement caractérisées par des biomasses phytoplanctoniques importantes jusqu'à 5 mg Chla m^{-3} (Holm-Hansen *et al.* 1977, Lutjeharms *et al.* 1985, El-Sayed 1986, Nelson *et al.* 1987, Jacques et Panouse 1989, 1991, Sullivan *et al.* 1993, Bathmann *et al.* 1997), et des productions primaires élevées aussi hautes que 2.9 gC m^{-2} d^{-1} (Mathot *et al.* 1994, Mathot *et al.* soumis).

2.2. Région océanique ouverte (Open Ocean Zone, OOZ)

Cette zone non influencée par la retraite de la glace, inclut essentiellement le courant circumpolaire antarctique (CCA) localisé entre la convergence antarctique (ou le front polaire) et la limite nord de la banquise. Cette région est fréquemment soumise aux tempêtes avec pour conséquence un entraînement en profondeur des eaux de surface et une couche de mélange profonde. Ainsi même si les concentrations en nutriments majeurs sont élevées, les biomasses phytoplanctoniques et les productions primaires sont faibles. Les valeurs de chlorophylle a sont de l'ordre de 0.5 mg m^{-3} et les productions primaires sont insignifiantes et varient entre 0.01 et 0.45 gC m^{-2} d^{-1} (Smith 1987, Smith & Sakshaug 1990, Tréguer & Jacques 1992, Mathot *et al.* soumis).

2.3. Zone marginale de fonte de glace (Marginal Ice Zone, MIZ)

Cette zone est définie comme l'aire de transition entre la région océanique ouverte et l'aire couverte par la banquise de manière permanente (plus de 85 % de couverture de glace). Son étendue géographique varie saisonnièrement selon la dynamique de formation et de retraite de la glace s'étendant sur 20 10^6 km^2 durant l'hiver austral (août) et reculant jusqu'à 4 10^6 km^2 en été (février) (Zwally *et al.* 1983). Cette zone est reconnue comme très productive et caractérisée par de développements importants de phytoplancton. Ces derniers sont favorisés par la formation d'une couche de surface de faible profondeur de la colonne d'eau dû à l'apport d'eau de salinité faible résultant de la fonte de la banquise (Sullivan *et al.* 1988). Néanmoins la profondeur et la stabilité de la couche de surface sont très variables dépendant des conditions météorologiques qui régissent la fonte de la banquise. En conséquence, la biomasse phytoplanctonique et la production primaire sont très variables mais occasionnellement élevées. La chlorophylle a varie entre 1 et 5 mg m^{-3} (El-Sayed et Taguchi 1981) et la production primaire entre 0.02 et 1.4 gC m^{-2} d^{-1}.

2.4. Zone couverte de manière permanente par la banquise (Closed Pack Ice Zone, CPIZ)

Cette zone est définie comme la zone dont la surface est couverte à plus de 85 % par de la glace. Des valeurs faibles de biomasses phytoplanctoniques (< 0.05 mg de Chl-a m^{-3}, Bianchi *et al.*, 1992) et de production primaire (0.06 -0.54 gC m^{-2} d^{-1}, Cota *et al.* 1990, Mathot *et al.* 1992, 1994, soumis) sont typiquement trouvées due à la limitation de la lumière.

2.5. Plateau continental et côtier (Coastal and continental Shelf Zone, CCSZ)

Cette région généralement d'une profondeur maximale de 500 m, est caractérisée par des développements phytoplanctoniques importants favorisés par une stabilité verticale importante de la colonne d'eau dû à de vents faibles et par un apport continu en fer à partir des sédiments du continent. La chlorophylle a variant entre 2 et > 25 mg m^{-3} (El-Sayed 1986, Wright 1987, Holm-Hansen et Mitchell 1991, Goeyens & Dehairs 1993, Mathot 1993, Sullivan *et al.* 1993) et la production primaire entre 0.25 et 6.2 gC m^{-2} d^{-1} (revue par Mathot *et al.* soumis).

3. Présentation des campagnes océanographiques

Le support expérimental de ce travail a été acquis lors de 4 campagnes océanographiques occupant des régions différentes de l'océan Antarctique à différentes périodes de la saison végétative. Une des campagnes a été réalisée dans la région mers de Weddell et d'Ecosse du 22 novembre 1988 au 9 janvier 1989 lors d'une étude européenne sur le bateau océanographique le "Polarstern" (**EPOS leg 2**). Dans le secteur Atlantique, des radiales ont été échantillonnées le long du méridien 6° W, du 29 septembre au 29 novembre 1992 dans le cadre du programme "Joint Global Ocean Flux Study" (JGOFS) de l'Océan Austral (Polarstern **ANT X/6**). Deux autres campagnes océanographiques se sont déroulées dans le secteur Indien le long du méridien 62° E dans le cadre du programme français ANTARES (JGOFS-France). La première, **ANTARES 2**, était du 26 janvier au 23 mars 1994. La seconde, **ANTARES 3**, du 10 octobre au 27 octobre 1995. La position géographique des campagnes océanographiques est représentée sur la figure 4 .

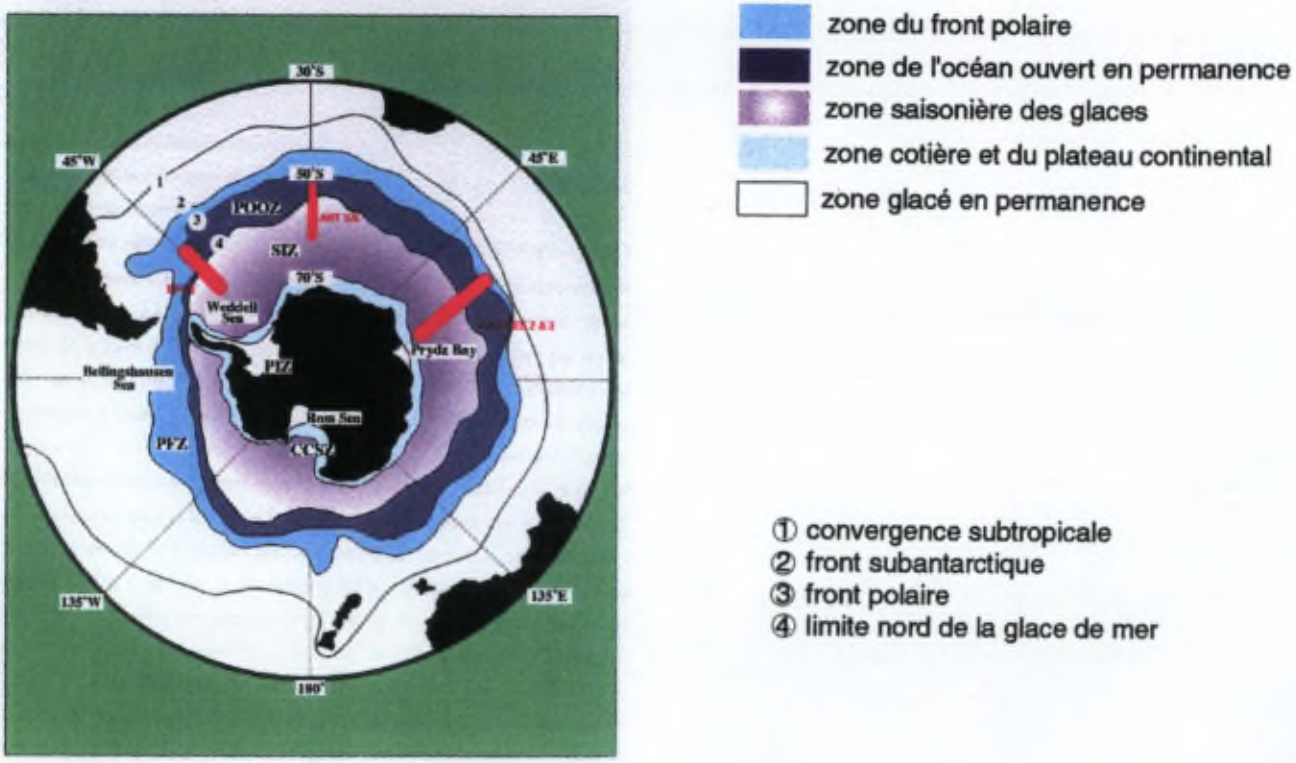

Figure 4. *Position géographique des campagnes océanographiques (EPOS, ANT X/6, ANTARES 2 et 3) (d'après Tréguer et Jacques 1992).*

3.1. Mers d'Ecosse et de Weddell au printemps et en été 1988 (EPOS leg 2)

L'objectif d'EPOS "European Polarstern Study" organisée à l'initiative de l'A.W.I. (Alfred-Wegener-Institut, Bremerhaven) et patronnée par l'E.S.F. (European Science Foundation) était d'étudier la glace de mer et son rôle sur l'écosystème pélagique, le benthos et les poissons. L'objectif du 2ème leg était plus spécifiquement l'étude des activités pélagiques lors de la retraite de la banquise.

Cette campagne était localisée entre la pointe de la péninsule antarctique et les îles Orcades Sud (Fig.5).

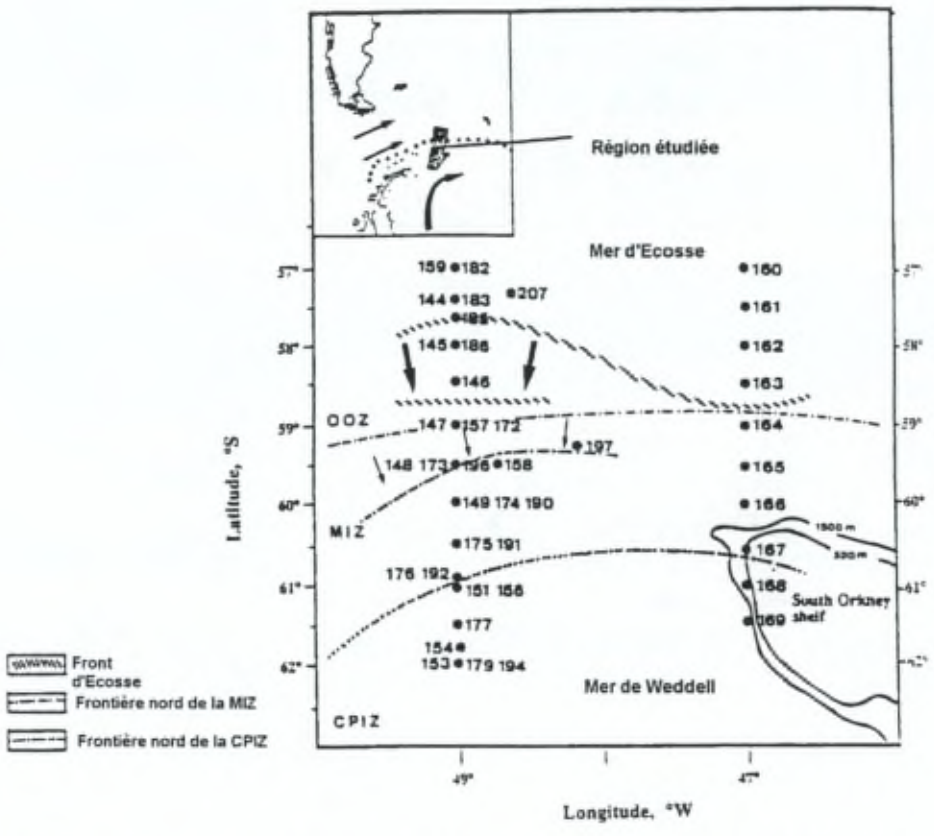

Figure 5. *Représentation de la zone d'échantillonnage lors d'EPOS leg 2. Les différents radiales sont indiquées: au méridien 49°W (stations 100-113 du 26 au 30 octobre, stations 143-153 du 26 au 30 novembre, stations 172-179 du 20 au 24 décembre, stations 182-194 du 27 au 31 décembre) et au méridien 47°W (stations 130-139 du 11 au 13 novembre, stations 160-169 du 13 au 17 décembre) entre les latitudes 57°S et 62 °S. La confluence Weddell-Ecosse est approximativement localisée. Les provinces biogéochimiques (OOZ, MIZ, CPIZ) sont indiquées.*

Dans cette région, les eaux du courant circumpolaire antarctique s'écoulant dans la mer d'Ecosse rentrent en contact le long d'une zone frontale avec les eaux circulant d'est en ouest du bord nord du gyre de Weddell. Cette zone frontale est la confluence Weddell-Ecosse (Gordon,

1967). La structure hydrodynamique de la région de la confluence est dominée par un gradient abrupte en température au nord (le front d'Ecosse) s'étendant de 200 à 2500 mètres. A la fin novembre, le front d'Ecosse était localisé entre 57.5°S et 58°S et un mois plus tard, il s'était élargi jusqu'à 59°S (Cederlöf *et al.* 1989). Lors de cette campagne, la confluence Weddell-Ecosse se surimposait à la OOZ ainsi qu'à la MIZ. Les stations d'échantillonnage et les limites géographiques des provinces biogéochimiques sont reprises sur la figure 5.

Au début de la campagne, la limite de la banquise était situé à la latitude 58 30°S. Deux mois plus tard, la limite de la banquise s'était retirée à la latitude 61°S. La retraite de la banquise s'effectuait à une vitesse moyenne de 5.5 km par jour, minimal au début de la campagne (fin octobre) ainsi qu'à la fin de la campagne (fin décembre). La couche océanique mélangée par le vent était peu profonde dans les régions associées à la banquise, 14 et 18 mètres respectivement pour la CPIZ et pour la MIZ (Table 1). Les profils verticaux de la salinité montrent clairement une couche de faible salinité résultant de la fonte de la banquise (Veth, 1991b). Dans la OOZ, la couche océanique mélangée par le vent était également peu profonde (en moyenne 24 m, Table 1) comparée à la profondeur de la couche de surface généralement observée dans la OOZ (supérieure à 100 m). En effet, lors de cette campagne la stabilité de la colonne d'eau engendrée par la fonte de la banquise dans la MIZ se maintenait au nord dû à un apport de chaleur (Veth *et al.* 1992). La vitesse du vent était faible (2 m sec^{-1}) à modérée (16 m sec^{-1}), avec une valeur moyenne de 8 m sec^{-1} (Lancelot *et al.*, 1997).

Table 1. *Résumé des caractéristiques physico-chimiques des différentes provinces biogéochimiques identifiées dans la région des mers d'Ecosse et de Weddell au printemps 1988. Valeurs moyenne, minimale et maximale dans la couche océanique mélangée par le vent sont présentées. Couche océanique mélangée par le vent (Veth, 1991), NO_3 et SiO_3 (Quéguiner et al. 1991, Tréguer & Jacques 1991) NO_3 et NH_4 (Goeyens et al. 1991), Fe (Nolting et al. 1991).*

	Régions associées à de la glace de mer		Régions océaniques ouvertes	
	CPIZ	MIZ	OOZ	WSC
Nombre de stations	14	18	9	3
Température, °C	-1.8 - -1.6	-1.5 - 0	+0.2 - +3.3	- 1.2 - -0.3
Couverture de glace de mer, %	> 75	0 - 75	0	0 - 4
Couche océanique mélangée par le vent , m	**14** (5 - 26)	**18** (8 - 37)	**24** (10 - 42)	**24** (16 - 30)
NO_3, µM	**30.3** (26.6 - 31.7	**25.2** (18.4 - 31.7)	**26.8** (24.6 - 27.4)	**23.5** (19.5 - 28.1)
PO_4, µM	**2.0** (1.8 - 2.1)	**1.6** (1.2 - 1.9)	**1.8** (1.6 - 1.9)	**1.4** (1.1 - 1.8)
SiO_3, µM	**77.4** (74.9 - 80.8)	**69.0** (54.8 - 82.5)	**29.4** (15.0 - 41.7)	**59.3** (55.7 - 63.3)
NH_4, µM	**0.26** (0.18 - 0.61)	**0.62** (0.08 - 2.04)	**0.41** (0.16 - 0.49)	**0.29** (0.10 - 0.49)
Fe, nM	**4.24** (2.87 - 5.30)	**7.54** (3.32 - 18.35)	**4.75** (3.05 - 7.55)	

Les valeurs moyennes des nutriments majeurs sont typiquement celles mesurées lors d'un début de printemps. Les concentrations en ammonium étaient en moyenne très faibles (0.08 - 0.61 µM), à l'exception de celles mesurées à la fin de décembre dans la MIZ (jusqu'à 2.04 µM). Les concentrations en fer dissous étaient bien au dessus de 1 nM, avec des valeurs maximales dans la MIZ. Ces concentrations en fer dissous élevées résulteraient de remontées d'eaux enrichies en fer en contact récemment avec les sédiments côtiers de la péninsule antarctique mais aussi de la fonte de la banquise où du fer d'origine éolienne se serait accumulé (de Baar *et al.* 1997).

3.2. Secteur atlantique au printemps 1992 (ANT X/6)

La campagne océanographique ANT X/6 fessait partie du programme international JGOFS (Joint Global Ocean Flux study) dans l'Océan Austral, dont l'objectif premier est d'étudier le cycle globale du carbone et des éléments biogènes associés dans des régions différentes de l'océan Antarctique. L'objectif spécifique de la campagne ANT X/6 était d'étudier le développement phytoplanctonique au printemps à la retraite de la banquise, dans le courant circumpolaire antarctique et dans la région du front polaire, afin de déterminer le rôle dans les échanges de CO_2 entre la mer et l'atmosphère de ces régions distinctes .

Les courants majeurs rencontrés dans le secteur atlantique étaient successivement du nord vers le sud, le front sub-antarctique, le front polaire, la partie sud du courant circumpolaire antarctique et la frontière entre le courant antarctique circumpolaire et le gyre de Weddell (Smetacek *et al.*, 1997). Le front polaire, défini comme une transition abrupte principalement en température, est une région hautement dynamique et associée à de nombreux tourbillons recouvrant une étendue approximative de trois degrés de latitude (Veth *et al.*, 1997). Durant cette campagne, la frontière entre le courant circumpolaire antarctique et le gyre de Weddell et la divergence antarctique se surimposait à la MIZ et à la CPIZ. La région océanique ouverte comprenait la partie du courant circumpolaire antarctique continuellement libre de glace.

Les stations d'échantillonnage et les limites géographiques des provinces biogéochimiques sont reprises sur la figure 6.

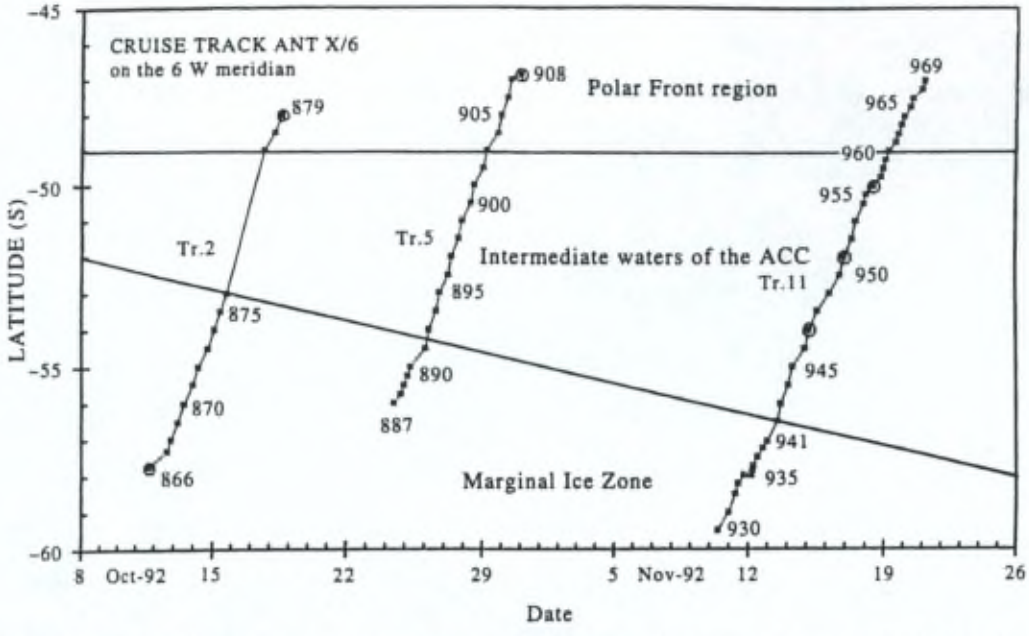

Figure 6. *Radiales réalisées lors de la campagne océanographique SO-JGOFS (ANT X/6) à bord du RV "Polarstern" dans le secteur atlantique de l'océan Antarctique au printemps (29 septembre - 29 novembre 1992).*

Lors de cette campagne, les conditions météorologiques étaient particulièrement mauvaises. La vitesse du vent excédait souvent 10 m sec^{-1}, avec des maxima de 35 m sec^{-1}. D'autre part des tempêtes étaient fréquemment observées dans la MIZ, avec pour conséquence un entraînement en profondeur des eaux de surface et une couche océanique mélangée par le vent profonde en dépit de la fonte de la banquise (Table 2). La retraite de la banquise était abrupte de 54°30 S à 58° S de latitude. Dans la région du front polaire, par contre, le mélange avec les eaux plus chaudes sub-antarctiques permettait la formation d'une couche océanique de surface plus stable (Table 2) où le phytoplancton était concentré et maintenu dans les eaux de surface (Veth *et al.* 1997).

Table 2. *Résumé des caractéristiques physico-chimiques des différentes provinces biogéochimiques identifiées dans le secteur atlantique au printemps 1992. Valeurs moyenne, minimale et maximale dans la couche océanique mélangée par le vent sont présentées. Données provenant d'une issue spéciale du journal Deep- Sea Research (Vol. 44, n°1-2, 1997).*

	Régions associées à de la glace de mer		Régions océaniques ouvertes	
	CPIZ	**MIZ**	***OOZ***	**PFr**
Nombre de stations	5	19	18	17
Température, °C	-1.8	-1.8 - -1.2	-1.6 - 1.2	1.3 - 3.7
Couverture de glace, %	> 85	0 - 85	0	0
couche océanique mélangée par le vent, m	**72** (60 - 100)	**113** (80 - 150)	**108** (40 - 150)	**45** (20 - 100)
NO_3, µM	**28.5** (28.1 - 29.1)	**27.4** (26.9 - 28.5)	**27.1** (26.3 - 28.3)	**23.7** (19.4 - 26.1)
PO_4, µM	**1.97** (1.9 - 2.0)	**1.9** (1.7 - 2.0)	**1.9** (1.7 - 2.0)	**1.5** (1.2 - 1.8)
SiO_3, µM	**58.5** (53.3 - 65.2)	**47.7** (39.5 - 79.1)	**35.8** (21.1 - 43.2)	**13.1** (0.7 - 20.6)
NH_4, µM	**0.10** (0.08 - 0.13)	**0.14** (0.07 - 0.5)	**0.22** (0.11 - 0.36)	**0.12** (0.08 - 0.18)
Fe, nM		**0.37** (0.22 - 1.25)	**0.43** (0.37 - 0.55)	**1.7** (1.43 - 1.87)

La distribution des nutriments majeurs montrait un gradient nord-sud en silicate, avec des valeurs faibles au nord du front polaire (0.7 µM) ainsi qu'une diminution en nitrate et en phosphate dans la région du front polaire à la fin novembre (Table 2). Des concentrations maximales en ammonium étaient mesurées au bord de la retraite de la banquise (Table 2).

Dans la partie la plus au sud du courant circumpolaire antarctique (51 - 56 °S), les concentrations en fer dissous étaient faibles et diminuaient en trois semaines de 0.49 nM en moyenne à 0.31 nM en moyenne (Löscher *et al.* 1997). Par contre, au voisinage de la retraite de la banquise, un apport de 0.5 nM de fer dissous était mesuré (de Baar *et al.* 1998). Dans la région du front polaire à approximativement 49-50°S, des concentrations élevées en fer dissous, approximativement 1.87 nM, étaient mesurées au début novembre. Deux à trois semaines plus tard, les concentrations en fer dissous diminuaient à approximativement 1.14 nM (de Baar *et al.* 1995, de Baar et Boyd 1998). L'origine de ces concentrations en fer dissous élevées au niveau de la partie est du front polaire ("Polar Frontal Jet") pourrait résultée des remontées d'eaux enrichies en fer en contact récemment avec les sédiments côtiers du basin argentin (de Baar *et al.* 1995, Löscher *et al.* 1997).

3.3. Secteur indien à la fin de l'été 1994 et au début du printemps 1995 (ANTARES 2 & 3)

ANTARES 2 et 3 étaient respectivement la deuxième et la troisième campagne du projet ANTARES (ANTArctic RESearch) du programme JGOFS-France, contribution française à SO-JGOFS. Ces campagnes étaient axées sur l'étude des processus contrôlant les flux de matière dans la couche photique et la colonne d'eau.

La radiale étudiée lors de ces campagnes traversait successivement, du nord au sud, le front polaire (51°S), le courant circumpolaire antarctique incluant la divergence antarctique (63-64°S) (Fig. 7).

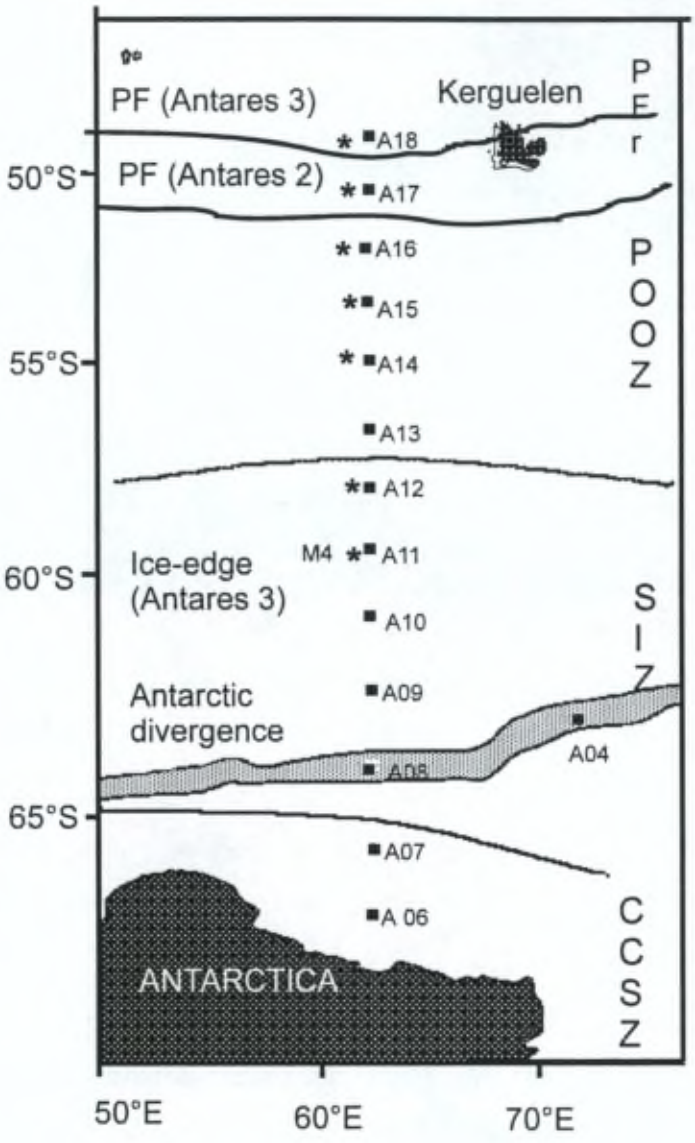

Figure 7. *Radiale réalisée durant ANTARES 2 (carré) et ANTARES 3 (étoile) dans le secteur indien de l'océan Antarctique. Les différentes provinces biogéochimiques rencontrées sont indiquées: PFr (Polar Frontal region), SIZ (Sea Ice Zone) et CCSZ (Coatal and Continental Shelf Zone).*

Au début du printemps (ANTARES 3), la banquise s'étendait jusqu'à 58°30S de latitude. Les couches océaniques de surface étaient peu stables (Descolas-Gros et Mayzaud 1997) et leurs

profondeurs excédaient le plus souvent 100 m, excepté à une station située dans la MIZ où la profondeur de la couche océanique mélangée par le vent était de 25 m. Cette station localisée à approximativement 167 km au nord de la retraite de la banquise (58°S) était influencée par l'apport d'eau moins salée provenant de la fonte de la banquise. Les concentrations en nutriments, particulièrement la silice, augmentaient du nord au sud. Les concentrations en silicate et en nitrate étaient respectivement 3.2 fois (13.9 à 44.0 µM SiO_3) et 1.1 fois (26.0 à 29.5 µM NO_3) plus élevées aux stations les plus au sud. Les concentrations en ammonium étaient faibles, < 0.005 µM dans la OOZ et entre 0.05 and 1.5 µM dans la PFr. Les concentrations en fer dissous variaient entre 0.1 et 0.5 nM (Blain *et al.* 1998).

Table 3. *Résumé des caractéristiques physico-chimiques des différentes provinces biogéochimiques identifiées dans le secteur indien au printemps 1995. Valeurs moyenne, minimale et maximale dans la couche océanique mélangée par le vent sont présentées. Données provenant d' Descolas-Gros & Mayzaud (1997).*

	Régions associées à de la glace de mer		**Régions océaniques ouvertes**	
	CCSZ	**MIZ**	***OOZ***	**PFr**
Nombre de stations		2	5	1
Température, °C		-1.8 - -1.3	2.3 - 3.2	2.3
Couverture de glace de mer, %		?	0	0
Couche océanique mélangée par le vent, m		**53** (25 - 80)	**118** (80 - 150)	**120**
NO_3, µM		**27.4** (27.9 - 28.8)	**26.7** (26.7 - 28.8)	**26.5**
PO_4, µM		**2.3** (2.1 - 2.4)	**2.0** (1.9 - 2.1)	**1.8**
SiO_3, µM		**41.5** (37.9 - 45.0)	**26.0** (17.9 - 32)	**13.9**
NH_4, µM		**0.25** (0.04 - 0.5)	**0.05** (0.00 - 0.12)	**0. 07**

Lors de la campagne océanographique réalisée dans la même région à la fin de l'été, l'aire marine d'étude était totalement libre de glace depuis un mois. Dans cette région de l'océan Antarctique, la retraite maximum de la couverture de glace dans cette région a lieu à la fin février (Hellmer & Berch 1985). La stabilité de la couche océanique mélangée par le vent diminuait du sud vers le nord, ainsi sa profondeur augmentait de 70 m en moyenne dans les régions associées à la banquise à 120 m dans la FZ (Table 4). Comme au printemps, un gradient des concentrations en nutriments , nitrate (23 à 29 µM NO_3), phosphate (1.55 à 1.95 µM PO_4) and silicate (3.5 à 45.1 µM SiO_3), était observé du nord vers le sud. Comme attendu, les concentrations en ammonium étaient d'un ordre de grandeur plus hautes que celles mesurées au printemps. La distribution spatiale de l'ammonium montrait des concentrations élevées aux stations situées les plus au sud (0.7 µM) et dans le front polaire (0.5 µM) (Semeneh 1997). Les concentrations en fer dissous

total (non filtré) étaient particulièrement élevées par rapport à celles mesurées le long de la même radiale au printemps, elles variaient de 0.9 à 2.0 nM (Sarthou *et al.* 1997).

Table 4. *Résumé des caractéristiques physico-chimiques des différentes provinces biogéochimiques identifiées dans le secteur indien en fin d'été 1994. Valeurs moyenne, minimale et maximale dans la couche océanique mélangée par le vent sont présentées. Données provenant de Fiala (1995) Données de fer provenant de Sarthou et al. (1995)*

	Régions associées par de la glace de mer		**Régions océaniques ouvertes**	
	CCSZ	**MIZ**	***OOZ***	**PFr**
Nombre de stations	2	5	4	2
Température, °C	0.1	0.7 - 1.5	2.3 - 3.2	4.1 - 5.3
Couverture de glace de mer, %	?	0	0	0
Couche océanique mélangée par le vent, m	**75**	**55** (50 - 75)	**110** (80 - 120)	**120**
NO_3, µM	**27.1**	**28.0** (27.5 - 28.6)	**26.2** (25.5 - 27.1)	**24.0** (23.4 - 24.6)
PO_4, µM	**1.75** (1.7 - 1.8)	**1.8** (1.7 - 1.9)	**1.7** (1.5 - 1.8)	**1.7** (1.6 - 1.8)
SiO_3, µM	**45.1**	**37.4** (31.1 - 47.7)	**15.1** (11.1 - 25.8)	**6.4** (3.5 - 9.2)
NH_4, µM	**0.64** (0.57 - 0.70)	**0.38** (0.25 - 0.45)	**0.4** (0.2 - 0.5)	**0.5**
Fe, nM	1.8 (n=1)	0.9-1.1(n=2)	2 (n= 1)	1.2 (n=1)

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Chapitre 3

Communautés microbiennes des glaces de mer et interaction avec les communautés microbiennes planctoniques

RESUME- La composition microbienne - incluant les micro-algues, les bactéries et les protozoaires - ainsi que l'activité métabolique potentielle du compartiment autotrophe étaient mesurées en décembre 1988 dans plusieurs micro-environnements caractérisant le secteur nord-ouest de la zone marginale de fonte de la banquise dans la mer de Weddell; "infiltration" et "band" assemblages de la glace de mer ainsi que les eaux adjacentes étaient examinés.

Au moment de la fonte de la glace de mer, la composition algale changeait d'une population dominée par des diatomées dans la glace vers une population dominée par des flagellés dans les eaux adjacentes. Cette modification de la population algale n'était néanmoins pas due à l'inhabilité des diatomées des glaces de croître dans les eaux adjacentes. Le broutage par le métazooplancton et/ou la sédimentation affectant préférentiellement les diatomées ont été suggérés comme causes possibles expliquant la disparition sélective des diatomées durant la fonte des glaces dans cette région de l'océan Antarctique. Les flagellés autotrophes relâchés de la glace lors de sa fonte pourrait par contre ensemencer significativement les eaux adjacentes et permettre la formation d'efflorescence nanophytoplanctonique à la retraite de la banquise.

La biomasse abondante d'organismes hétérotrophes tel que les bactéries et les protozoaires dans la banquise suggère la présence d'un réseau microbien actif dans la glace. D'autre part, il semble que ces organismes hétérotrophes soient peu affectés par le broutage ou la sédimentation, ce qui résulte à une augmentation relative de la biomasse hétérotrophe par rapport à la biomasse autotrophe dans les eaux adjacentes à la banquise.

Microbial communities from the sea ice and adjacent water column at the time of ice melting in the northwestern part of the Weddell Sea

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ABSTRACT- Microbial composition - including microalgae, bacteria and protozoans - and potential metabolic activity of its autotrophic compartment were measured in December 1988 in several micro-environments that characterize the North-West Sector of the marginal area of the Weddell Sea; infiltration and band assemblages of ice floes and adjacent waters were investigated. At the time of ice melting, a shift from a diatom dominated population (ice) to a flagellate dominated population (water column) was observed.
Nevertheless. this shift was not due to an "inability" of the ice-diatoms to grow in the water column. Macrograzing and/or sedimentation are suggested as possible causes of the disappearance of diatoms during ice melting. The remaining small autotrophic forms released by the ice would constitute a significant seeding stock for the growth of ice-edge blooms.

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INTRODUCTION

The annual sea ice of the Southern Ocean provides suitable microhabitats for microalgae (Whitaker 1977, Ackley *et al.* 1979, Palmisano & Sullivan 1983, Horner 1985, Garrison *et al.* 1986, Garrison & Buck 1989b), heterotrophic flagellates and other protozoans (Garrison & Buck 1989a, 1989b, Buck *et al.* 1990, Garrison & Gowing 1992), as well as bacteria (Sullivan 1985, Kottmeier & Sullivan 1987, Kottmeier *et al.* 1987). Indeed the sea ice offers a set of physicochemical conditions for microorganisms living in close association with it, either attached to ice crystals or suspended in the interstitial water between ice crystals (Horner 1985).

When released from the ice upon melting, the fate of ice-associated algae may be variable: part of the algae settles down (Schnack *et al.* 1985, von Bodungen *et al.* 1986), part is grazed by pelagic herbivores such as krill (Marschall 1988) or copepods (Fransz 1988), and part survives in the water column (Garrison & Buck 1985). The latter part should constitute an inoculum for ice-edge blooms that grow in the shallow, stable water column induced by the melting of pack ice (Garrison *et al.* 1986, 1987, Fryxell & Kendrick 1988, Smith & Nelson 1985, 1986, Sullivan *et al.* 1988). Accordingly, many of the nano- and microheterotrophic species are common to both ice and water (Garrison & Gowing 1992), and those which seem to grow in ice after their initial incorporation (Garrison & Buck 1989b) may produce an inoculum in the water column at the time of ice melting (Garrison & Gowing 1992).

This study presents data concerning the structure of microbial communities originating from sea ice biota at the time of ice melting during the period of retreat of the ice edge. We have compared microbial inhabitants (microalgae, bacteria and protozoans) of several ice environments and adjacent water columns in the Weddell Sector of the Antarctic Ocean.

The possible genesis of an ice edge bloom through the release of living cells seeded into the water column depends not only on the physical properties of the adjacent water column, but also on the ability of the released ice-algae to be metabolically active. Thus, the potential activity of the primary producers released by the melting process also bas been tested in a simulated seeding experiment under controlled conditions in filtered seawater.

MATERIAL AND METHODS

Sampling

Samples were collected during the European expedition EPOS leg 2 on board R/V POLARSTERN from 22 November, 1988, to 9 January, 1989.

Three sites were investigated in December 1988 in the marginal ice zone of the northwestern Weddell Sea in an area extending from 47° to 49°W between 61° and 62°S (Fig. 1A and B).

Referring to the terminology proposed by Horner *et al.* (1988), results presented here only concern the infiltration assemblage located at the snow-ice interface of floes (Stations 169 and 194), and the band assemblage which appeared as a brown colored band in the middle (60 to 80 cm from the top of the ice floe) of cores taken at Station 178 (Fig. 1C). Bottom assemblages were inconspicuous in the study area. To reduce osmotic shock (Garrison & Buck 1986), ice samples were melted in sterile, filtered seawater in the dark prior to fixative addition or experiment start. Ice assemblages were sampled randomly. For comparison between ice and water environments, samples of seawater were also collected directly under the ice floes.

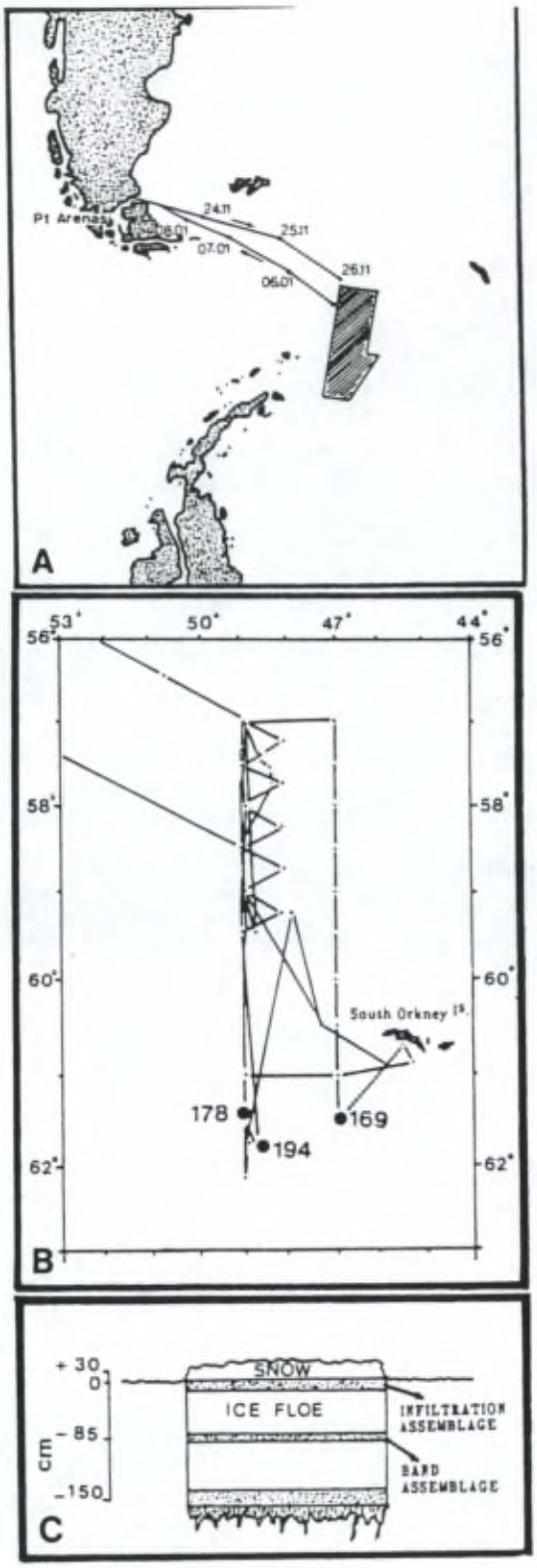

Figure 1. *Sampling area and sites: A. Location of the sampling area in the Southern Ocean; B. Cruise track of Nov. 1988- Jan. 1989 EPOS Leg 2 expedition in the Scotia/Weddell Sea area, showing the ice stations sampled; C. Schematic representation of the sea ice biota sampled with a vertical scale (in cm) of the thickness of ice floes.*

Microscopical analysis

Qualitative and quantitative analysis of plankton was carried out using two different microscopical methods: 1) Microplankton samples (mainly diatoms, ciliates, dinoflagellates), preserved with modified Lugol's solution (Thomas pers. comm.), were analysed in settling chambers using the inverted microscope technique of Utermöhl (1958); 2) Nanoplankton (mainly autotrophic and heterotrophic flagellates) and bacterioplankton samples fixed respectively with glutardialdehyde (0.5% final conc.) and formalin (2% final conc.) were analyzed by epifluorescence microscopy after 4'6 diamidino-2-phenylindole (DAPI) staining according to the procedure of Porter & Feig (1980).

In both methods, cell volumes were calculated from measurements of the dimensions and shapes of cells. In the case of diatoms, cell volumes were converted to carbon biomass according to Edler's (1979) recommendations using a conversion factor of 0.11 pgC μm^{-3}. For ciliates, cell volumes were converted to carbon values using the conversion factor of 0.08 pgC μm^{-3} (Sherr & Sherr 1984). The conversion factor of 0.11 pgC μm^{-3} (Edler 1979) was used for autotrophic and heterotrophic flagellates. Concerning the bacteria, biovolumes were estimated on the enlargements of microphotographs. Conversion into carbon was done using the biovolume dependent C/biovolume ratio proposed by Simon & Azam (1989).

Activity measurements

The experimental determination of photosynthetic parameters involved short-term ^{14}C incubation (Steemann-Nielsen standard method) performed at different light intensities (P-I curves). Bottles (Cel-Cult) tissue culture flasks of 60, 250 and 700 ml were incubated in a water bath with running seawater at in situ temperature illuminated by artificial light. Maximum irradiance reached 135 $\mu mol\ m^{-2}\ s^{-1}$, i.e. very close to the light saturation constant characteristic of Antarctic phytoplankton. ^{14}C incubations were conducted at *in situ* temperature for different fractions of light intensity (0, 1, 4, 6, 15, 20, 40, 60, 100%). Incubation times of 4-6 hours were chosen after a preliminary study of P-I curves for different incubation times. This choice minimizes losses by respiration and increases accuracy. After incubation, samples were filtered on GF/F filters. Radioactivity was measured on the filter (photosynthetic carbon fixation) and in the dissolved organic matter (excretion). However, radioactivity of the latter was never significantly different from that of the background. Excretion was therefore assumed to represent a maximum of 5% of total

photosynthesis. Photosynthetic parameters K_{max}, α, and β were then statistically estimated by means of the Platt *et al.* equation (1980).

RESULTS

Primary producers and potential activities

Figs. 2 and 3 show algal uptake of carbon as a function of irradiance for typical infiltration (Fig. 2A) and band (Fig. 3A) algal assemblages as well as their respective water column phytoplanktonic assemblages (Figs. 2B and 3B). Carbon uptake bas been normalized to "active" carbon biomass calculated from cell counts and biovolume measurements. Thus, only carbon associated with vegetative, healthy autotrophic cells bas been taken into account; this was a necessary correction since resting spores accounted for nearly half (45%) of the total autotrophic carbon in the band assemblage. Photosynthetic characteristics of the biomass populations as computed by statistical fitting of experimental data using the Platt *et al.* equation (1980) are presented in Table 1.

Table 1. *Photosynthetic characteristics of the infi1tration assemblage and the band assemblage (= vegetative cells only, with exclusion of the resting spores) from ice communities and of phytoplankton from the water column. n: number of samples. α: photosynthetic efficiency (h^{-1} ($\mu mol\ m^{-2}\ s^{-1}$)$^{-1}$). K_m: maximal specific rate of photosynthesis (h^{-1}) I_k : index of photoadaptation ($\mu mol\ m^{-2}\ s^{-1}$).*

	n	α	K_m	I_k
Infiltr. Ass.	2	0.00066 + 0.00007	0.049 + 0.003	7 5+ 12.8
Band. Ass	2	0.00018 ± 0.00007	0.012 ± 0.007	62 ±1 5.7
Phytoplankton	6	0.00042 ± 0.00016	0.041 ± 0.014	92 ± 19

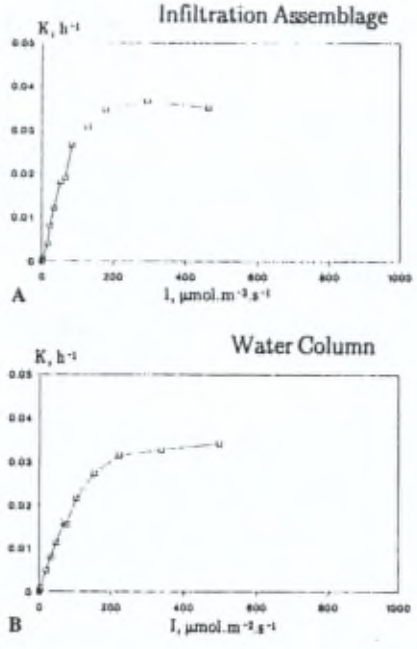

Figure 2. *Photosynthesis-irradiance relationship of natural populations sampled (A) in the infiltration assemblage and (B) in the adjacent water.*

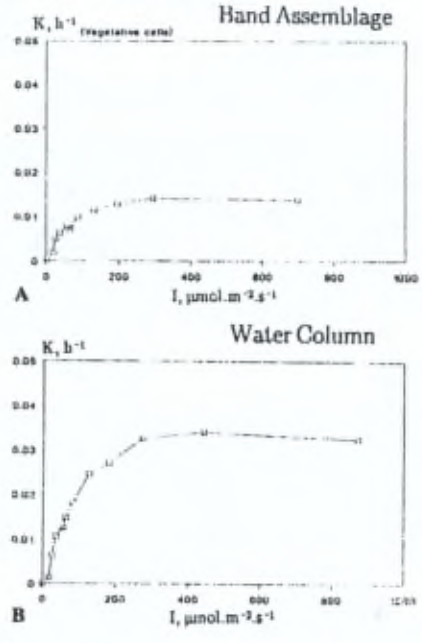

Figure 3. *Photosynthesis--irradiance relationship of natural populations sampled (A) in the band assemblage and (B) in the adjacent water column. For the band assemblage, only vegetative cells have been considered.*

From examination of the P-I curves, it is obvious that, apart from the band assemblages (Fig. 3A), which revealed a low maximum specific rate of photosynthesis (see Table 1, mean K_m = 0.012 h^{-1}), the infiltration assemblages exhibited similar values) (Fig. 2A, Table 1, mean K_m = 0.049 h^{-1}) to those of the water column phytoplankton (Fig. 2B and 3B, Table 1, mean K_m = 0.041 h^{-1}). Photosynthetic efficiencies were in the same order of magnitude for infiltration and water column assemblages, ranging between 0.00066 h^{-1} (µmol m^{-2} s^{-1})$^{-1}$ for the former and 0.00047 h^{-1} (µmol m^{-2} s^{-1})$^{-1}$ for the latter. I_k (index of photoadaptation) values were higher for infiltration and water column assemblages than for the band assemblages, being 75 and 92 µmol m^{-2} s^{-1} for the former, and much lower for the latter (Table 1). Thus photosynthesis-irradiance relationships did not exhibit clear variations between infiltration assemblage and the surrounding water column, and both communities were similarly well adapted to prevailing physico-chemical conditions.

"Taxonomic" composition

The dominant autotrophic taxons present in the different environments, i.e. ice assemblages and the adjacent water column, are summarized in Table 2A. Results are expressed as percentages of total autotrophic cell number.

Table 2. A. *Composition of the autotrophic community encountered in the different environments sampled. Results expressed as percentage of total autotrophic cell number. (-) = negligible.*

Taxon	Infilt. Assembage n=4 Range	mean	Band Assemblage n=2 Range	mean	Water column n= 3 Range,	mean
Pennate diatoms						
Nitzschia sp.	41-94	70.7 ± 15	57-82	70 ± 12.5	9-13	10.3 ± 1.8
Tropidoneis sp.	0-7	2.5 ± 2.5	1.6-2	1.8 ± 0.2	(-)	
Amphiprora sp.	0-1	0.3 ± 0.4	6.5-15	10.8 ± 4.3	(-)	
Centric diatoms	(-)		1.4-32	16.7±15.3	(-)	
Flagellates						
Dinoflagellates	0-2	1.0 ± 1.0	0-2.5	1.3 ± 1.3	2-3	2.7 ± 0.4
Nanoflagellates	0-51	25±13	(-)		85-89	87.8±1.6

Table 2 B. *Composition of the protozoan community encountered in the different environments sampled. Results expressed as percentage of total protozoan cell number. (-) = negligible.*

Taxon	Infilt. Assembage n=4 Range	mean	Band Assemblage n=2 Range	mean	Water column n= 3 Range,	mean
Ciliates	(-)		30-80	55 ± 25	(-)	
Flagellates						
Dinoflagellates	1-5	3.5 ± 1.3	20-70	45 ± 25	1-4	3 ± 1.3
Nanoflagellates	95-99	96.5 ± 1.3	(-)		96 - 99	97 ± 1.3

This table reveals a predominantly algal community with pennate diatoms always dominant in the ice assemblages (mean = 74% for infiltration assemblage; mean = 82% for band assemblage). The diatoms were mainly of the genus Nitzschia (up to 94% of autotroph cell number, e.g. *N. closterium*, *N. cylindrus* , *N. curta*, *N. kerguelensis*), but also genera such as

Tropidoneis and *Amphiprora*, which presented a certain variability within each type of ice assemblage as well as in between the two types studied, were present (Table 2A).

Centric diatoms were scarce - if at all present- in the infiltration assemblages, whereas they accounted for 1.4 and 32% of autotroph cell numbers in the band assemblages, both as vegetative cells and resting spores.

Autotrophic flagellates were not abundant in the ice assemblages, and even if they did reach 51% of the autotrophic cell number (Table 2A) in a particular infiltration sample. Their contribution to the autotrophic total biomass (Table 3A) remained negligible compared to that of diatoms. Thus, the autotrophic composition of the ice assemblages was highly variable and showed a patchy distribution of microalgae, reflecting the heterogeneity of the ice environment.

Table 3. A. *Composition of the autotrophic biomass encountered in the various environments sampled. Results expressed as percentage of total autotrophic carbon biomass. (-) = negligible.*

Taxon	Infilt. Assembage n=4		Band Assemblage n=2		Water column n= 3	
	Range	mean	Range	mean	Range,	mean
Diatoms	78-95	84 ± 5.6	98-99	98.5 ±0.5	19-25	21.3 ± 2.4
Flagellates						
Phaeocystis col.	0-4	1.5 ± 1.5	(-)		(-)	
Dinoflagellates	1-14	6.5 ± 4	0-0.5	0.3 ± 0.5	3-18	10.7 ± 5.1
Nanoflagellates	3-14	7.5 ± 4.5	0.5-1	0.8 ± 0.3	64-72	68.7 ± 3.1
Cyanobacteria	0.3-2.2	1 ± 0.6	(-)		(-)	

Table 3- B. *Composition of the heterotrophic biomass encountered in the various environments sampled. Results expressed as percentage of total heterotrophic biomass. (-) = negligible.*

Taxon	Infilt. Assembage n=4		Band Assemblage n=2		Water column n= 3	
	Range	mean	Range	mean	Range,	mean
Protozoa						
Ciliates	4-13	8 ± 3.6	6.2-69.3	38 ± 31.6	5-10	7.2 ± 2.1
Dinoflagellates	10-55	31 ± 19.7	0-1.3	0.1 ± 0.07	9-32	19.3 ± 8.3
Nanoflagellates	5-41	20 ± 10.6	(-)		19-31	25 ± 4
Bacteria	16-59	41 ± 12.6	29-94	62 ± 32.2	33-67	48.5 ±12.2

In contrast, the composition of autotrophic communities of the adjacent water column was constant and homogeneous, without any conspicuous differences between the different localities. Indeed, *Nitzschia* sp. was the only diatom present, accounting for only 9 to 13% (mean = 10%) of the autotroph cell numbers (Table 2A), whereas the bulk of the autotrophic population consisted of flagellated cells (85 - 89 % autotrophic nanoflagellates including *Cryptomonas* sp., *Pyramimonas* sp., *Phaeocystis pouchetii*; 1 - 3 % autotrophic dinoflagellates). In terms of biomass (Table 3A), diatoms represented about one-fifth of the total autotrophic biomass (range = 19 - 25 %, mean = 21 %). and autotrophic flagellates occupied the remaining four-fifths, with a net dominance of nanoflagellates (range = 64 -72 %, mean = 69 %) other than dinoflagellates (range = 3 - 18 %, mean = 10 %).

Concerning the protozooplankton abundance in the three environments considered (Table 2B), there were no differences between infiltration assemblages and water column assemblages in the composition of the groups, with net dominance of heterotrophic nanoflagellates (95 - 99 % of heterotrophic cell number) over heterotrophic dinoflagellates (1 - 5 %). The biomass of heterotrophic dinoflagellates (Table 3B) was higher (mean = 31 % of total heterotrophic carbon) than that of the heterotrophic nanoflagellates (mean = 20 % of total heterotrophic carbon) in the infiltration assemblages, whereas in the water column, the non-dinoflagellate heterotrophic nanoflagellates dominated the flagellated fraction (see Table 3B). Ciliates were not significant although this group did contribute to some extent to the total heterotrophic biomass (Table 3B), with mean values of 8 % for the infiltration assemblages, and 7 % for the water column.

In the band assemblages, heterotrophic nanoflagellates were present in negligible numbers compared to heterotrophic dinoflagellates and ciliates, which showed a great heterogeneity in their respective distributions (Table 2B).

DISCUSSION

Relative proportions - in terms of biomass - of autotrophs (diatoms, dinoflagellates, nanoflagellates and cyanobacteria) as well as heterotrophs (ciliates, dinoflagellates, nanoflagellates, and bacteria) are shown in Table 4 for both ice and water column communities.

Floristic analysis of the ice assemblages showed a clear dominance of diatoms over other autotrophs (65 - 95 % of total biomass). Moreover, comparison of ice assemblages indicated the presence of resting spores in the band assemblages, suggesting that these might be remnants from a sub-ice algal bloom from the previous year, which were "trapped" in two-year-old ice according to Ackley *et al.* (1979) and McConville & Wetherbee (1983).

In contrast, diatoms in the water column constituted a minor fraction never exceeding 15 % (Table 4) ; the bulk of the biomass was contributed by the autotrophic flagellates (45 to 57 %) with a net dominance of the nanoflagellated fraction (78 - 96 %).

These results seem to contradict observations made by Garrison & Buck (1985), Garrison *et al.* (1986) and Smith & Nelson (1986), all of whom found great similarity among assemblages from ice floes and from planktonic populations, supporting the seeding hypothesis from the ice to the water column. Our results, however, do not exclude the potential role of seeding, but do indicate that other factors (such as early grazing by macrozooplankton) can prevent seeding of the water column assemblages.

Note that unlike Fryxell & Kendrick (1988) who suggested that *Phaeocystis* colonies found in the water column in the same area could have been seeded from the melting ice, *Phaeocystis* colonies were present in two of our infiltration samples where they accounted for 1 and 3% of the total biomass, but no colonies were observed in the surrounding waters.

Table 4. *Composition of microorganisms in the sea ice and adjacent water column samples. Results expressed in percentage of total carbon biomass (autotrophs + heterotrophs). Diatoms R.S. = Resting Spores; Diatoms V C. = Vegetative Cells. (-) = negligible.*

Taxon	Infilt. Assembage n=4		Band Assemblage n=2		Water column n= 3	
	Range	mean	Range	mean	Range,	mean
Autotrophs						
Diatoms R.S.	(-)		12-45	29 ± 16.2	(-)	
Diatoms V.C.	65-93	77 ± 8.7	50-63	56.5 ± 6	11-15	13.4 ± 1.6
Phaeocystis col.	0-3.3	1.2 ± 1.2	(-)		(-)	
Dinoflagellates	1-11	5.6 ± 3.2	0-0.3	0.2 ± 0.2	2-10	6.7 ± 3.2
Nanoflagellates	3-13	6.9 ± 4.3	0.2-1	0.6 ± 0.4	38-50	43.6 ± 4
Cyanobacteria	0.1-1.8	0.9 ± 0.6	(-)		(-)	
Total	**82-97**	**92 ± 4.8**	**76-96**	**86 ± 10**	**60-71**	**64 ± 14.7**
Heterotrophs						
Ciliates	0.1-2.4	0.9 ± 0.7	1.4-2.9	2.2 ± 0.8	1.9-3	2.5 ± 0.4
Dinoflagellates	0.4-4.5	2.1 ± 1.2	0-0.1	0.05 ±0.05	3.8-9	6.5 ± 1.8
Nanoflagellates	0.2-3	1.6 ± 0.7	0-0.6	0.3 ± 0.3	7-12	9 ± 2.1
Bacteria	1.3-11	3.8 ± 3.5	1.3-22	12 ±1 0.4	9-27	18.2 ± 5.9
Total	**3-18**	**8.3 ± 4.9**	**4-24**	**14 ± 31.6**	**29-40**	**36.3 ± 4.9**

In the ice assemblages, the autotroph/heterotroph biomass ratio was quite different from one sample to another, ranging between 3 and 33. In contrast, water samples presented a lower and remarkably constant ratio (1.5 - 2.5). The relative proportions of heterotrophs were always more important in the water column than in the ice environment, although protozoans (including flagellates and ciliates) and bacteria are regular and abundant components of the ice biota (Garrison *et al.* 1986). The abundance of heterotrophs in the ice environment indicates an active food web within the ice community (Garrison & Buck 1989b). In fact, the relative proportions of heterotrophs were greater in the water column since only a part of total autotrophic biomass remained in the water column at the time of ice melting.

This accounts for the shift observed from a diatom dominated population (ice) to a flagellate dominated population (water column) at the time of ice melting. However, as bas been shown previously (Table 1, Fig. 2), this shift cannot be explained by an " inability" of the ice communities, at least for their autotrophic constituents, to grow in the water column, but rather

by an effective disappearance from the water column, either by grazing pressure (macrozooplankton) or sedimentation processes.

Indeed, euphausiids have been shown to follow the retreating ice edge, taking advantage of the elevated food supply when the ice is melting (see Sakshaug & Skjoldal 1989). During the EPOS Leg 2 expedition, Cuzin-Roudy & Schalk (1989) reported an abundance of krill under ice floes, indicating that sea ice can provide a nursery ground for larval krill (Marshall 1988) which feed on particles released by the melting infiltration and band assemblages. Smetacek *et al.* (1990) even presents a hypothetical annual cycle where krill switch from scraping ice algae to filtering phytoplankton. The disappearance of diatoms but not of flagellates does not seem to reflect selection of "species" but rather of particle size.

As seen in Fig. 4, the distribution of autotrophs in the various size ranges is inverted when going from the ice environment to the water column. This figure shows an example of autotrophic biomass distribution in three size ranges (2 - 10 µm, 10 - 20 µm, > 20 µm) for an infiltration assemblage (Fig. 4A), a band assemblage (Fig. 4B) and a water column phytoplanktonic community (Fig. 4C), with separation between diatom and flagellate biomass contribution within each size range. Although krill is capable of feeding on very small particles, large cells are taken more efficiently (Segawa *et al.* 1983, Boyd *et al.* 1984).

Meyer & El-Sayed (1983) also showed the preferential feeding on micro-sized (20-200 µm) particles by krill.

On the other hand, because of the spatial constraint of living in the ice environment, the growth of ice algae can occur in aggregated entities between ice crystals (*Tropidoneis vanheurckii* often aggregated in our samples). These observations are in accordance with experimental results obtained by Riebesell *et al.* (1991) collected during the same EPOS expedition. Being heavier, these aggregates could, together with larger cells, sink out of the surface mixed layer leaving small cells and flagellates in the adjacent water column. In fact, high sedimentation following spring blooms bas been reported as being one of the fates (Schnack *et al.* 1985) if not the dominant one (von Bodungen *et al.* 1986) of ice-edge blooms.

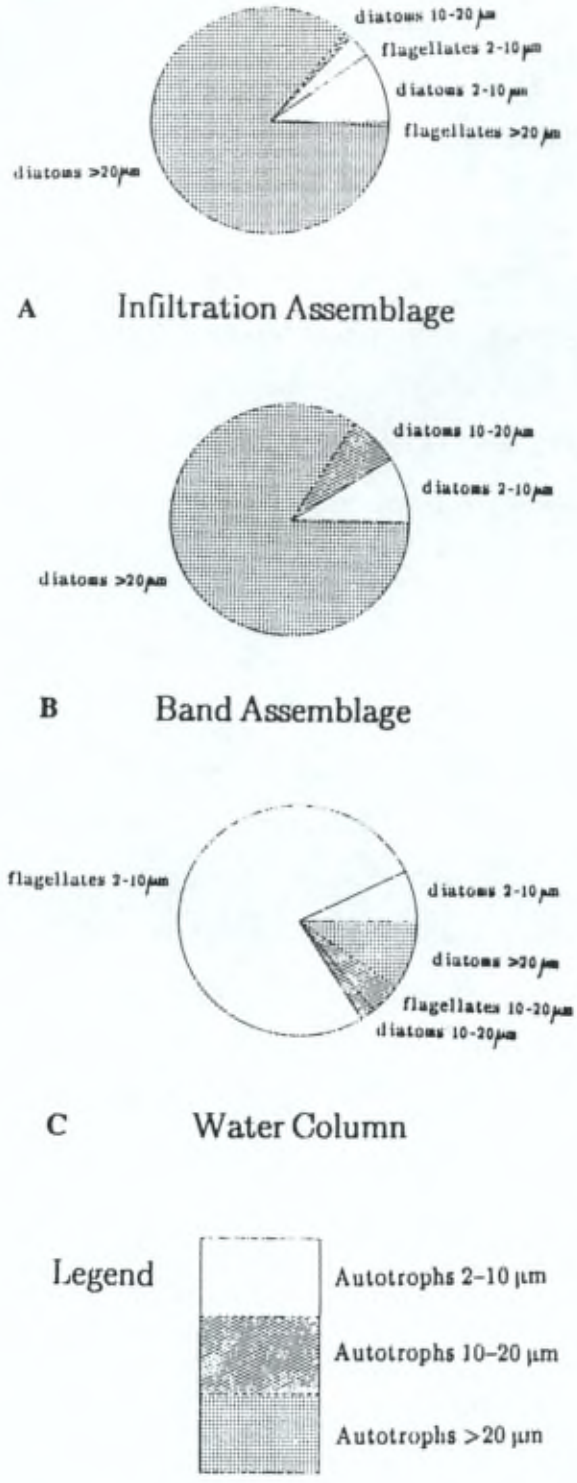

Figure 4. *Composition of the total autotrophic biomass in three size classes of distribution. with distinction between diatoms and flagellates in each size range: A. Infil1tration assemblage 169/1; B. band assemblage 178/1; C. water column assemblage 194.*

In summary, by comparing the floristic composition of the ice environment with that of the water column following ice melting, an obvious shift from a diatom dominated population in the ice environment to a flagellated one in the water column was observed, with an apparently negligible seeding effect of ice algae into the water column. When analyzing the photosynthetic capabilities of these ice algal communities (infiltration assemblages being largely dominant over band assemblages in the area of the Weddell Sea we visited), there is clear evidence that they could grow at the same rate as the water column assemblages. Thus, other factors such as grazing by pelagic herbivores or sedimentation at very early stages during and after melting of the ice might significantly modify the structure of ice-associated microbial communities entering the water column.

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Chapitre 4

Interactions trophiques microbiennes planctoniques

Chapitre 4.1.

Interaction trophique entre le phytoplancton et les bactéries

RESUME- Des séries temporelles des biomasses phytoplanctoniques et bactériennes lors de la retraite de la banquise à plusieurs latitudes dans la mer de Weddell et la baie de Prydz montrent un retard dans le développement bactérien par rapport à celui du phytoplancton. L'utilisation d'un modèle écophysiologique décrivant la dynamique bactérienne (modèle H.S.B.) incluant la dégradation de la matière organique par les bactéries ainsi que la croissance et la mortalité bactérienne, a permis de simuler le développement bactérien dans les zones explorées de l'océan Antarctique. Afin de comprendre la cause du retard du développement bactérien par rapport à celui de phytoplancton, les effets des différents paramètres sur le développement bactérien ont été testés par l'intermédiaire du modèle H.S.B. Les résultats ont suggérés que le non couplage entre les développements phytoplanctoniques et bactériens ne résultait pas des faibles températures caractérisant l'océan Antarctique mais plutôt de la nature macromoléculaire de la matière organique dissoute dérivant du phytoplancton par l'intermédiaire de sa lyse et/ou de sa consommation par le zooplancton.

Phytoplankton-bacteria relationship in the Antarctic marine ecosystem

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ABSTRACT- Time series data of phytoplanktonic and bacterial biomass during the ice retreat period at different latitudes in the Weddell Sea and Prydz Bay areas show a distinct delay in the development of bacteria with respect to phytoplankton. Use of a general ecophysiological model of bacterial growth, along with direct in situ measurements of growth and mortality rates, allowed the simulation of the observed timing of bacterial development. It is suggested that the uncoupling between phytoplanktonic and bacterial development at the earliest stage of the spring ice-edge related algal bloom is not the result of the low temperatures occurring in the Southern Ocean but rather is due to the macromolecular nature of the dissolved organic matter released from phytoplankton.

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INTRODUCTION

That planktonic bacteria directly depend on phytoplankton in aquatic systems devoid of allochtonous input of organic matter is now widely recognized. Evidence for this statement is provided by the correlation which exists between bacterial biomass and chlorophyll a concentration (Linley *et al.* 1983, Bird & Kalff 1984) or between bacterial production and both chlorophyll a concentration and planktonic primary production (Cole *et al.* 1988), over a large range of temperate and tropical aquatic environments. However, the exact nature of the trophic relationship between phytoplankton and bacteria is still a matter of controversy. Exudation by algae of low molecular weight photosynthates bas long been considered as the dominant dissolved organic carbon (DOC) flux to heterotrophic bacteria (Larsson & Hagström 1979, Wolter 1982, Moller Jensen 1983). Recently, however, Björnsen (1989) suggested that exudation should be interpreted as a passive leakage of small metabolites across cellular membranes and should represent no more than 1 - 5 % of phytoplankton biomass per day (0.0005- 0.002 h^{-1}). Other processes producing DOC therefore probably account for an additional and often dominant part of the organic matter transfer to the bacterial compartment, as e.g. direct lysis of phytoplankton cells (Jassby & Goldman 1974, Billen 1984) or rapid diffusion from incompletely digested fecal material of macro- or micrograzers (the so-called sloppy feeding of Lampert 1978) (Jumars *et al.* 1989). These processes mainly produce dissolved organic substances with high molecular weight which require extracellular hydrolysis before they can be taken up by bacterioplankton. For this reason, a looser coupling between bacteria and phytoplankton can be expected in situations where the latter processes of DOC-supply are dominant rather than in situations where bacteria live mainly on algal exudation products (Billen 1990).

How these ideas apply to polar systems at low temperatures is the subject of this paper. Contradictory observations bave been published in previous literature concerning the role of bacteria in Arctic and Antarctic marine ecosystems. Some authors (Hodson *et al.* 1981, Azam *et al.* 1981, Hanson & Lowery 1983, Hanson *et al.* 1983, Sullivan *et al.* 1990) reported measurements of bacterial activities in the Antarctic ocean of the same order of magnitude as those observed in temperate seas. They concluded that the microbial loop performs a similarly important role in the Antarctic marine system as in temperate and tropical systems. On the other hand, situations with high phytoplanktonic biomass and low bacterial numbers and activities bave been reported in both the Arctic and Antarctic systems (Kriss *et al.* 1969, Sorokin 1971, Mullins & Priddle 1987, Davidson 198S, Pomeroy *et al.* 1990).

Pomeroy & Deibel (1986) explained this by a dramatic decrease of bacterial activity below 2°C, while algae continued to be active at these temperatures. This could explain the preservation of DOC, which bas sometimes been found in high concentrations in Antarctic waters (Bolter & Dawson 1982). This organic matter would then be exported to lower latitudes by deep oceanic circulation (Sorokin 1971).

As observations of low bacterial activity most often concern early spring situations, a possible explanation reconciling these contradictory observations may be that a time lag exists in the response of bacterioplankton to algal development. Only rather one time-series observations could confirm this hypothesis. Such time series are difficult to obtain, however, for obvious logistic reasons. In this paper we present such data on phytoplankton and bacterioplankton development obtained during the period of ice retreat in two sectors of the Antarctic Ocean. We discuss them in the light of a simplified ecophysiological model of bacterioplankton development.

BIOTOPES AND METHODS

The two data sets used in this paper result from the participation of Belgian teams, in an Australian cruise to Prydz Bay area (Marine Science Voyage 7 of the Australian Antarctic Division on board of the *R/V NELLA DAN*) and in the European EPOS cruise to the Weddell Sea, on board the *R/V POLARSTERN* (Fig. 1).

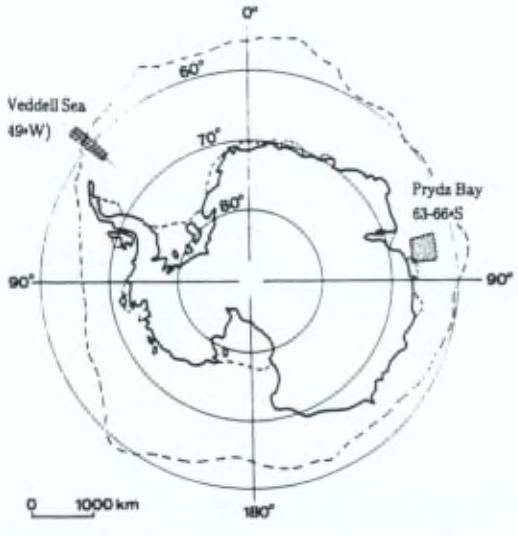

Figure 1 *The two areas in the Southern Ocean where the data sets discussed in this paper were collected.*

The Prydz Bay area was first visited in mid-January 1987 by Joiris *et al.* (1987) on board the R/V MARION DUFRESNE during the French Indigo III cruise. At that time, the position of the ice edge was about 65°S. From mid-February to end-March 1987, the area between 62 and 66°S was free of ice. In the Weddell Sea area, several successive transects along the meridian 49°W were sampled from mid-November 1988 to the beginning of January 1989. The ice edge location varied during this period from about 60°S to 61.5°S.

Chlorophyll a determinations were carried out according to Lorenzen (1967). Conversion into carbon biomass was made by using a constant C/ Chlorophyll a ratio of 30. This represents the median value derived from comparison of chlorophyll a determination and algal carbon content calculated from microscopic cell size determination using Edler's (1979) formulas (Mathot pers. comm.).

At most stations, samples were taken at la, 20, 40, 60, and 120 m depth. The results reported here are the means of the duplicate determinations performed at the depths located in the upper homogeneous layer, as determined from the CTD vertical profile (range 15-50 m). For only a few stations, samples were only taken at l0 m depth. In these cases the results reported are the means of the duplicate determinations.

Bacteria were enumerated by epifluorescence microscopy after either acridine orange (Hobbie *et al.* 1977) (Prydz Bay data) or DAPI staining (Porter & Feigh 1980) (Weddell Sea data). Biovolumes were estimated on enlargements of microphotographs. Conversion into carbon biomass was done using the biovolume dependent C/biovolume ratio proposed by Simon & Azam (1989). Differences in the bacterial biomass values reported here for the Prydz Bay area with previously reported values (Lancelot *et al.* 1989) originate from the use of this new conversion factor.

Bacterial production rates were measured according to the ^{3}H-thymidine incorporation method of Fuhrman & Azam (1982). ^{3}H-thymidine was added at a final concentration of l0 nmol l^{-1}, a concentration shown saturating for the process of incorporation. The uptake of radioactivity in the cold TCA fraction was determined after 3-4 hours incubation. Empirical calibration with cell number increase in 0.2 µm filtered seawater reinoculated with 2 µm filtered water (Riemann *et al.* 1987) was carried out several times at both sites. The conversion factors were 5.0 10^{9} and 1.25 10^{9} cells/nmol thymidine incorporated in the Prydz Bay area and the Weddell Sea, respectively.

Maximum growth rate of bacteria was measured after addition of a mixture of amino acids and monosaccharides in the following final concentrations: glucose (4 mg l^{-1}), galactose (4 mg l^{-1}), casamino acids (15 mg l^{-1}), ammonium acetate (1.5 mg l^{-1}), ammonium hydrogenophosphate (2.5 mg l^{-1}).

Bacterial mortality was estimated according to the method developed by Servais *et al.* (1985, 1989). The part of grazing in overall mortality rate was estimated by comparing the mortality rate of an untreated sample with a sample filtered through a 2 µm membrane and treated with a colchicine and cycloheximide (concentration 100 and 200 mg l^{-1}, respectively) (Becquevort *et al.* unpublished data).

RESULTS AND DISCUSSION

Relationship between bacterial and phytoplanktonic biomass

When plotted against each other, no distinct relationship is apparent between bacterial and phytoplankton biomass (Fig. 2a) as would be expected in the case of a direct response of bacteria to phytoplankton.

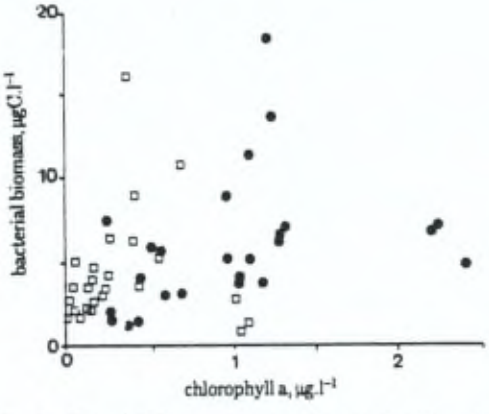

Figure 2a. *Bacterial biomass plotted against chlorophyll a values in the Weddell Sea (closed circle) and Prydz Bay (open circle) area during the period of ice retreat.*

Data from successive situations in the same area, however, describe counterclockwise trajectories, indicating that phytoplankton development precedes bacterial response by about 15-30 days (Fig. 2b).

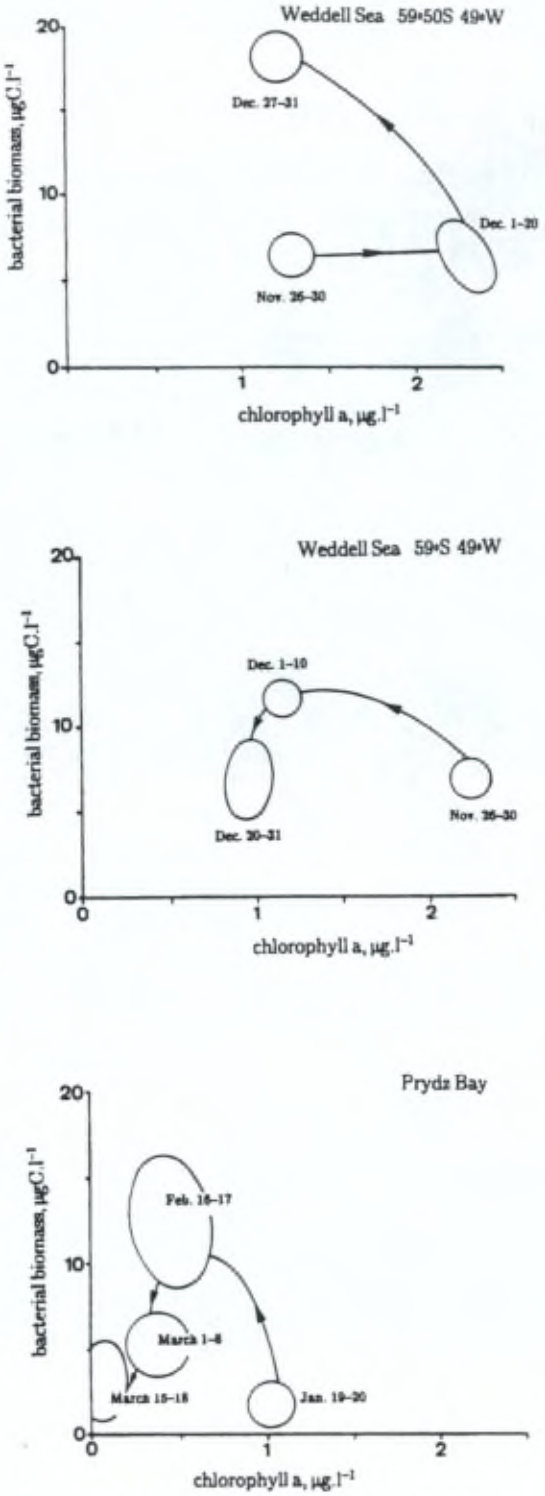

Figure 2b. *Counterclockwise trajectories of bacterial and phytoplankton biomass values at 3 sites in the Southern Ocean. The counterclockwise trajectories indicate a delayed response of bacteria to algal development.*

This delay in the bacterial response to phytoplankton is quite clear in the Prydz Bay data set, which shows a clear chlorophyll maximum in mid-January, while bacterial biomass peaks only about one month later (Fig. 3).

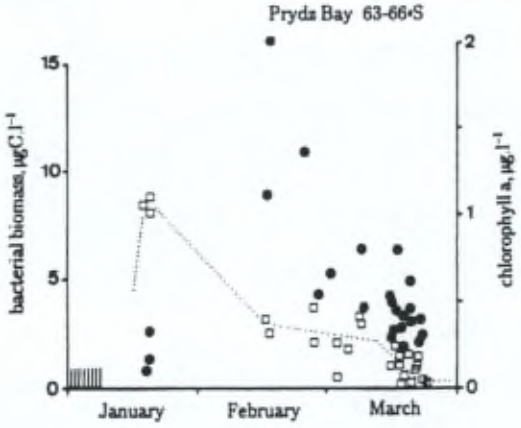

Figure 3. *Temporal variations of chlorophyll a (open square) and bacterial biomass (closed circle) during the 1987 ice-retreat period in an area of Prydz Bay between 62 and 66°S.*

In the Weddell Sea data set, a delay is also quite apparent in the response of bacteria to the algal bloom which follows the southward retreat of the ice edge (Fig. 4).

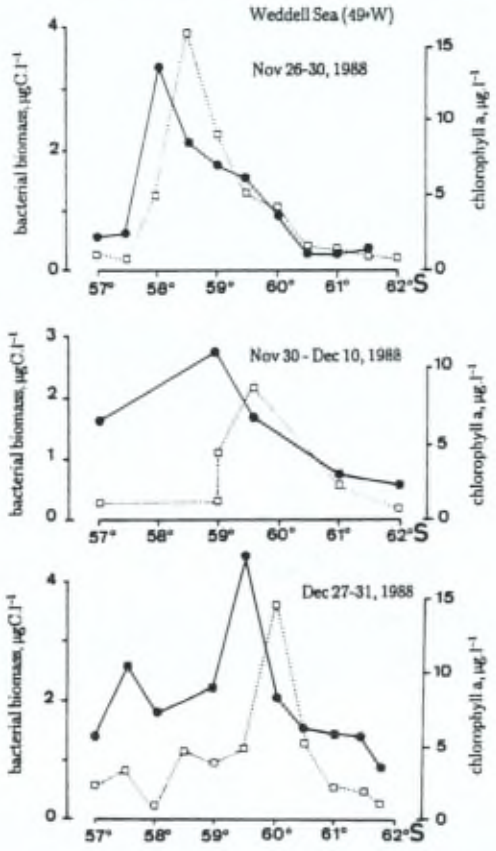

Figure 4. *N-S transects of chlorophyll a (open square) and bacterial biomass (closed circle) values observed at different times during the 1989 ice retreat period in the Weddell Sea area (meridian 49°W).*

Growth and mortality rates of bacterioplankton

Specific growth rate of bacteria, as estimated by the ratio between thymidine incorporation measurements during 4 hours incubation at in situ temperature and bacterial biomass, varied between 0.05 and 0.001 h^{-1}. An immediate increase of this growth rate was observed when amending the samples with a mixture of amino acids and monosaccharides at a final concentration of 10 mgC l^{-1} and a C : N : P ratio of 16 : 4 : 1 by weight. We considered that the value of the specific growth rate measured with this amendment represents the maximum growth rate of the natural bacterial assemblage. Use of short incubation times (4 hours) minimizes the risk of modifications in the bacterial populations.

Fig. 5 shows the value of this maximum growth rate measured at different incubation temperature for samples from the Weddell Sea and the Prydz Bay area. Also shown are the results of similar measurements carried out in the Belgian coastal zone of the North Sea (Billen 1990).

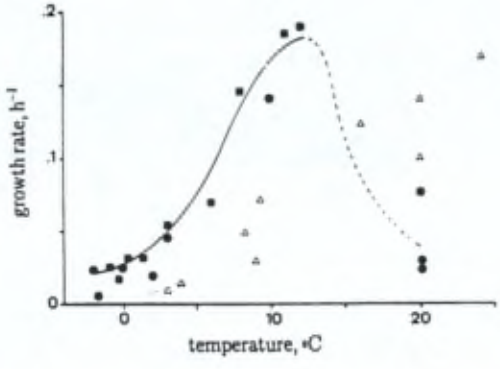

Figure 5. *Maximum specific growth rate of natural assemblages of antarctic bacteria as determined by short term thymidine incorporation measurement after amendment with direct monomeric substrates. as a function of incubation temperature. Closed circle = Prydz Bay; closed square = Weddell Sea. Also shown are the results of similar determinations carried out on bacterial assemblages from the Southern Bight of the North Sea (open triangle).*

Clearly, the temperature range of the Southern Ocean (-2 to +2°C) is suboptimal for bacterial growth, in contrast to what is observed for phytoplankton growth (see e.g. Lancelot *et al.* 1989). Nevertheless, when compared with the temperature response of bacterial communities at temperate latitudes, a remarkable adaptation to lower temperatures is found in Antarctic bacteria, with an optimum temperature 18°C lower with respect to the former. Antarctic bacteria at negative temperatures are able to grow as fast as North Sea bacteria in early spring conditions (8-10°C). Measured rates of bacterial mortality in the two areas studied are remarkably constant, varying between 0.002 and 0.005 h^{-1} in the range -2 to +2°C. A clear effect of temperature on

mortality rate bas been observed (Fig. 6). Grazing by protozoans contributed to 22 to 100% of the total bacterial mortality.

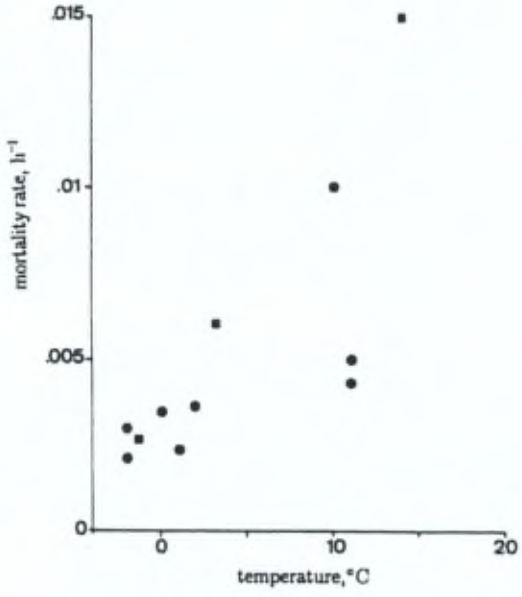

Figure 6. *Grazing rate of natural bacterial assemblages of the Weddell Sea (closed circle) and the Prydz Bay (closed square) as a function of temperature.*

Modeling bacterial response to phytoplankton development

In order to better understand the causes of the delay observed in the bacterial response to phytoplanktonic development in the Antarctic ecosystem, we used an idealized model of bacterioplankton dynamics, described and justified in details elsewhere (Servais 1986, Billen & Fontigny 1987, Billen & Servais 1989, Billen 1991). The basic assumption of this model is that bacterial growth rate is directly dependent on the concentration of small, monomeric substrates, while most of the DOC is under the form of macromolecules requiring extracellular hydrolysis. Uptake of direct substrates is assumed to obey an overall Michaelis-Menten kinetics (Parsons & Strickland 1962, Wright & Hobbie 1965). A constant fraction Y of the amount of substrate taken up is used for biomass production, the remaining part being respired (Servais 1986).

Extracellular hydrolysis of biopolymers was also shown to obey a Michaelis-Menten kinetics (Somville & Billen 1983, Somville 1984). Bacterial exoenzymes are mostly attached to bacterial envelopes and are present in constant amount with respect to biomass (Fontigny *et al.* 1987).

Servais (1986) showed that it is possible to describe the bacterial utilization of phytoplanktonic derived organic matter by assuming that it is made of two fractions (Hl, H2) with different

susceptibilities to extracellular hydrolysis, hence different parameters of their Michaelis-Menten degradation kinetics. The process of bacterial mortality can be represented, as a first approximation, by a first order kinetics (Servais *et al.* 1985).

The following equations can therefore be written for describing the dynamics of bacterial growth :

$$\frac{dH_1}{dt} = -e_{1max}\frac{H_1}{H_1 + KH_1}B + pH_1 \quad (1)$$

$$\frac{dH_2}{dt} = -e_{2max}\frac{H_2}{H_2 + KH_2}B + pH_2 \quad (2)$$

$$\frac{dS}{dt} = e_{1max}\frac{H_1}{H_1 + KH_1}B + e_{2max}\frac{H_2}{H_2 + KH_2}B - b_{max}\frac{S}{S + K_S}B + P_{ex} \quad (3)$$

$$\frac{dB}{dt} = Yb_{max}\frac{S}{S + K_S} - k_dB \quad (4)$$

where

e_{1max}, e_{2max} are the maximum rates of polymers hydrolysis per unit bacterial biomass

KH_1, KH_2 are the half-saturation constants of polymer hydrolysis;

pH_1, pH_2 are the rate of production of polymers through phytoplankton lysis;

b_{max} is the maximum rate of substrate uptake by bacteria;

K_s is the half-saturation constant of substrate uptake ;

Y is the growth yield;

k_d is the mortality constant;

P_{ex} is the rate of production of direct monomeric substrate through phytoplankton exudation.

The value of most of the parameters involved in these equations bas been determined experimentally.

From the data shown in Fig. 5, the maximum growth rate of bacteria (μmax), and its temperature dependency can be estimated as follows:

$$\mu_{max}(T) = 0.018 h^{-1} \left\{ 0.1 + 0.9 \exp\left[-\left(\frac{T - T_{opt}}{T_i - T_{opt}} \right)^2 \right] \right\}$$

with $T_{opt} = 12°C$

$T_i = 5°C$

The value of Y, in the absence of nutrient limitation, is generally close to 0.3 (Servais *et al.*1987). b_{max} is calculated as $\mu_{max}/Y.K_s$ is taken arbitrarily as 0.01 mgC l^{-1}, as this parameter does not significantly influence the results of the calculations.

The parameters characterizing the rate of exoenzymatic hydrolysis of macromolecules from phytoplanktonic origin bave been estimated as follows, on the basis of experiments in which the kinetics of bacterial degradation of a sonicated and filtered algal culture is measured after inoculation with a natural assemblage of bacteria (Servais 1986; Billen 1990):

$el_{max}(T_{opt}) = 0.75\ h^{-1}$, $K_{H1} = 0.1$ mgC l^{-1}

$e2_{max}(T_{opt}) = 0.25\ h^{-1}$, $K_{H2} = 2.5$ mgC l^{-1}

The same dependence to temperature (T) as described above for μmax bas been considered.

On the basis of experimental determinations of the total mortality rate constant k_d, the following relationship with temperature bas been considered :

$k_d = 0.004\ h^{-1} + 0.0005\ h^{-1} . T.$

On the other hand, it bas been assumed that organic matter is produced by phytoplankton through two distinct processes: (i) exudation, producing low molecular weight substrates (S) at a rate proportional to its biomass (k_{ex}); and (ii) lysis and/or sloppy feeding, producing high molecular weight biopolymers of two classes of utilisability (H_1, H_2) in a ratio 1: 1. In the basic simulation,

k_{ex} bas been maintained at the lowest value suggested by Björnsen (1989) (0.0005 h^{-1}). The rate of DOC production through lysis or sloppy feeding is the only adjustable parameter of the model. Forcing functions for the simulation are the observed variation of water temperature and phytoplankton biomass.

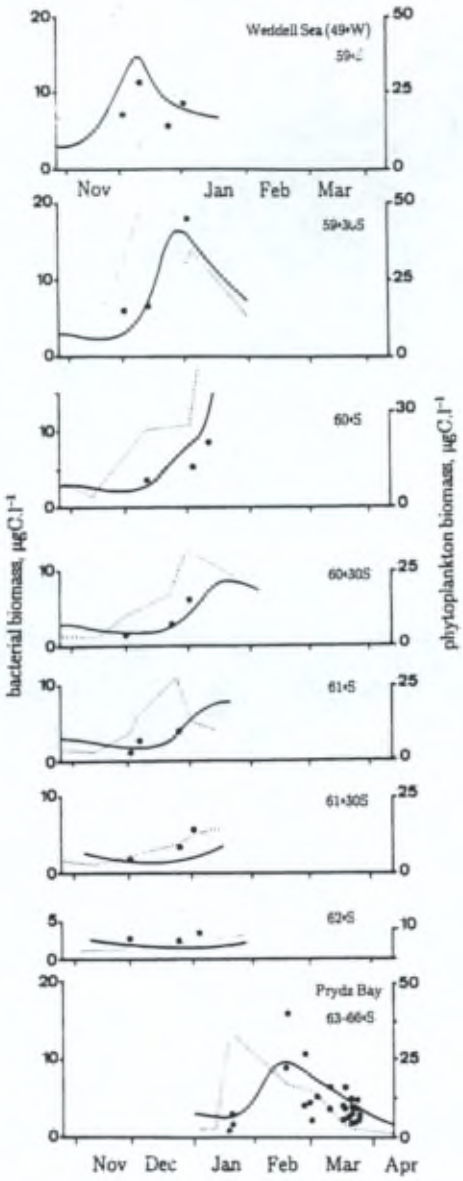

Figure 7. *Simulation of the seasonal variations of bacterial biomass in response to observed phytoplankton development (dotted curve) at different latitudes. according to the HSB model for a single value of the rate of phytoplankton macromolecular DOC release (klys = 0.004 h^{-1}) and a rate of phytoplankton exudation of 0.0005 h^{-1}. The black dots represent the observed values of bacterial biomass.*

Figure 7 shows that the general trends of the observed bacterioplanktonic response to phytoplankton development both in Prydz Bay and in the Weddell Sea can be satisfactorily simulated with a single value of the first order rate constant of macromolecular DOC production

by phytoplankton (k_{lys} = 0.004 h^{-1}). In particular the model predicts a lag of about 10 to 30 days between the peaks of algal and bacterial biomass, as observed.

The rates of bacterial production calculated by the model are compared in Fig. 8 with the measured values. Agreement is generally within a factor of 2, and again, the major trends of geographical and seasonal variations are correctly simulated. As the measurements of bacterial biomass and production rates are quite independent of each other, this overall agreement constitutes a further validation of the model.

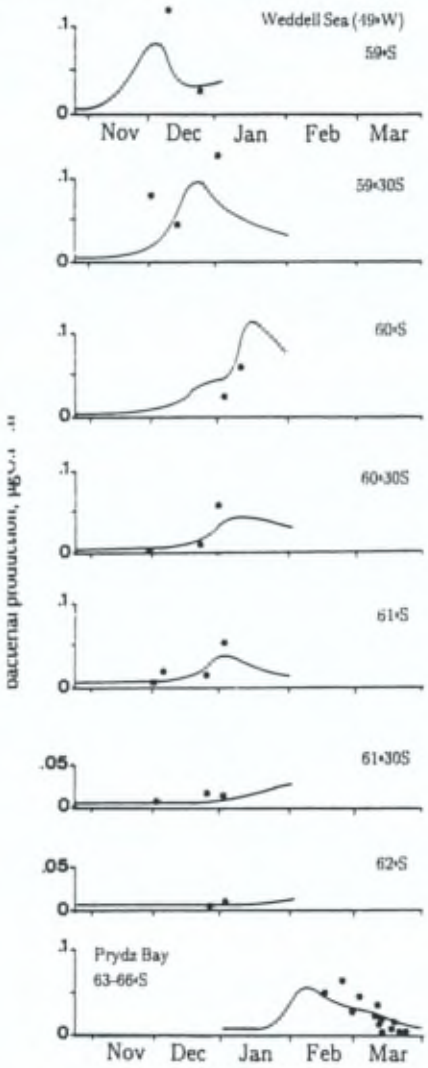

Figure 8. *Simulation of the seasonal variations of bacterial production rate in response to observed phytoplankton development (dotted curve) at different latitudes according to the HSB model for the same values of the parameters as in Fig.7. The black dots represent the observed values of bacterial production rates.*

In order to obtain further insight into the factor responsible for the time lag between phytoplankton and bacterioplankton, the effect of varying some parameters or forcing variables in the model were tested. Fig. 9 shows the effect of increasing the temperature to a constant value of 5°C: the timing of the bacterial development is hardly modified. On the other hand, if the rate k_{ex}

of algal exudation of low molecular weight DOC is increased (at the expense of the production rate of macromolecular material, k_{lys}), the model predicts a much more rapid bacterial response.

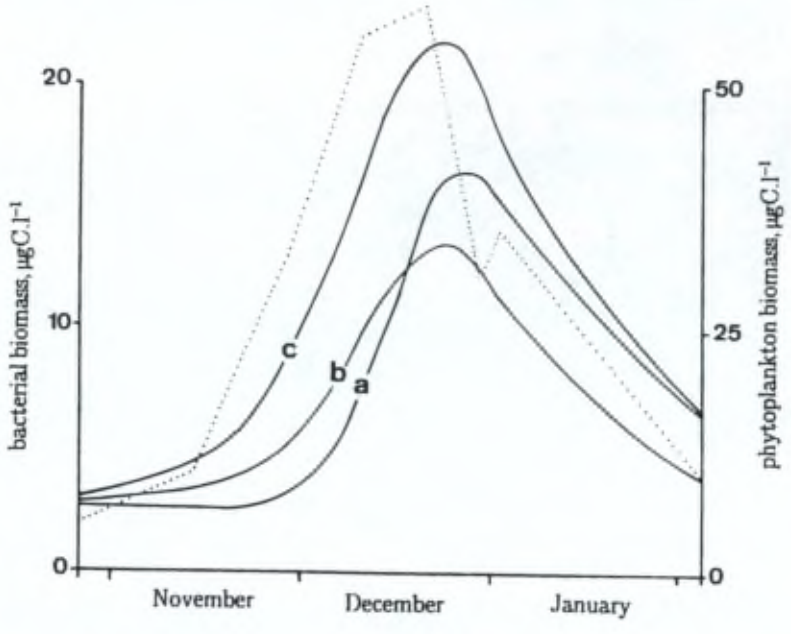

Figure 9. *Simulation of the effect of temperature b) and nature of the organic matter released by phytoplankton c) on the dynamics of bacterioplankton development in the Weddell Sea.*
a) basic simulation. as in Fig. 7. k_{lys} *= O.OO4* h^{-1}*.* k_{ex} *= 0.0005* h^{-1} *observed in situ temperature.*
b) simulation of the effect of increasing the temperature up to 5°C.
c) simulation of increased proportion of algal exudation in DOC release: k_{lys} *= 0.0005* h^{-1}*;* k_{ex} *= 0.004* h^{-1} *observed in situ temperature.*

CONCLUSION

Our observations in the Prydz Bay and Weddell Sea areas have shown clearly that a significant time lag exists in the response of bacterioplankton to the early spring phytoplankton development.

Application of our model of bacterioplankton dynamics, with measured values of the kinetic parameters involved, suggests that this time lag is not the result of a reduction of bacterial activity due to low temperatures. The fact that DOC produced by phytoplankton is mostly under the form of macromolecular material requiring extracellular hydrolysis before being taken up by bacterioplankton is a more likely explanation.

The occurrence of a delay between phytoplankton and bacterioplankton development does not, therefore, appear to be a specific feature of polar systems. Accordingly, a similar, though shorter

delay in bacterioplankton response to the spring phytoplankton bloom bas been also described in temperate marine ecosystems (Billen 1990, Billen *et al.* 1990).

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Chapitre 4.2.

Interactions trophiques entre le bactérioplancton/ le phytoplancton et le protozooplancton

RESUME- Quantifications des biomasses des pico, nano micro-organismes planctoniques - phytoplancton, bactérioplancton et protozooplancton - ont été réalisées lors de 4 campagnes océanographiques; EPOS leg 2 dans la mer de Weddell à la fin du printemps et en été 1988 (**Chapitre 4.2.a.**), ANT X/6 dans le secteur atlantique de l'océan Antarctique au printemps 1992 (**Chapitre 4.2.b.**), ANTARES 2 à la fin de l'été 1994 et ANTARES 3 au début du printemps 1995 dans le secteur indien de l'océan Antarctique (**Chapitre 4.2.c**).

Le réseau trophique microbien était ubiquiste, généralement caractérisé par de faibles biomasses. En effet dans la zone marginale de fonte de la banquise de la mer de Weddell, une efflorescence de flagellés autotrophes était observée. Des efflorescences de diatomées de grande taille initiant la chaîne trophique linéaire étaient des phénomènes très transitoires et localisés dans la zone du front polaire (ANT X/6), dans la confluence des mers de Weddell et d'Ecosse (EPOS leg 2) et dans la zone marginale de fonte de la banquise (printemps, EPOS leg 2).

Au sein du réseau planctonique microbien, les protozoaires constituaientt une biomasse significative (16 - 30 % de la biomasse microbienne totale) principalement dominée par des taxons de la taille du nanoplancton. Parmi ceux-ci, les dinoflagellés hétérotrophes toujours présents de manière significative dans les régions explorées à l'exception du secteur Indien en été, sont des organismes particulièrement intéressants par leur capacité à consommer des particules alimentaires de taille similaire à la leur. Dans des régions dominées par ces organismes, le spectre de taille des particules alimentaires était très similaire à celui du protozooplancton.

Les distributions spatio-temporelle très semblables du protozooplancton et de leur nourriture potentielle (bactéries et phytoplancton < 20 µm) suggèrent de manière indirecte le rôle du protozooplancton dans le contrôle du développement des bactéries et du pico- et nanophytoplancton. Des corrélations significatives entre protozooplancton et de leur nourriture potentielle étaient reportées.

D'autre part par des mesures des taux d'ingestion de nanoflagellés et de bactéries par les protozoaires, réalisées lors des 3 dernières campagnes océanographiques, nous avons pu estimer directement le rôle du protozooplancton dans le contrôle du développement nanophytoplanctonique et bactérien. Le broutage par le protozooplancton contrôlait entre 32 et > 100 % (moyenne des différentes études) de la production bactérienne et entre 28 et 54 % (moyenne des différentes études) de la production phytoplanctonique.

Interactions in the microbial community of the northwestern Weddell Sea of the marginal ice zone through size distribution analysis

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ABSTRACT- Enumeration and identification of planktonic microorganisms (phytoplankton, bacteria, protozoa) were carried out for 16 stations sampled in the marginal ice zone of the northwestern Weddell Sea during sea-ice retreat in 1988 (EPOS Leg 2). From these data, carbon biomass distribution among various classes, chosen according to size and trophic mode, bas been determined. This analysis reveals the general dominance of nano-phytoplankton (74 %), mainly *Cryptomonas* sp. In two stations only, significant microphytoplanktonic biomass occurred. Bacterioplankton biomass was 16 % of the phytoplanktonic biomass. Protozooplankton appeared as a significant group whose biomass represented an average of 23 % of the total microbial biomass. Maximum phytoplankton and protozooplankton biomass was reached at about 100-150 km north of the receding ice edge whilst bacteria did not show marked spatial variations. From these results, indirect evidence for close relationships between protozoa and bacteria, as well as protozoa and autotrophs, is given. The size range of autotrophic prey and predators overlaps (equivalent spherical diameter range = 6 to 11 µm). This size overlapping increases the complexity of the trophic organization of the microbial community. Our results thus support the idea of a flux of energy not always oriented towards an increasing particle size range. Potential ingestion rate, calculated from a mean clearance rate in the literature, indicated that protozooplankton might ingest as high as 48 % of the daily phytoplankton production in the marginal ice zone.

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INTRODUCTION

The intensification of research effort in the Southern Ocean and the application of new methods have considerably revised the classical view of the antarctic food web structure dominated by carbon flow from the large diatoms to krill. Recently, Hewes *et al.* (1985) introduced the concept of an alternate carbon pathway at lower trophic levels in the antarctic food web coexisting in parallel with the classical food chain. In agreement with this, recent studies show that pico- and nano-sized primary (Von Bröckel 1981, Weber and El-Sayed 1987, Hewes *et al.* 1990) and secondary (Miller *et al.* 1984, Sullivan *et al.* 1990) producers are quantitatively important in the Southern Ocean. As a link between these auto-and heterotrophic microorganisms and the grazing zooplankton such as krill, the protozooplankton forms an intermediate group (Nothig 1988, Garrison and Buck 1989, Hewes *et al.* 1990, Garrison 1991). However, there is still little information about the abundance, distribution and activity of protozoa in the antarctic marine ecosystem or about their seasonal and regional variations (see the review by Garrison and Gowing 1992). Moreover, the information available is often scattered due to interest in specific taxonomic groups rather than in the whole community structure, and in numerical abundance rather than biomass estimate. Assessing the role and importance of protozoa in the trophic dynamics of the whole microbial assemblage, however, requires consideration of both biomass and cellular density of various taxonomic groups (Garrison and Gowing 1992). This paper presents data on the abundance and size distribution of planktonic microorganisms (phytoplankton, bacterioplankton and protozoa) in the marginal ice zone of the northwestern Weddell Sea in spring 1988, and gives additional evidence of the importance of the microbial food web in the Southern Ocean. Owing to the release of active sea-ice microbes in very stable surface waters, marginal ice zones have been reported as regions of enhanced biological activity at all trophic levels (Cota *et al.* 1991, Smith and Nelson 1985, 1986, 1990, Schalk 1990, Smetacek *et al.* 1990, Ainley *et al.* 1986). The physical processes operating within the marginal ice zone greatly stimulate primary production by providing phytoplankton with optimum light conditions through the formation of shallow upper layers due to the addition of meltwater (Smith and Nelson 1985, 1986, Lancelot *et al.* 1991). Protozoa from the melting sea-ice (Garrison and Buck 1985, 1989, 1991, Garrison *et al.* 1987, Mathot *et al.* 1991), due to their high potential growth, are therefore expected to quickly respond to the enhanced primary production associated with the receding pack-ice (Garrison and Buck 1989). This hypothesis was tested in this study by analysis of trophic relationships between microbial planktonic organisms. These interactions were indirectly determined from the statistical regression analysis relating taxonomic groups selected

according to their size (pico-, nano- and micro-) and trophic mode (autotroph versus heterotroph).

MATERIAL AND METHODS

Studied area and sampling

Samples were collected during EPOS (European Polarstern Study) Leg 2, in the Scotia/Weddell Sea area of the Southern Ocean from 22th November 1988 to 5th January 1989. This paper refers in particular to two transects performed respectively along the meridian 49°W and 47°W between 59° and 62°S (Fig. 1) as well as to two stations located at 59°S and 61°S which were visited several times during the cruise. During the investigated period. the ice edge moved southwards from 58.5°S in late November to 61°S in early January (Lancelot *et al.* 1991).

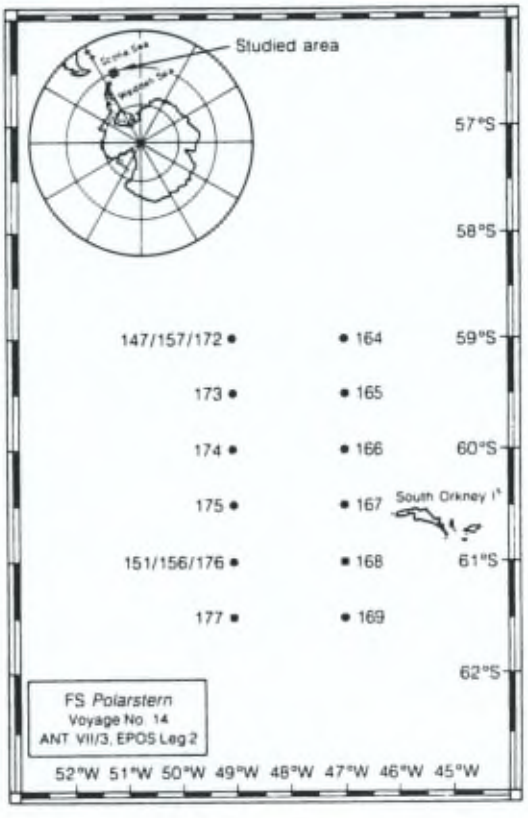


Figure 1. *Partial cruise track of the EPOS Leg 2 (November 1988 January 1989), showing the position of the sampling stations. Inset shows location of the study area in the Southern Ocean.*

Planktonic communities were collected by a Rosette sampler equipped with 12 l Niskin bottles and were preserved with an appropriate fixative immediately after collection. The sampling depth

was chosen as deep enough to prevent any strong influence from the ship's hull but always in the upper mixed layer as given by CTD profiles.

Identification and biomass determination

Due to the broad range of sizes covered by microbial assemblages (0.2-200 µm). Sampling volume, preservation solution and microscopical technique were chosen according to the average size and the trophic mode of selected taxonomic groups. Bacteria, heterotrophic and autotrophic flagellates were examined under an epifluorescence microscope following the method of Porter and Feig (1980). From 2 to 5 ml of water sample were fixed with formaldehyde-40 % (final concentration 2 %) and 10 to 20 ml with glutaraldehyde-25% (final concentration 0.5 %), respectively, for bacteria and flagellates. Both samples were stained with 4'6 diamidino-2-phenylindole (DAPI) and filtered onto Nuclepore black filters (0.2 µm pore size) under a gentle (< 50 mmHg) vacuum (Haas 1982). The filters were rinsed with sterile filtered water, air-dried for 30 s, mounted in paraffin oil and stored in a freezer (- 20°C) until examination. The organisms were observed within 6 months of sampling. Bacteria were counted on a minimum of 20 different fields at 1000x magnification. Biovolumes were calculated by treating rods and cocci, respectively, as cylinders and spheres (Watson *et al.* 1977), and converted to cell carbon by using the biovolume dependent conversion factor established by Simon and Azam (1989). A minimum of 100 flagellates per filter were counted and autotrophs were discriminated from heterotrophs by the red chlorophyll autofluorescence. Cell sizes were measured visually by comparison with an ocular micrometer. Biovolumes were calculated from cells shapes and converted to cell carbon by multiplying by 0.11 pgC μm^{-3} (Edler 1979).

Diatoms and ciliates were analysed in settling chambers using the inverted microscope technique of Utermöhl (1958). Samples were preserved with glutaraldehyde-lugol (35%, v/v) solution (final concentration 10%) and stored in the dark at 4°C until examination (within 9 months of the cruise) with a Fluovert inverted microscope (Leitz). Between 10 and 100 ml of sample were settled for a period varying between 8 and 60 h. Magnification was chosen according to cell size: 400x for cells less than 20 µm, 320x for cells ranging between 20 and 50 µm and 100x or 200x for larger cells. According to Elder's recommendations (1979) and as far as possible, 500 cells per sedimented volume were counted in total, with at least 50 cells of the most abundant species. Cell sizes were measured visually by comparison with an ocular micrometer, and cell volumes were calculated from the stereometric shapes of the cells (Edler 1979). For diatoms, cell volumes were

transformed to plasma volumes by assuming the plasma volume to be a homogeneous layer of 1 µm thickness inside the cell wall. Plasma volumes were converted to carbon values by considering a carbon density of 0.11 pgC μm^{-3} (Edler 1979). For ciliates, cell volumes were converted to carbon values using the factor 0.08 pgC μm^{-3} proposed by Beers and Stewart (1970). Statistical analysis of the results consisted of measuring the Pearson's correlation coefficient(r), i.e. the linear association between the variables which are normally distributed. The significance level of the correlation was tested by the Student test.

RESULTS

Biomass distribution of main taxonomic groups

Average carbon biomass distribution among the principal components of the microbial assemblages of the marginal ice zone of the northwestern Weddell Sea is shown in Table 1. These components were chosen according to size (nano-, micro-) and trophic mode (phyto-, protozoo-, bacterioplankton). Within each trophic mode, the most abundant groups of organisms were considered.

Table 1. *Mean and extreme values of biomass for main microbial groups. Units are µgC l^{-1} * = % of the total microbial biomass*

Organisms	Nano–size (< 20 µm) Mean (min. – max.)	Micro–size (> 20 µm) Mean (min. – max.)	Total Mean (min. – max.)
Phytoplankton			
Diatoms	2.0 (0.1 –18.6)	6.7 (0.0 – 50.3)	8.7 (0.1 – 68.9)
Dinoflagellates	0.5 (0.0 – 2.1)	0.0 (0.0 – 0.5)	0.5 (0.0 – 2.1)
Other flagellates	16.4 (4.4 – 79.1)	0.1 (0.0 – 2.0)	16.5 (0.2 – 79.1)
Total	18.9 (3.4 – 79.3)	6.8 (0.0 – 2.0)	25.7 (7.7 – 79.8)
%	**49**	**17**	**66**
Protozooplankton			
Choanoflagellates	0.1 (0.0 – 0.4)		0.1 (0.0 – 0.7)
Dinoflagellates	1.3 (0.3 – 3.4)	1.3 (0.0 – 7.4)	2.6 (0.7 – 7.7)
Other flagellates	3.4 (0.3 – 20.3)		3.4 (0.3 – 20.3)
Ciliates	0.2 (0.0 – 1.0)	1.6 (0.5 – 6.5)	1.8 (0.5 – 6.7)
Amoeba	1.2 (0.0 – 5.6)		1.2 (0.0 – 5.6)
Total	6.2 (0.7 – 27.6)	2.9 (0.5 – 11.2)	9.1 (1.8 – 29.2)
%	**16**	**7**	**23**
Bacterioplankton	6.2 (0.7 – 27.6)	2.9 (0.5 – 11.2)	4.2 (1.4 – 10.0)
%	**16**	**7**	**11**

Phytoplankton biomass, ranging between 7.7 and 79.8 µgC l^{-1} with a mean value of 25.7 µgC l^{-1}, constituted by far the bulk of the microbial biomass, contributing an average of 66 % of the total microbial carbon (Table 1). Among the autotrophs, the nanophytoplankton were the most important, representing 74% of the total phytoplankton biomass with an average of 18.9 µgC l^{-1}.

As a general trend, flagellates dominated this community (87 %), whilst diatoms constituted the bulk of microphytoplankton (99 %). In one case however (station 147), when a small Chaetoceros was abundant, diatoms significantly contributed to the nanophytoplankton. Naked flagellates identified as *Prasinophyceae*, *Cryptophyceae* and *Prymnesiophyceae* were the dominant autotrophic nanoplankton.

Among these, *Cryptomonas* was the most important genus, contributing most to the bulk of the nanophytoplankton. Centric diatoms constituted the bulk of the microphytoplankton, with *Corethron*, *Thalassiosira* and *Rhizosolenia* being the principal genera.

The protozooplankton accounted for 9.1 $\mu gC\ l^{-1}$, contributing 23 % of the total microbial biomass. On average, it represented 35 % of the phytoplankton biomass. Like the phytoplankton, the protozooplankton was dominated by nano-sized taxa, in which heterotrophic dinoflagellates and other flagellates contributed, respectively, to 29 and 37 % of the total nanoprotozooplankton biomass. The microzooplankton was composed of dinoflagellates and ciliates, the latter constituting 55 % of the biomass of this component.

The bacterioplankton biomass generally varied around 4.3 $\mu gC\ l^{-1}$. On one occasion however (station 157), a particularly high bacterial biomass of 10 $\mu gC\ l^{-1}$ was observed; this was 1.3 times greater than the phytoplanktonic standing stock. This elevated bacterial biomass followed the passage of a krill swarm.

Size spectrum of phyto- and protozooplankton C biomass

Size distributions of microbial carbon biomass were expressed, according to Sheldon and Parsons (1967), on a logarithmic scale of particle diameter, i.e. the calculated equivalent spherical diameter (ESD). Essentially three patterns of phytoplankton size distribution were observed in the investigated area (Fig. 2). At most stations (11 stations out of 16, Table 2), phytoplankton was dominated by organisms for which the ESD ranged between 6 and 10 µm (Fig. 2a). Two stations (stations 147 and 176) clearly displayed a different phytoplanktonic size spectrum characterized by three peaks: one located in the nano-size range, identical to that reported for most of the stations, and two others situated in the micro-size range (Fig. 2b).

Unlike all other stations, three stations (151, 156 and 157) had very low total phytoplanktonic biomass (7.7-14.4 $\mu gC\ l^{-1}$, mean = 11 $\mu gC\ l^{-1}$) and did not show any distinct peak in the phytoplankton size spectrum (Fig. 2c).

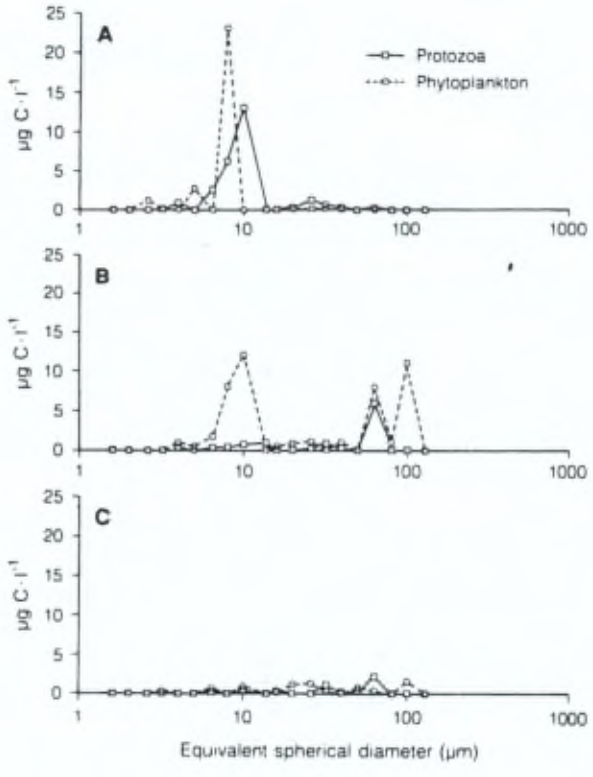


Figure 2A-C. *Typical C biomass (expressed as µg carbon per liter) distribution of phytoplankton and protozooplankton plotted against equivalent spherical diameter. A station 172, B station 176, C station 157.*

The size distribution of protozoa carbon biomass appeared less regular than for the phytoplankton. As a general trend, however, at stations of nano-autotrophic dominance, protozooplankton was also dominated by nano-sized organisms. For those stations, the highest protozooplanktonic biomasses were recorded together with highest nano-sized phytoplanktonic biomasses (Fig. 2a). On the other hand, stations characterized by high biomass of both nano- and micro-sized phytoplankton (stations 147 and 176) were dominated by a peak of protozooplankton in the micro-sized range whilst nanosized protozooplankton were insignificant (Fig. 2b). All the other stations analysed presented low biomasses of protozooplankton equally distributed up to 64 µm ESD (Fig. 2c).

Table 2. *Classification of stations according to C biomass distribution of phytoplankton plotted against equivalent spherical diameter.*
A: see Fig. 2A, B: see Fig. 2B, C: see Fig. 2C.

Stations	A	B	C
Transect 49°W			
147		*	
151			*
156			*
157/6			*
172	*		
173	*		
174	*		
175	*		
176		*	
177	*		
Transect 49°W			
164	*		
165	*		
166	*		
167	*		
168	*		
169	*		

Biomass distribution of auto- and heterotrophic microorganisms and ice retreat

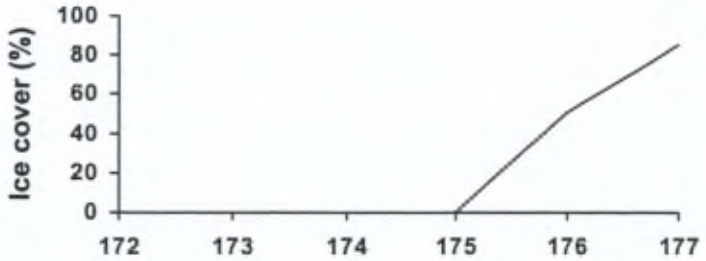
Figure 3 shows carbon biomasses of phytoplankton, bacterioplankton and protozooplankton measured during a 2 day cross-section conducted along meridian 49°W, perpendicular to the ice retreat.

A high phytoplanktonic biomass of 80 µgC l^{-1} was recorded in the area recently free of ice, about 100-150 km north of the receding ice edge (Fig. 3a, b). North as well as south of this maximum phytoplankton position, biomass was very low, particularly in the heavy ice covered areas (more than 80% ice cover) where phytoplankton was about one order of magnitude lower than the observed maximum.

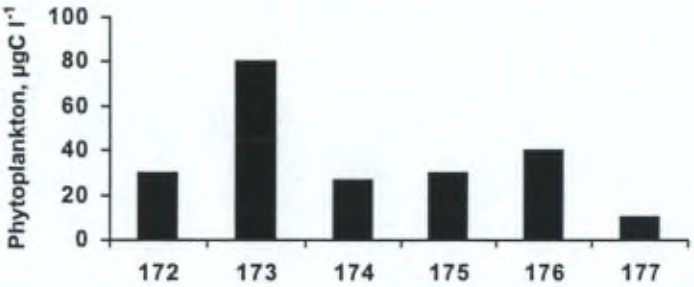
Protozooplankton biomass closely followed phytoplankton biomass by increasing at the time of phytoplankton bloom and maintaining levels during the decline of the autotrophs (Fig. 3b, c). At phytoplankton maxima, protozoan biomass reached 30 µgC l^{-1}, i.e. 26% of the total microbial carbon. At the northern station, however, protozoan biomass was identical to phytoplankton biomass suggesting than these grazers do control phytoplankton development in this area.

Bacterioplankton biomass varied between 2.5 and 5.5 µgC l^{-1} representing, on average, 7% of the total microbial carbon (Fig. 3d). No clear relationship between spatial variation of bacterioplankton and those of phytoplankton and protozooplankton is evidenced by Fig. 3.

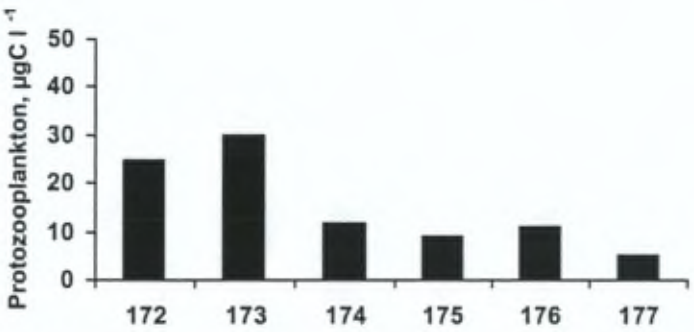
A.



B.



C.



D.

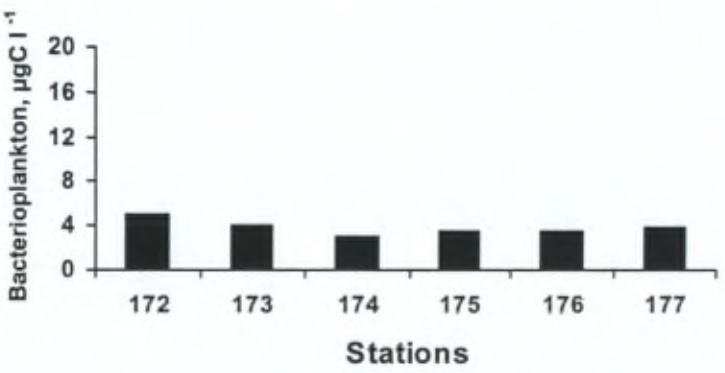


Figure 3A-D. *Distribution of (A) sea ice cover. (B) phytoplankton. (C) protozooplankton and (D) bacterioplankton biomasses along the transect 49°W.*

DISCUSSION

Biomass distributions and interactions in the microbial community

Quantitative analysis of the phytoplankton community of the marginal ice zone of the northwestern Weddell Sea indicates that phytoplankton biomass was maintained at a low level during the period of ice retreat, with values ranging between 7.7 and 79.8 µgC l^{-1}. Maximum values were observed in the marginal ice zone, at about 100-150 km north of the receding ice edge, as is often observed in this area (Smith and Nelson 1986). Accordingly, corresponding chlorophyll a concentrations were generally less than 1µg l^{-1}(Jacques and Panouse 1989, 1991). Taxonomic analysis revealed that low phytoplankton biomass was accompanied by the dominance of nanoplanktonic flagellates (mainly *Cryptomonas* sp., see also Buma *et al.* 1989), in agreement with observations by Hewes *et al.* (1990) in the same area. According to these authors, nanophytoplanktonic forms dominate in regions with low chlorophyll a values (< 1 µg l^{-1}) and the increase in phytoplankton biomass results from an increase of the microphytoplanktonic forms, mainly diatoms. On two occasions (stations 147 and 173), high chlorophyll a concentrations of 2.2 and 2.4 µg l^{-1} were measured (Jacques and Panouse 1989, 1991). However, even though microphytoplankton was an important component of station 147, station 173 was largely dominated by nanoplanktonic forms. Thus, obviously, the ice edge phytoplanktonic blooms can be dominated by either micro- or nanophytoplanktonic forms. According to Jacques and Panouse (1991), the dominance of a nanoplanktonic community results from a heavy grazing pressure on the diatoms and a little appetence of the herbivorous zooplankton for cryptophyceans. The occurrence of nanophytoplankton in the studied area was accompanied by the simultaneous development of protozoa (Fig. 3). Accordingly, a significant positive correlation between protozoa biomass and the combined biomass of phytoplankton and bacteria was found (Fig. 4).

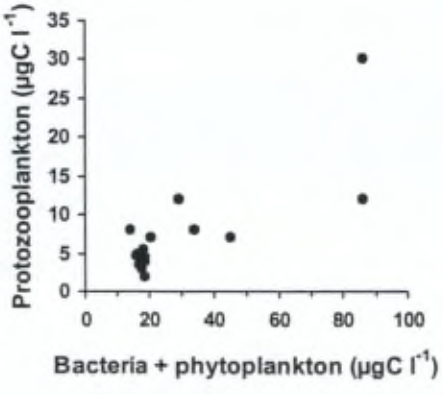


Figure 4. *Relationship between total protozooplankton biomass and combined biomass of bacterio- and phytoplankton. Units are µg carbon per litre. Equation: y =0.54+0.24 x, R =0.85.*

The protozoa contributed 26% of the total microbial carbon (phyto and protozooplankton), and hence must be considered as a key component of the planktonic food web.

The co-occurrence of nanophytoplankton and protozoa seems to be a general feature of the marginal ice zone of the Weddell Sea, with protozoa accounting for 10-58% of the total carbon biomass (Table 3).

Table 3. *Relative abundance of protozoa and particularly heterotrophic flagellates in the Scotia and Weddell Seas.*

% of combined phyto and protozoo plankton biomass	Heterotrophic flagellates fraction (%)	Period	Site	Source
42 – 15	33	January 1985	Southeastern Weddell Sea	Nöthig 1988
16 – 11	50	February 1985	Southeastern Weddell Sea	Nöthig 1988
10 – 2	50	Nov. Dec. 1983	Scotia–Weddell Sea area	Garrison and Buck 1989
10 – 2	71	March 1986	Western Weddell Sea area	Garrison and Buck 1989
33	52	January 1981	Scotia Sea	Hewes et al. 1990
58 – 10	88	June = August 1988	Scotia–Weddell Sea area	Garrison et al. 1992
26 – 10	67	Nov. Dec. 1988	Northwestern Weddell Sea	This study

Table 3 suggests a general dominance of flagellates, including naked flagellates, dinoflagellates and choanoflagellates, contributing 33-88% of total protozoan biomass.

The trophic role of protozoa was indirectly estimated from the correlation analysis of the data presented here.

According to Fenchel (1987) and Longhurst (1989), the size of ingested food depends on the feeding mechanisms of protozoa. To further investigate trophic relationships between consumers and their food, multiregression analysis of each dominant taxonomic group of either nano- or micro-sized protozooplankton on each different potential food resource (bacterioplankton and both nano- and micro-sized phytoplankton) was carried out. Correlation coefficients specific to each food-consumer analysis are given in Table 4.

Table 4. *Correlation analysis between microbial organisms calculated according to the method of Pearson followed by the Student test. Coefficients r and (P) are reported for the significant correlations *P<0.05, **P<0.005, ***P <0.0005; n.s.= not significant (P > 0.05).*

Food resource Consumer	Bacterio–plankton	Nanophyto–plankton	Microphyto–plankton	Total phyto–plankton
Bacterioplankton	–	–	–	n.s.
Nanoprotozooplankton				
Choanoflagellates	0.86***	n.s.	n.s.	n.s.
Other flagellates	n.s.	0.85***	n.s.	n.s.
Ciliates	0.44*	n.s.	n.s.	n.s.
Total	n.s.	0.80**	n.s.	n.s.
Microprotozooplankton				
Dinoflagellates	n.s.	n.s.	0.84***	n.s.
Ciliates	n.s.	n.s.	0.67**	n.s.
Total	n.s.	n.s.	0.95***	0.63**
Total protozooplankton	n.s.	0.83	n.s.	0.68**

In this table, bacteria are considered both as potential consumers of organic matter of phytoplankton origin either produced by excretion or by lysis, and as food for protozoa (Table 4). The lack of correlation between bacterial and phytoplanktonic biomasses indicates either heavy grazing on bacteria as well as on phytoplankton or that the bulk of dissolved organic matter utilizable by bacteria is not provided by direct phytoplankton exudation but rather by phytoplankton lysis (autolysis or diffusion from uncompletely digested fecal material of macro- or micrograzers). According to Billen and Becquevort (1991), a strong coupling between phytoplankton and bacteria is expected when organic matter of phytoplankton origin is produced as a monomeric substance, directly utilizable by bacteria. These monomers are produced mainly by exudation whilst lysis releases macromolecular substances. Utilization of the latter by bacteria thus requires prior extracellular enzymatic hydrolysis of the material, which considerably delays the response of bacteria to the supply of organic matter of phytoplankton origin. An alternative hypothesis is that the bulk of dissolved organic matter does not originate from local phytoplankton lysis but from release, at the time of ice melting, of dissolved organic matter from sea-ice assemblages. Among protozoa, only the filter-feeding ones, i.e. choanoflagellates (0.86, $P < 0.0005$) and to a lesser extent nano-sized ciliates (0.44, $P < 0.05$), should be active bacteria consumers as suggested by the significant correlations relating these taxonomic groups to bacteria (Table 4).

However, the significant positive correlation between total protozooplankton and total phytoplankton (0.68, $P < 0.005$) suggests that these microheterotrophs quickly respond to phytoplankton, thus maintaining the low phytoplankton biomass. Moreover, the highly

significant correlations existing between distinct taxonomic groups indicate a strong trophodynamic relationship between protozoa and phytoplankton within the same size range, especially between heterotrophic nanoflagellates and nanophytoplankton (0.85, P <0.0005) and between heterotrophic dinoflagellates and microphytoplankton (0.84, P <0.0005). This is particularly evident from the superposition of Fig. 2a, b in which peaks of both protozoan biomass and phytoplankton biomass clearly overlap. In this case, the size of predator of about 10 times that of their prey as suggested by Azam *et al.* (1983) does not hold, mostly due to the abundance of heterotrophic dinoflagellates. In microcosm experiments carried out with samples taken in the same area during the same period, Björnsen and Kuparinen (1991) indeed found an average linear size ratio less than 1 : 2 between nanophytoplankton prey and the heterotrophic dinoflagellates which were by far the dominant predators. Moreover, these microorganisms have been shown to feed on particles that approach or exceed their own sizes (Gaines and Elbrachter 1987, Hansen 1991). No significant relationship between the various selected taxonomic groups of protozoa could be deduced from our data (Table 4).

Role of protozoa in controlling phytoplankton and bacteria development: an assumption

The role of protozoan grazing in controlling bacteria and phytoplankton development at the receding ice edge bas been assessed by comparing the potential ingestion rate of protozoa with the net primary (Mathot *et al.* 1992) and bacterioplankton (Billen and Becquevort 1992) productions measured simultaneously. Potential ingestion rate of protozoa on bacteria and phytoplankton was calculated from protozoan biovolume measurements, abundance and food (bacteria and phytoplankton) concentrations using a maximum volume-specific clearance rate. According to Fenchel (1987), a maximum hourly clearance rate of 10^5 body volume per protozoa is characteristic of protozoa feeding on particle suspension. This values agrees very well with that experimentally determined by Björnsen and Kuparinen (1991) during the same cruise but for one protozoan taxon in particular. Indeed, these authors evaluated the range of maximum hourly clearance rate per heterotrophic dinoflagellate to be 0.8 - 1.2 10^5 body volume.

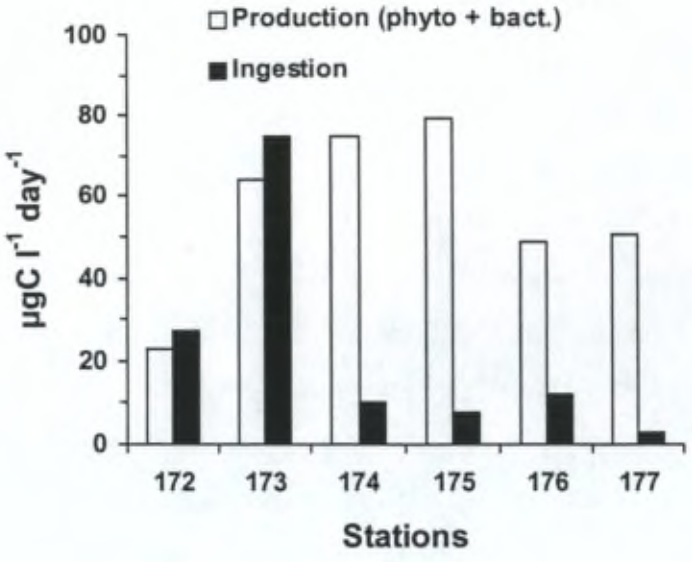


Figure 5. *Potential carbon utilization by protozoa (estimated from ingestion rates) of the combined net primary and bacterioplankton production, along the transect 49°W. Horizontal bars show the contribution of the bacterioplankton production to the combined bacterio-and phytoplanktonic production*

Results of this calculation, a typical example of which is illustrated by Fig. 5, clearly indicate that protozoan food requirements are primarily met by primary production, which contributes more than 95% of the total food production (combined phyto- and bacterioplankton production). Results shown in Fig. 5 suggests, in addition, that protozoa do actively control phytoplankton development at the receding ice edge, particularly in the recently free of ice area where calculated protozoan ingestion rates are higher than primary production. Within the marginal ice zone, potential ingestion rate by protozoa represents on average 48% of the net primary production.

The contribution of protozoa to food resources available to krill and other zooplankton can be grossly evaluated from the above calculations using the protozoa growth efficiency value of 0.38 experimentally determined by Björnsen and Kuparinen (1991) for local populations of heterotrophic dinoflagellates. Budget calculations indicate that protozoa in the marginal ice zone of the northwestern Weddell Sea provide 18% of food resources available to mesoplankton during spring.

CONCLUSION

The determination of size distribution and abundance of auto-and heterotrophic microorganisms in the marginal ice zone of the Weddell Sea during spring 1988 gives additional evidence for the dominance of nano-sized autotrophic communities and the quantitative importance of protozooplankton in this sector of the Southern Ocean. However, the specific analysis of the trophic relationships between the various dominant taxonomic groups revealed a microbial network of high complexity, mainly due to a size overlapping of the various consumers and their respective food. This gives rise to a network of microbial pathways in which the energy flow is not only directed towards larger particles.

Under these circumstances, grazing measurements of each dominant taxonomic group are needed to accurately assess the carbon utilization by protozoa, but results of calculations already suggest that protozoa are potentially able to utilize significant portions of the daily production of bacterioplankton and phytoplankton.

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Nanoprotozooplankton in the Atlantic sector of the Southern Ocean during early spring: biomass and feeding activities

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ABSTRACT- The dynamic of early spring nanoprotozoa was investigated in three characteristic water masses of the Southern Ocean: the Marginal Ice Zone, the intermediate waters of the Antarctic Circumpolar Current and the Polar Frontal Zone. Biomass and feeding activities of nanoprotozoa were measured as well as the biomass of their potential prey - bacteria and phototrophic flagellates - on the 6° W meridian in the Southern Ocean along three repetitive transects between 47° and 60 ° South from October to November 1992.

On average, nanoprotozooplankton biomass accounted for 77 % of the combined biomass of bacteria and phototrophic flagellates and was dominated by dinoflagellates and flagellates smaller than 5 µm. As a general trend, low protozoan biomass of 2 mgC m^{-3} was typical of the ice covered area while significantly higher biomasses culminating at 15 mgC m^{-3} were recorded at the Polar Front. Biomasses of bacteria and total phytoplankton were distributed accordingly with larger values at the Polar Front. Phototrophic flagellates did not show any geographical trend. No seasonal trend could be identified in the marginal ice zone and in the intermediate waters of the Antarctic Circumpolar Current. On the other hand, at the Polar Front region, a three-fold increase was observed within a 2-month period for nanoprotozooplankton biomass. Such a biomass increase was also detected for bacterioplankton and total phytoplankton biomass.

Half-saturation constants and maximum specific ingestion of nanoprotozoan taxons feeding on bacteria and phototrophic flagellates were determined using the technique of fluorescent labeled bacteria (FLB) and algae (FLA) over a large range of prey concentrations. Maximum ingestion rates ranged between 0.002 and 0.015 h^{-1} for bacterivorous nanoprotozoa and heterotrophic flagellates larger than 5 µm feeding on phototrophic flagellates. The markedly high maximum ingestion rates of 0.4 h^{-1} characterising nanophytoplankton ingestion by dinoflagellates evidenced the strong ability of dinoflagellates for feeding on nanophytoplankton.

Daily ingestion rates were calculated from nanoprotozoan grazing parameters and carbon biomass of prey and predators. This indicated that nanoprotozoa ingestion of daily bacterioplankton and phytoplankton production in early spring ranged from 32 % to 40 %.

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INTRODUCTION

In 1985, Hewes *et al.* (1985) introduced the concept of an alternative carbon pathway at the lower trophic levels of the pelagic Antarctic food web coexisting in parallel with the usual view of a food web structure dominated by carbon flow from the large diatoms to krill. Accordingly, recent observations suggest that pico-and nanoautotrophic and heterotrophic planktonic organisms, present in low biomasses, are more typical during the Austral growing season (Bröckel 1981, Weber & El-Sayed 1987, Hewes *et al.* 1985, 1990, Becquevort *et al.* 1992) than blooms of large diatoms which should be restricted to particular areas such as the Ross Sea (Smith & Nelson 1985, Comiso *et al.* 1990) and the Prydz Bay (Goeyens & Dehairs 1993). Trace metal deficiency, in particular iron (Martin *et al.*, 1990), and selective grazing of krill swarms (Smetacek *et al.* 1990) have been mentioned as potential chemical and biological factors controlling diatoms bloom development and favouring the dominance of fast growing nanophytoplankton species in the Southern Ocean (Lancelot *et al.* 1993b, Morel *et al.* 1991).

Indirect evidence based on controlled experiments in microcosms (Hewes *et al.* 1985, Bjornsen & Kuparinen 1991), statistical regression analyses between protozoan biomass and its food (Garrison & Gowing 1992, Nöthig 1988, Becquevort *et al.* 1992), and estimates of potential protozoan ingestion deduced from measured biomass and clearance rates reported in literature, suggest that fast growing protozoa of the Southern Ocean are strongly controlling the development of bacteria and nanophytoplankton, giving rise to a regenerated-type planktonic microbial community despite the presence of large concentrations of nitrate (Lancelot *et al.* 1993a, Goeyens *et al.* 1991).

To assess the trophic role of protozoa in controlling phytoplankton and bacterioplankton in the Southern Ocean, biomass data of both protozoa and their potential food are required, as well as direct measurements of feeding activity on the various sources of food offered to nanoprotozooplankton in natural environments. Protozoan grazing has not been investigated much up to now due to the lack of suitable experimental procedures. Dual radioactive labelling tracer experiments (Lessard & Rivkin 1986) and the application of Landry and Hassett's (1982) dilution grazing technique (Taylor & Haberstroh 1988) gave some preliminary field measurements. These two techniques, however, do not take into account the food selectivity of protozoa and do not give kinetic parameters of their specific functional feeding responses i.e. the response of ingestion rate to food availability.

On the other hand, when applied over a large range of concentrations of specific food- bacteria and nanophytoplankton- the method based on the protozoan uptake of added fluorescently labelled prey (Sherr *et al.* 1987, Rublee & Gallegos 1989) allows direct measurements of the ingestion rate of protozooplankton on bacteria and nanophytoplankton as well as the physiological parameters characterising feeding behaviour of protozoa.

This experimental procedure has been applied for the first time in the Atlantic sector of the Southern Ocean, in early spring, a season for which little information exist on protozooplankton. Results are presented here and discussed in terms of trophic web structure and functioning.

MATERIAL AND METHODS

Data were collected during the SO-JGOFS cruise (ANT X/6) of R.V. *Polarstern* in the Atlantic sector of the Southern Ocean in early spring (29 September - 29 November 1992). Transects were repeatedly sampled along the 6° W meridian from the ice-covered Weddell Sea (Marginal Ice Zone, MIZ), across the southern Antarctic Circumpolar Current (ACC) and into the Polar Front region (PFr). The data presented in this paper are referring to three transects along 6°W sampled between 47°S and 60 °S (Fig.1).

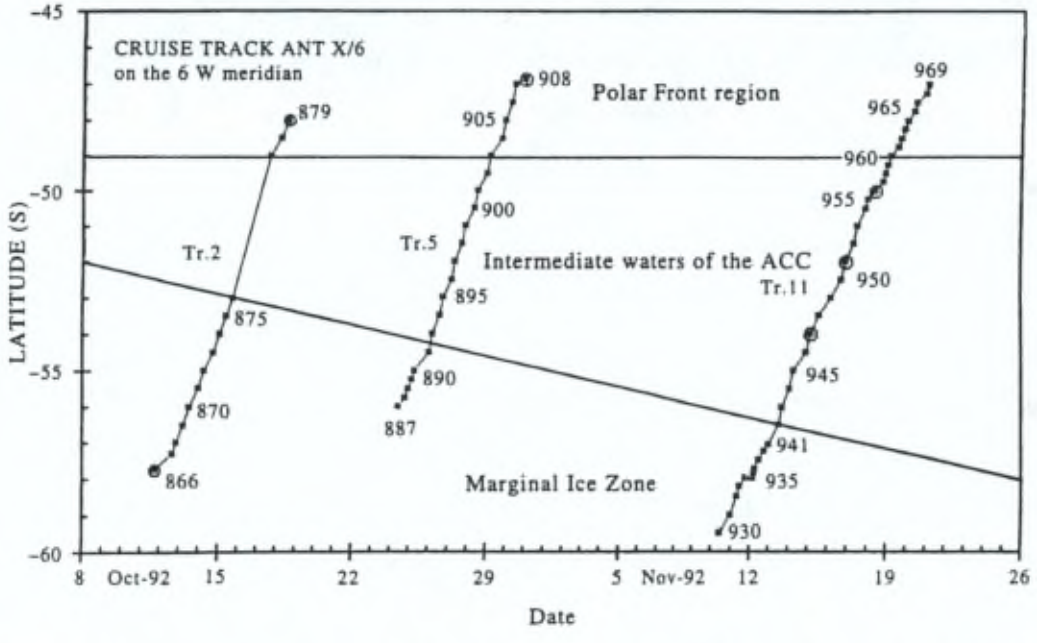


Figure 1. *Transects sampled during the SO-JGOFS cruise (ANT X/6) of RV "Polarstern" in the Atlantic sector of the Southern Ocean in early spring (29 September - 29 November 1992). The three sub-areas identified as Polar Front region (PFr), intermediate waters of the Antarctic Circumpolar Current (ACC) and Marginal Ice Zone (MIZ) are also indicated.*

The transects were : Transect 2, Stations 866 to 879 (Oct 12 to 18); Transect 5, Stations 887 to 908 (Oct 24 to 30); and Transect 11, Stations 930 to 969 (Nov 10 to 21). Salinity, temperature, pressure, oxygen, nutrients and chlorophyll concentrations were measured at every station (Bathmann *et al.*, 1994) in accordance with JGOFS core measurement recommendations (see SCOR, JGOFS report 6, 1990); the collected results are given in this issue.

Surface waters (20 m depth) microorganisms were sampled at each half or quarter degree of latitude using a standard CTD rosette sampler equipped with 12 L Niskin bottles.

Identification and biomass determination

Bacteria were fixed with formaldehyde- 40 % (2 % final concentration). Glutaraldehyde (0.5 % final concentration) was used to preserve phototrophic and heterotrophic flagellates. Biological samples were stored at 4°C before staining (within 12 hours after collection). Cell density and biovolume of photo- and heterotrophic microorganisms were determined by epifluorescence microscopy (Leitz, Laborlux D) after DAPI staining (Porter & Feig 1980).

Staining procedure. Fixed samples (2 -5 ml for bacteria and 5-20 ml for flagellates) were stained with 4'6 diamidino-2-phenylindole (DAPI) and isolated by filtration on 0.2 µm Nuclepore polycarbonate black membranes under gentle vacuum (<50 mmHg) (Haas 1982). The filters were rinsed with sterile filtered sea water, air-dried for 30 s and mounted in Olympus immersion oil. Microscopic slides were stored at -40 °C until examination.

Microscopic analysis and carbon biomass estimate. Microorganisms were observed within 6 months of collection. Bacteria were enumerated on a minimum of 20 different fields at 1000x magnification. Cell sizes were measured on photomicrography and biovolumes were calculated by considering rods and cocci, respectively, as cylinders and spheres (Watson *et al.* 1977). Biovolumes were converted to cell carbon by using the biovolume-dependent conversion factor established by Simon and Azam (1989).

A minimum of 100 flagellates per filter were counted and phototrophs were discriminated from heterotrophs by the presence of photosynthetic pigments. Cell sizes were measured visually by means of an ocular micrometer. Biovolumes were calculated from cell dimensions and shapes. Ratios to convert biovolume to biomass appears to be influenced by the fixation and staining method as well as by taxon, so that various ratios have been proposed in the literature. These are range between 0.08 and 0.22 pgC μm^{-3} (Beers & Stewart 1971, Edler 1979, Parsons *et al.* 1984, Borsheim & Bratbak 1987, Choi & Stoecker 1989, Putt & Stoecker 1989). Lessard (1991) suggested a conversion factor of 0.14 pgC μm^{-3} for dinoflagellates fixed with glutaraldehyde. In this study, we decided to use this conversion factor for all taxa. The biomass of total phytoplankton was estimated from chlorophyll data (Bathmann *et al.*, this issue) assuming a C/Chl a ratio of 35 proposed by Dehairs *et al.* (1992).

Biological activities

Ingestion rate of protozooplankton. Ingestion rates of bacteria and nanoplanktonic algae by protozooplankton were measured using the method based on the uptake of fluorescent prey (Sherr *et al.* 1987, Rublee & Gallegos 1989). Natural protozoan populations are incubated in the presence of added prey (bacteria and nanophytoplankton), previously stained with DTAF (5-(4,6-dichlorotriazin-2-yl) aminofluorescein). The number of prey ingested by protozoa per unit of time is kinetically measured during the incubation experiment through the microscopic identification of fluorescent prey within the protozoan vacuoles. Grazing rates (number of prey ingested by protozoa per hour) is deduced from the initial slope of the time-dependence curve.

Preparation of FLB and FLA.. Fluorescent labelled bacteria (FLB) - mean biovolume of 0.06 μm^3 - were prepared from natural assemblages of bacterioplankton according to the procedure of Sherr *et al.* (1987). Fluorescent labelled algae (FLA) were obtained from cultures of Antarctic Phaeocystis cells (equivalent spherical diameters of 4 µm and mean biovolume of 33.5 μm^3) using the procedure of Rublee and Gallegos (1989). Stock solutions of FLB and FLA were kept at -4°C before feeding experiments.

Ingestion experiments. The functional feeding response of phagotrophic nanoprotozoa was investigated in the different water masses, in the PFr, the intermediate water of the ACC and the MIZ. For each experiment, 3 replicates were done. All experiments were carried out in 500 ml polycarbonate (Nalgene) bottles decontaminated in 10% (vol/vol) HCl during 12 hours and rinsed thoroughly with deionized water. Experiments were run in the dark at in situ temperature (in sea water circulation). After an acclimation period of 30 min, natural assemblages of protozoa were inoculated with various concentrations of FLA (10^6 to 10^9 FLA l^{-1}) and FLB (10^7 to 10^{12} FLB l^{-1}). The precise number of added FLA and FLB was determined within a subsample at time zero.

Subsamples of 50 ml were removed every 15-60 minutes during the incubation periods (2 and 8 hours for FLB and FLA experiments, respectively). Biological activity was immediately stopped through the sequential addition of the following preservatives: alkaline lugol solution (0.5 % final concentration), borate buffered formalin (3% final concentration), and a drop of 3% sodium thiosulfate. According to Sherr *et al.* (1989), this fixative does not cause the egestion of prey. Samples were stored in glass vials at 4°C in the dark until preparation for microscopic analyses (within a few days).

Ten to 20 ml of the preserved samples were stained with DAPI (Porter & Feig 1980). Protozoa were isolated by filtration through Nuclepore black polycarbonate membranes of 0.8 µm porosity. Protozoan abundance and biomass, and average number of FLB or FLA ingested per protozoa were determined by

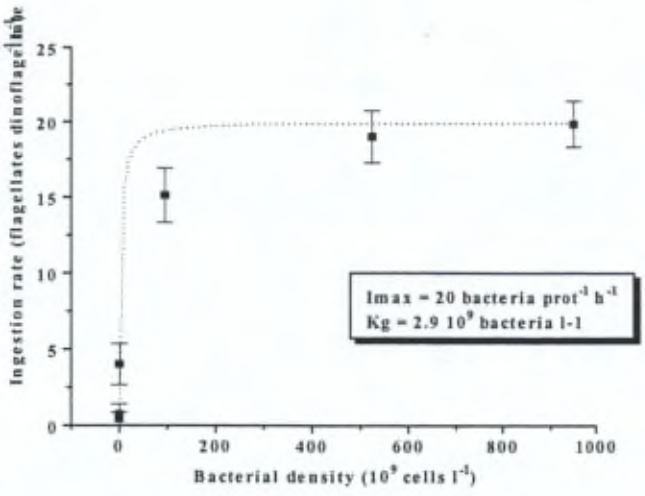
epifluorescence microscopy. Ingestion rates of bacteria and phototrophic flagellates were then calculated for different groups of protozoa from linear slopes of the time dependent curve of average FLB and FLA number ingested per protozoa (Sherr *et al.*, 1987). Since the early work of Fenchel (1982, 1987), it has been recognized that protozoa ingestion rate obeys a hyperbolic kinetics (Holling type II model) as a function of the prey concentration.

The prey concentration dependent ingestion rates -the functional feeding response- were thus analysed by the following kinetics:

$$I = I\max \cdot \frac{N}{(N + Kg)}$$

This equation is described by two parameters, the maximum ingestion rate *I*max and the half-saturation constant *K*g. *I*max can be expressed as the numbers of prey consumed per protozoa per hour and/or as maximum specific ingestion (µgC of prey per µgC of protozoa per hour). Unit for *K*g is number of prey per liter or µgC of prey per liter. *N* is the prey concentration (number of prey per liter or µgC of prey per liter). The kinetic parameters were estimated from the best fitting curve (calculated by the least-squares method) of the protozoan ingestion rates as a function of bacterial and flagellate prey concentrations (as shown in Fig.2).

A.



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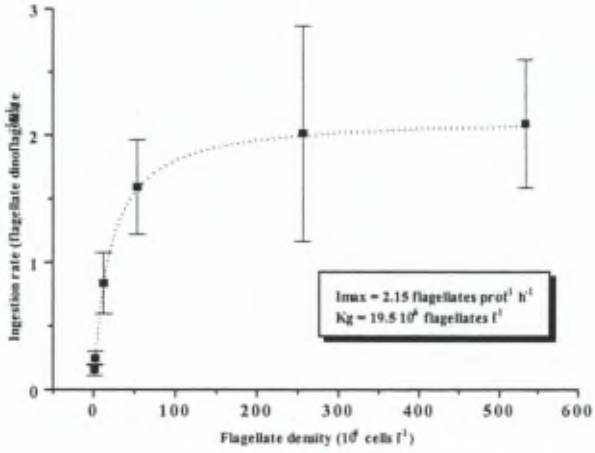

Figure 2. *Functional feeding responses of heterotrophic dinoflagellates ingesting bacteria (a) and flagellates (b) with 3 replicates at the station 907. Vertical bars represented standard error of mean ingestion rate estimates. Data were fitted by Holling type II curves, with given maximum ingestion rates (Imax) and half-saturation constants (Kg).*

Integrated daily bacteria and phototrophic flagellate ingestion rates by nanoprotozoa (mgC m^{-2} d^{-1}) have been calculated from estimated ingestion parameters (*I*max and *K*g), carbon biomasses of food (bacteria and phototrophic flagellates) and protozoa. They were integrated to the depth of the upper mixed layer water mass as calculated by Lancelot and Veth (1997).

Bacterial production.

Bacterial production was estimated by measuring the incorporation of ^{3}H-Leucine into cold trichloroacetic acid-TCA insoluble fraction. Data from Lochte *et al.* (1997). Integrated daily bacterial production (mgC m^{-2} d^{-1}) was calculated by integration of bacterial production to the depth of the upper mixed layer water mass.

Phytoplanktonic production.

Phytoplanktonic production was estimated by measuring the $NaH^{14}CO_3$ assimilation following the protocol recommended by JGOFS (see SCOR, JGOFS report 6, 1990). These results are presented and discussed in Jochem *et al.* (1995). Integrated daily phytoplankton production (mgC m^{-2} d^{-1}) was calculated by integration of phytoplankton production to the depth of the upper mixed layer water mass.

RESULTS

Distribution of nanoprotozooplankton and its potential food

Bacteria and autotrophic flagellates predominate largely the nanoprotozooplankton diet. Spatio-temporal distribution of nanoprotozooplankton, bacteria and autotrophic flagellates observed in early spring in the Atlantic sector are illustrated respectively by Fig.3, 4 and 5.

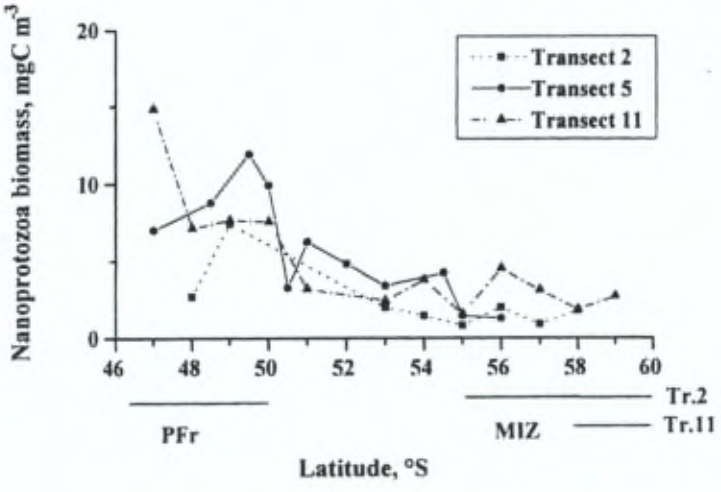

Figure 3 *Spatio-temporal distribution of nanoprotozooplankton biomass along the three investigated transects. The position of the PFr and the MIZ are indicated.*

In the investigated areas, nanoprotozoan carbon biomass ranged between 0.81 and 14.85 mgC m^{-3} with the lowest values in the MIZ and highest values in the PFr, particularly in mid-November. No clear seasonal trend was observed in the sea-ice associated and ACC water masses, where average values of 1.62 and 4.07 mgC m^{-3}, respectively, were observed. On the other hand, in the PFR, a threefold increase of protozoa biomass was recorded within 44 days.

Among the nanoprotozoan community, three main groups were considered as based either on their size (< and > 5 µm) or their feeding behaviour (dinoflagellates, choanoflagellates and other flagellates) (Table 1). The size limit of 5 µm was selected from ingestion experiments showing no uptake of *Phaeocystis* cells-FLA by protozoa smaller than 5 µm.

Table 1. *Mean and extreme values of biomass (units are mgC m^{-3}) and percent of the total nanoprotozoan biomass for main nanoprotozooplankton groups .*

	Carbon biomass	**%**
	Mean (min.-max.)	Mean (min.-max.)
Flagellates < 5 µm	1.36 (0.22-8.66)	34 (7-81)
Flagellates > 5 µm		
Dinoflagellates	8.26 (0.37-10.13)	61 (19-93)
Choanoflagellates	0.15 (0.01-1.21)	4 (0-13)
Other flagellates	0.10 (0.01 -0.08)	1 (0-6)

Heterotrophic dinoflagellates were important in the whole area ranging from 19 to 93 % (on average 61 %) of the total nanoprotozooplankton biomass. Other significant taxa were flagellates smaller than 5 µm, contributing to 34 % of the total nanoprotozooplankton biomass. Choanoflagellates represented only 4 % of the total nanoprotozooplankton biomass. Ciliates were insignificant in the nano-sized range. Bacterioplankton ranged between 2 and 18 mgC m^{-3} with highest values in the PFr (Fig.4).

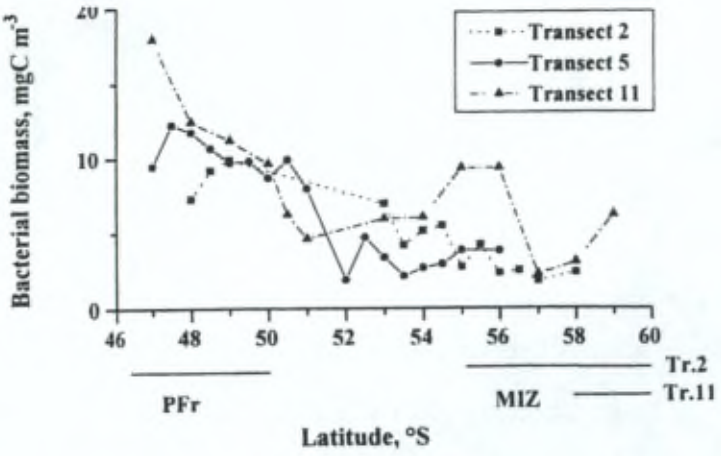

Figure 4. *Spatio-temporal distribution of bacterioplankton biomass along the three investigated transects. The position of the PFr and the MIZ are indicated.*

Lowest biomass was recorded at the receding ice edge. The largest bacterial biovolumes (mean value of 0.08 μm^3 per cell) were observed in the PFr and near the ice (on average 0.07 μm^3 per cell). In the intermediate waters of the ACC, the mean biovolume was 0.04 μm^3 per cell. No significant seasonal trend in bacterial cell volume could be observed in the different water masses.

Biomass of phototrophic flagellates ranged between 1.3 to 17.8 mgC m^{-3} with small variations between the different water masses (Fig.5).

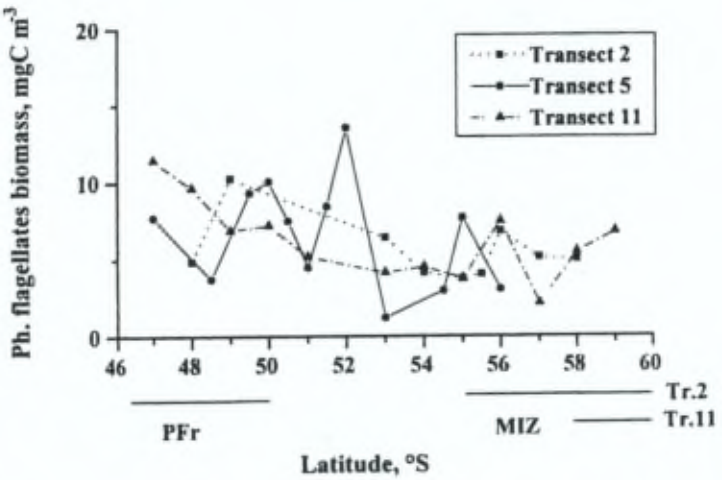

Figure 5. *Spatio-temporal distribution of the phototrophic flagellate biomass along the three investigated transects. The position of the PFr and the MIZ are indicated.*

The flagellate biomass was dominated (84 %) by small organisms (< 5 µm, mean equivalent spherical diameter = ESD), mostly Prymnesiophytes (Table 2).

Table 2. *Mean and extreme values of biomass (units are mgC m^{-3}) and percent of the total nanoprotozoan biomass for main phototroph nanoflagellates groups .*

	Carbon biomass	**%**
	Mean (min.-max.)	Mean (min.-max.)
Flagellates < 5 µm	6.46 (1.12-16.03)	84 (68-100)
Flagellates > 5 µm		
Dinoflagellates	0.98 (0.03-4.90)	11 (0-38)
Other flagellates	0.32 (0.01 -0.76)	5 (0-38)

Their relative contribution in the total phytoplanktonic biomass was significant , particularly in the marginal ice zone (82 %) and in the intermediate waters of the ACC (95 %) at the beginning of October (Table 3). On the other hand, the PFr was dominated from the end of October by non-flagellated phytoplankton. This is particularly obvious in November where they contributed 83 % of the total phytoplankton biomass (Table 3).

Table 3. *Mean percentages of phototrophic flagellates in the total phytoplankton biomass estimated from chlorophyll a) in three water masses during the transects 2, 5 and 11.*

	Transect 2	**Transect 5**	**Transect 11**
Polar Front region	53 %	23 %	17 %
Int. waters of the ACC	95 %	58 %	70 %
Marginal Ice Zone	82 %	-	60 %

Ingestion rates of nanoprotozooplankton

The prey concentration dependent ingestion rates of protozoa were measured in the three different water masses, the PFr, the intermediate water of the ACC and the MIZ.

Abundance and biomass of field microbial assemblages used for grazing experiments are reported on Table 4.

Table 4. *Microbial composition (abundance and biomass) of natural assemblages used for protozoan grazing experiments. Polar Front region, station 907; Intermediate waters of ACC, stations 895 and 945; Marginal Ice Zone, stations 887 and 930.*

Taxons	Polar Frontal Zone	Intermediate waters of ACC	Marginal Ice Zone	Mean
Phototrophic flagellates < 5 µm				
number, 10^6 l^{-1}	3.8	1.7	2.7	2.7
biomass, µgC l^{-1}	10.0	3.9	7.7	7.2
Bacteria				
number, 10^8 l^{-1}	6.4	5.7	4.3	5.5
biomass, µgC l^{-1}	12.4	9.3	6.2	9.3
Protozooplankton				
Flagellates < 5µm (25 µm^3)				
number, 10^5 l^{-1}	14.3	4.6	3.3	6.3
biomass, µgC l^{-1}	3.3	1.7	1.9	2.3
Flagellates > 5 µm(318 µm^3)				
number, 10^5 l^{-1}	1.6	0.6		1.1
biomass, µgC l^{-1}	1.0	2.7		1.9
Dinoflagellates (188 µm^3)				
number, 10^5 l^{-1}	1.1	1.6	0.1	0.93
biomass, µgC l^{-1}	3.6	4.2	0.1	2.6

Physiological parameters of protozoan feeding on bacteria and flagellates calculated for the different protozoan groups and in the three different water masses are gathered in Tables 5 and 6. As expected from their physiological significance, calculated feeding parameters were quite similar for the protozoan populations developing in the three different water masses.

As a general trend, bacteria could be ingested by every group of heterotrophic flagellate (Table 5). Half-saturation constants for bacteria ingestion by the different protozoan groups show little variations around an average value of 54 µgC l^{-1}. Conversely, maximum ingestion rates, *I*max, were typical of each protozoan group, ranging between 1.1 bacteria per protozoa h^{-1} for the heterotrophic flagellates < 5 µm, 7.3 bacteria per protozoa h^{-1} for the heterotrophic flagellates > 5 µm and 17.7 bacteria per protozoa h^{-1} for the heterotrophic dinoflagellates. Accordingly, the maximum carbon-specific ingestion rate was significantly higher for the heterotrophic dinoflagellates (mean value of 0.011 h^{-1}) than for the other heterotrophic flagellates (mean value of 0.005 h^{-1} for the heterotrophic flagellates < 5 µm and 0.007 h^{-1} for the heterotrophic flagellates >5 µm).

Table 5. *Calculated physiological parameters of nanoprotozoan feeding on bacteria i.e. maximum ingestion (Imax) and half-saturation constant rate (Kg). Polar Front region, station 907; Intermediate waters of ACC, stations 895 and 945; Marginal Ice Zone, stations 887 and 930.*

Ingestion of bacteria	Polar Frontal Zone	Intermediate waters of ACC	Marginal Ice Zone	Mean
by Flagellates < 5 µm				
Imax, bact.prot^{-1}h^{-1}	1.3	1.2	0.9	1.1
Imax, µgC µgC^{-1} h^{-1}	0.008	0.006	0.002	0.005
Kg, 10^8 bact.l^{-1}	53	24	36	38
Kg, µgC l^{-1}	85	38	58	61
by Flagellates > 5 µm				
Imax, bact.prot^{-1}h^{-1}	4.2	10.3		7.3
Imax, µgC µgC^{-1} h^{-1}	0.010	0.004		0.007
Kg, 10^8 bact.l^{-1}	29	35		32
Kg, µgC l^{-1}	46	55		51
by Dinoflagellates				
Imax, bact.prot^{-1}h^{-1}	20	20	13	17.7
Imax, µgC µgC^{-1} h^{-1}	0.009	0.013	0.010	0.011
Kg, 10^8 bact.l^{-1}	29	34	31	31
Kg, µgC l^{-1}	46	54	50	50

Flagellates on the other hand were ingested only by the heterotrophic flagellates > 5 µm and heterotrophic dinoflagellates (Table 6).

The calculated half-saturation constants of flagellates ingestion by protozoa show small variations between the different consumers, so that a mean value of 69 µgC l^{-1} being considered as typical for the half-saturation constant of flagellates ingestion by nanoprotozoa. As observed for bacteria, maximum ingestion rates of flagellates differed remarkably between protozoa taxons. A very high ingestion rate of an average of 1.95 flagellates consumed per protozoa h^{-1} was found for heterotrophic dinoflagellates, corresponding to a maximum specific ingestion rate of 0.35 h^{-1}. Maximum ingestion of flagellates by the heterotrophic dinoflagellates were more than an order of magnitude greater than by other heterotrophic flagellates (Table 6) stressing the very high ability of dinoflagellates to feed on flagellates.

Table 6. *Calculated physiological parameters of nanoprotozoan feeding on autotrophic flagellates i.e. maximum ingestion (Imax) and half-saturation constant rate (Kg). Polar Front region, station 907; Intermediate waters of ACC, stations 895 and 945; Marginal Ice Zone, stations 887 and 930.*

Ingestion of phototrophic flagellates	Polar Frontal Zone	Intermediate waters of ACC	Marginal Ice Zone	Mean
by Flagellates > 5 µm				
Imax, bact.prot^{-1}h^{-1}	0.02	0.08		0.05
Imax, µgC µgC^{-1} h^{-1}	0.015	0.008		0.012
Kg, 10^5 bact.l^{-1}	142	202		35
Kg, µgC l^{-1}	53	74.5		64
by Dinoflagellates				
Imax, bact.prot^{-1}h^{-1}	2.15	2.2	1.5	1.95
Imax, µgC µgC^{-1} h^{-1}	0.30	0.40	0.34	0.35
Kg, 10^5 bact.l^{-1}	195	200	195	197
Kg, µgC l^{-1}	72	74	72	73

DISCUSSION

The microbial network in early spring: the importance of dinoflagellates

The analysis of the specific composition of the early spring microbial biomass developing in the Atlantic sector of the Southern Ocean suggests the occurrence of different trophic networks with respect to water mass distribution. In the MIZ and in the intermediate waters of the ACC, the microbial community was dominated by pico-sized and nano-sized auto -and heterotrophic microorganisms giving rise to an active microbial network. As an average, bacterioplankton and phototrophic nanoflagellates were contributing 67 % and 86 % of the combined biomass of bacterioplankton and total phytoplankton, respectively in the MIZ and in the intermediate waters of the ACC. In both areas, nanoprotozooplankton biomass represented respectively 16 % and 17 % of the combined biomass of bacterioplankton, total phytoplankton and nanoprotozooplankton.

In the PFr, on the other hand, the phytoplankton community was largely dominated by non-flagellated phytoplankton identified principally as net-sized diatoms giving rise to occasional blooms with chlorophyll a concentrations higher than 1 µgC l^{-1} (Bathman *et al.* 1997). Consequently, the nanoprotozooplankton biomass was relatively less significant, contributing only 10 % of the combined total phytoplankton, bacterioplankton and nanoprotozooplankton biomass.

Less proportion of primary material seems, therefore, to flow through the microbial network in this zone.

These data are consistent with previous information showing that high phytoplankton biomass is usually associated with net plankton, whereas low biomass waters are generally dominated by nanoplankton (Hewes *et al.* 1990). Indeed, during the 4 months of the RACER (Research on Antarctic Coastal Ecosystem Rates) programme, investigation of the phytoplankton population in the coastal region showed a concomitant change in cell size distribution and biomass from high biomass of predominantly microplankton in December to low biomass of predominantly nanoplankton in February and March (Holm-Hansen & Mitchell 1991). At EPOS (European Polarstern Study), in the Marginal Ice Zone, low phytoplanktonic biomass dominated by the nanoplankton community was observed during the whole investigated period (end of November to the beginning of January) (Jacques & Panouse 1991). In contrast, in the Weddell/Scotia Confluence area, a high biomass net-plankton community rapidly changed toward a uniform nanoplankton system.

Contrary to the EPOS (Becquevort *et al.* 1992), in this study, bacterioplankton constituted a large component of the total microbial biomass, in the ACC and in the MIZ, and thus represented a significant amount of food for protozooplankton.

Nanoprotozooplankton biomass was significantly correlated with its potential food, i.e. bacteria and phototrophic flagellates (Fig.6). Nanoprotozooplankton biomass represented 77 % of the combined biomass of bacteria and phototrophic flagellates and hence is to be considered a key component of the planktonic food-web.

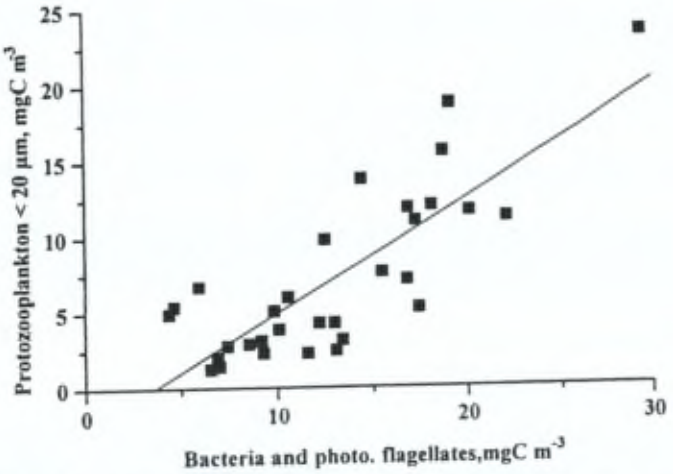

Figure 6. *Relationship between nanoprotozooplankton biomass and combined biomass of bacterio-and phototrophic flagellates. Regression line: y = 0.77 x-0.68 (R= 0.81). N= 31.*

Compared to existing data of spatio-temporal distribution of protozoan biomass in the Southern Ocean (Garrison 1991, Becquevort *et al.* 1992), the measured biomass of protozooplankton appears very low; but, this work reports first early spring data on nanoprotozooplankton in the Southern Ocean. Accordingly, the review by Garrison (1991) suggests the occurrence of maximum protozoan biomass in the summer period.

In all investigated water masses, the nanoprotozooplankton biomass was dominated by dinoflagellates and flagellates smaller than 5 µm, in agreement with previous taxonomic analysis of protozoan assemblages in the vicinity of the investigated area (Becquevort *et al.* 1992, Mathot 1993).

Flagellates smaller than 5 µm were principally bacterivorous while heterotrophic dinoflagellates were observed to feed on bacteria as well as on flagellates. In this case the size of predator is not around 10 times of that of their prey as suggested by Fenchel (1987). The predator - prey size ratio was less than 2 with observed dinoflagellates characterised by a mean equivalent spherical diameter of 7 µm (ESD) compared to fluorescent prey of 4 µm (ESD). In microcosm experiments carried out in the north-western Weddell Sea area, Bjornsen and Kuparinen (1991a) also found an average linear size ratio less than 1:2 between nanophytoplankton prey and heterotrophic dinoflagellates which were the dominant predators. Moreover, heterotrophic dinoflagellates have been reported to feed on a large size range of prey such as bacteria, flagellates, diatoms, other dinoflagellates, ciliates and metazoans (Gaines & Elbrächter 1987, Hansen 1991).

The maximum ingestion rates of dinoflagellates consuming phototrophic flagellates were very high. Indeed, assuming a gross growth efficiency of 30 %, a maximum growth rate of 2.5 d^{-1} was estimated. In the literature, for heterotrophic dinoflagellates, the mean value of the maximum growth rate was 0.8 d^{-1} (Jacobson 1987, Goldman *et al.* 1989, Bjornsen & Kuparinen 1991, Strom, 1991). Our higher estimated value could be the result of a protozoan selection for the fluorescent non-living and non-motile prey (Landry *et al.* 1991, Putt 1991, Gonzales *et al.* 1993). Now, Putt (1991) proposed the use of live fluorescently labelled algae as tracers in microzooplankton herbivore. But till now, the FLB, FLA method constitutes an experimental approach to identify the trophic relationships between microorganisms on the one hand and to give an estimation of protozoan grazing impact on field phytoplankton and bacterioplankton developments on the other hand.

Carbon budget estimation: the trophic role of nanoprotozoa

Spatio-temporal distributions of calculated integrated daily ingestion rates of protozooplankton, illustrated by Fig. 7 and 8 are compared to bacterial and primary production rates.

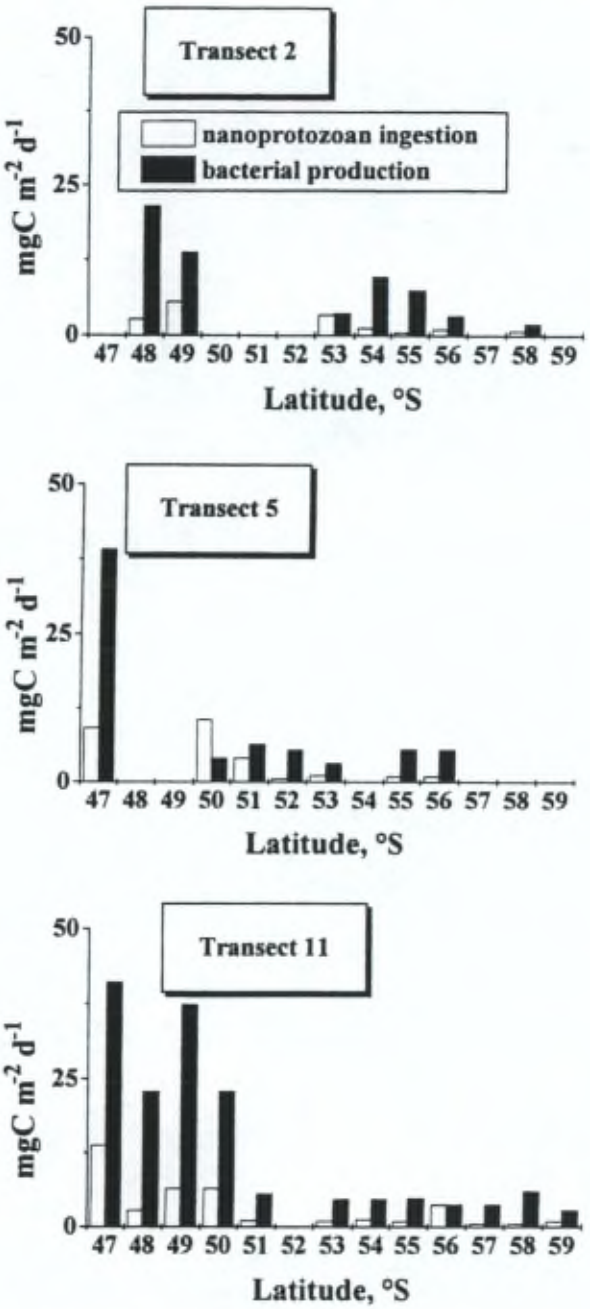

Figure 7. *Spatio-temporal distribution of daily bacterial ingestion rate by nanoprotozoa compared to the daily bacterial production along the three investigated transects.*

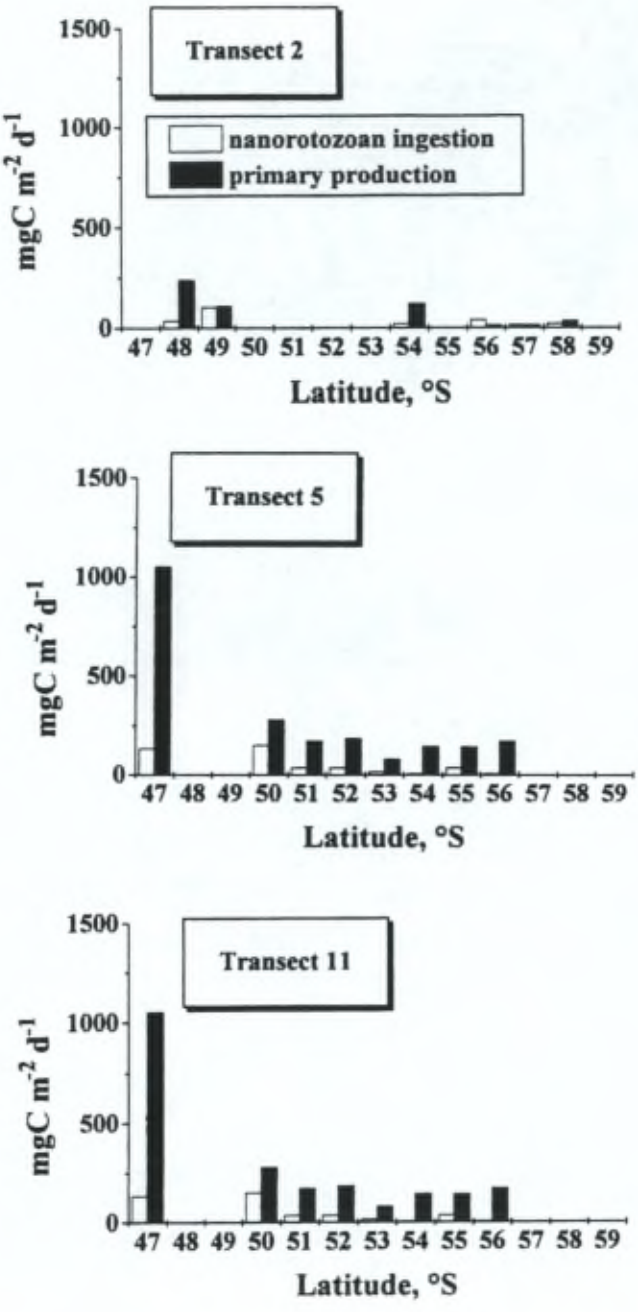

Figure 8 *Spatio-temporal distribution of autotrophic flagellate ingestion by nanoprotozoa compared to the daily primary production along the three investigated transects.*

Examination of Fig. 7 indicates little control of nanoprotozooplankton on bacterioplankton development. Daily bacterial production is always significantly higher than daily ingestion rates of bacteria by protozooplankton, except at one station. As an average, nanoprotozooplankton controls 32 % of bacterial development with an even higher value (mean value of 46 %) in the ACC intermediate waters (Table 7).

Table 7. *Mean and extreme percents of bacterial and phytoplankton production ingested by nanoprotozoa in the polar frontal zone, in the intermediate waters of ACC and in the marginal ice zone*

	Bacterial production % ingested by nanoprotozoa min - max., mean	**Phyto. production % ingested by nanoprotozoa** min - max., mean
Polar Frontal Zone	12 - 40, 24	5 - 95, 27
Int. waters of ACC	6 - 256, 46	1 - 54, 14
Marginal Ice Zone	8 - 39, 27	3 - 295, 78

Among protozoa, dinoflagellates are by far the most active predators, ingesting 81 % of the grazed bacteria, followed by the flagellates smaller than 5 µm (15 %) and the flagellates larger than 5 µm (4%) (Table 8).

Table 8. *Mean percent of ingested bacteria and phototrophic flagellates by three nanoprotozoan taxon.*

Protozoan taxon	**% of bacteria**	**% of phytoplankton**
flagellates < 5 µm	15	-
dinoflagellates	81	99
flagellates > 5 µm	4	1

Phytoplankton loss by nanoprotozooplankton ingestion is mainly due to dinoflagellates with a feeding activity representing 99 % of the total protozooplankton grazing on nanophytoplankton (Table 8). The control of phytoplankton development exerted by nanoprotozooplankton is, however, quite variable accounting for 2 - 295 % of primary production (Fig.8). In the PFr as well as in the intermediate waters of the ACC, nanoprotozoan feeding was in fact not very effective in controlling the early spring development of phytoplankton, consuming respectively 27 % and 14 % of the measured primary production. On the other hand, in the MIZ, 78 % of phytoplanktonic production was controlled by nanoprotozoan feeding. This suggests that the low phytoplankton

biomass observed in the marginal ice zone could partly be the result of the grazing control by nanoprotozooplankton. However, the nanoprotozoan feeding can not explain the phytoplanktonic biomass level observed in the intermediate waters of the ACC. Wind has been suggested as a factor controlling the primary production in this area (Lancelot & Veth 1997). Indeed, in this wind-stressed area, small events of localised production can take place near the surface and are rapidly followed by sinking due to the instability of the water column (deep mixed layer).

Comparison of these data with existing measurements or indirect estimates of daily auto- and heterotrophic microbial activities in the Southern Ocean (Table 9) gives some insight into the trophic role of protozooplankton along a seasonal cycle.

Table 9. *Estimated percents of daily primary and bacterial production ingested by protozoa in Antarctic waters.*

% of primary production	% of bacterial production	Period	Source
40	32	Oct-November	This study
48		Nov-December	Becquevort et al. ,1992
	35	Nov-December	Becquevort ,pers. com.
75		Dec-January	Taylor and Habertroh, 1988
41	68	March	Garrison, 1991

Indeed, from Table 9, it is obvious that control of phyto-and bacterioplankton development by protozoan grazing increases along the seasonal cycle, from 40-32 % in early spring to 75-68 % in summer with some delay between maximum control of bacteria and phytoplankton development during the latter. Strongest control of phytoplankton development seems to occur in summer while maximum bacterial development control is taking place at the end of summer-early fall, in good agreement with the observed time delay between phytoplankton and bacteria blooms (Billen and Becquevort, 1991; Lancelot *et al.*, 1991).

Additional direct measurements of protozooplankton feeding activities are, therefore, needed for estimating on a seasonal scale the trophic role of protozooplankton in the Southern Ocean, in particular its importance in controlling phytoplankton bloom development and its link between microbes and copepods and krill.

CONCLUSION

This study, during early spring in the Southern Ocean, shows the dominance of nanosized planktonic organisms - phototrophic flagellates, bacteria, heterotrophic protozoa - in water masses characterised by low biomasses. Nanoprotozoa, dominated principally by heterotrophic dinoflagellates and flagellates < 5 µm, was significantly correlated with its potential food (bacteria and phototrophic flagellates).

Moreover, the high measured ingestion rates of heterotrophic dinoflagellates on phototrophic flagellates indicated a control by these organisms on the primary production in the MIZ.

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Comparative study of the protozoan dynamics during early spring 1995 and late summer 1994 in the Indian sector of the Southern Ocean

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ABSTRACT- The dynamics of protozoa were investigated during two cruises in the Indian sector of the Southern Ocean: the early spring ANTARES 3 cruise (28 September - 08 November 1995) and the late summer ANTARES 2 cruise (6 February - 8 March 1994). Biomass and feeding activities of protozoa were measured as well as the biomass of their potential prey - bacteria and phototrophic flagellates - along the 62°E meridian from the Polar Frontal region (PFr) to the Coastal and Continental Shelf Zone (CCSZ) for ANTARES 2 and to the ice-edge for ANTARES 3, crossing the Antarctic Divergence.

Protozooplankton biomass was low, however, it contributed to 30 % and 20 % of the total microbial biomass (bacteria, phytoplankton and protozooplankton) in early spring and late summer, respectively. Nanosize protozoa was dominating in the whole protozoa biomass. The geographical and seasonal distribution of protozoa biomass was correlated with that of phototrophic flagellates. On the other hand, bacterial and phototrophic flagellate biomass were inversely correlated, phototrophic flagellates dominated in the Sea Ice Zone although bacteria in end-summer in the PFr and in the CCSZ. Futhermore, bacteria were the most important component of the microbial community (57 % of the total microbial community) in late summer. Phototrophic flagellates were ingested by nano-and microprotozoa, although bacteria were only ingested by protozoa < 10 µm. Protozooplankton was controlling up to 90% of the bacterial daily production over the whole seasonal period. On the contrary, protozoa didn't control totally the primary production. In spring, it consumed 54 % of the total primary production but more than 100 % of phototrophic flagellate daily production. At the end of summer, protozoan grazing was controlling the primary production to a less extent, i.e. only 42 % of the phototrophic flagellate daily production.

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INTRODUCTION

It is now well admitted that much of the pelagic ecosystem in the Southern Ocean is dominated by a recycling small-sized community, where protozooplankton plays a key role as consumers of phytoplankton and bacterioplankton and as prey for metazooplankton (Smetacek *et al.* 1990). Silicate (Queguiner *et al.* 1997) and/or iron deficiency (Martin *et al.* 1990, de Baar *et al.* 1990, van Leeuwe *et al.* 1997, Scharek *et al.* 1997) and/or the high grazing pressure by krill (Graneli *et al.* 1993) or their combination have all been suggested to affect mainly larger phytoplankton species (diatoms), explaining the predominance of smaller cells in the Southern Ocean (Lancelot *et al.* 1993, 1997, submitted).

Small phytoplankton is typically ingested by protozoa with generation times of the same order of magnitude (day). This leads to a severe control of pico-and nanophytoplankton populations by micro-grazers and explains the strikingly constant and relatively low concentration of pico- and nanophytoplankton populations in marine environments (Frost & Franzen 1992, Lancelot *et al.* 1993, Price *et al.* 1994, Becquevort 1997). The same feature of bacterial populations has likewise been explained by predation control from heterotrophic flagellates (Becquevort 1997).

In the scope of Southern Ocean-JGOFS (Joint Global Fluxes Studies) addressing the role of the Southern ocean in the carbon cycle, the quantification and the understanding of the carbon flow through the microbial network is very important. The latter flux allows to estimate the part of primary production recycled in the surface water through rapid metabolism of heterotrophic microorganisms (protozoa and bacteria) versus the part which escapes this rapid cycling and might be exported to the deep ocean.

To properly assess the trophic role of protozoa in controlling phytoplankton and bacterioplankton in the Southern Ocean, data of both protozoa biomass and their potential food are required, as well as direct measurements of feeding activity of protozoa. Protozoa are an ubiquitous component of the plankton assemblages in the the Southern Ocean and are now recognized as significant and major consumers of bacterioplankton (Becquevort 1997) and nanophytoplanktonic (Garrison *et al.* 1991 , 1993, Burkill *et al.* 1995, Bjornsen & Kuparinen 1991, Becquevort 1997, Klaas 1997) production. A experimental and modelling study conducted in the marginal ice zone of the northwestern Weddell Sea has shown that herbivorous protozoa is determining the magnitude and the extent of the nanophytoplankton dominated ice edge bloom of 1988 (Becquevort *et al.* 1992, Lancelot *et al.* 1993b). In the other part of the Southern Ocean as for instance the Indian ocean's sector, the control of bacterial and algal biomasses by protozoa

grazing is poorly documented. In the Indian ocean's sector Some measurements of protozoan grazing were reported for coastal Antarctic waters (Leakey *et al.* 1996, Archer *et al.* 1996).

As part of the JGOFS-France program, this paper presents data on protozooplankton biomass and activity collected in the Indian sector of the Southern Ocean during early spring 1995 (ANTARES 3) and late summer 1994 (ANTARES 2).

From these data, the trophic relationships between protozoa and prey i.e. bacteria and phototrophic flagellates as well as the role of protozoa in controlling the phytoplankton and bacterioplankton productivity in the Indian ocean's sector of the Southern Ocean are discussed.

MATERIAL AND METHODS

Data were collected during two SO-JGOFS cruises of R/V Marion Dufresne 1 and 2 in the Indian ocean's sector of the Southern Ocean: the late summer ANTARES 2 cruise (6 February - 8 March 1994) and the early spring ANTARES 3 cruise (28 September - 08 November 1995). Transects were sampled along the 62° E meridian from the Polar Front region (PFr) to the Coastal and Continental Shelf Zone (CCSZ) for ANTARES 2 and to the ice edge for ANTARES 3, crossing the Antarctic Divergence (AD). The location of the stations and the geographical position of water masses and ice-edges is shown on Fig. 1.

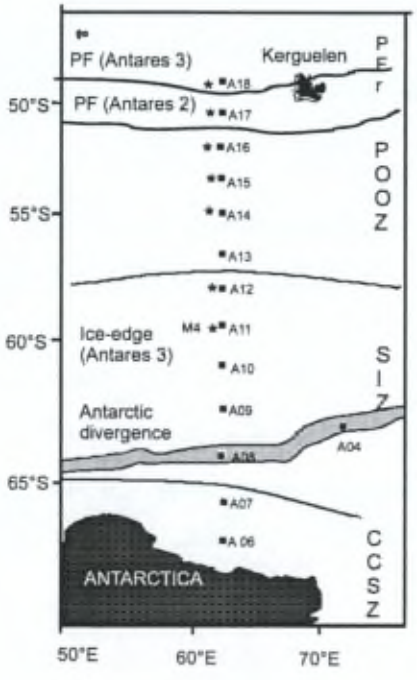


Figure 1. *Stations sampled during ANTARES 2 (closed square) and ANTARES 3 (star) in the Indian sector of the Southern Ocean. Four sub-areas identified as Polar Front region (PFr), Permanently Open Ocean Zone (POOZ), Sea Ice Zone (Sea Ice Zone) and Coastal and Continental Shelf Zone (CCSZ) are also indicated.*

Salinity, temperature, pressure, oxygen, nutrients and chlorophyll concentrations were measured at each station according to JGOFS recommendations (see SCOR, JGOFS report 6, 1990) for core parameters measurement (Fiala 1995, Descolas-Gros & Mayzaud 1997).

Microorganisms were sampled using a standard CTD rosette sampler equipped with 12 L Niskin bottles. Depths were chosen according to the physical and optical structure of the water column. This paper focuses on samples collected in the upper wind mixed layer.

Methods

Microbial numbers and biomass

The abundance and biomass of microorganisms was determined by epifluorescence microscopy (Leitz, Laborlux D) after DAPI staining.

Bacteria

2-20 ml of formalin-fixed (2% final concentration) seawater was stained with 4'6 diamidino-2-phenylindole (DAPI, 0.1 µg/l, final concentration) for 15 min (Porter & Feig 1980). Stained bacteria were collected by filtration on 0.2 µm pore-size black polycarbonate filters (Nuclepore). Filters were mounted on microscopic slides and stored at -20 °C until examination. Bacteria were enumerated on a minimum of 20 different fields at 1000x magnification. Their cell volume was calculated from the measurement of the shortest and longest axes, considering rods and cocci, respectively, as cylinders and spheres. Between 300-600 bacteria were measured for each sample. Biovolumes were converted to cell carbon after the biovolume-dependant conversion factor established by Simon and Azam (1989).

Protists

20 ml of glutaraldehyde-preserved (0.5% final concentration) seawater was stained with 4'6 diamidino-2-phenylindole (DAPI, 0.1 µg/l, final concentration) for 15 min. Stained protists were collected by filtration on a 0.4 µm and 10 µm Nuclepore black filter. Nano sized (2-20 µm in diameter) microorganisms were identified, counted and measured at a magnification of x 1250 while micro sized (20-200µm in diameter) microorganisms were analysed on the 10 µm pore size filter at a magnification of x 125. A minimum of 100 organisms per filter was counted. Autotrophic species were distinguished from heterotrophs by the red autofluorescence of chlorophyll a observed under blue light excitation. Mixotrophic species were distinguished from strictly heterotroph or autotroph organisms by the combined presence of chloroplastes and ingested bacteria and/or nanophytoplankton (Bouvier *et al.* 1998). Cell sizes were estimated visually by comparison with an ocular micrometer. Biovolumes were calculated from cell dimensions and shapes. Ciliate carbon contents were computed using a carbon to volume

conversion factor of 0.08 pgC μm^{-3} (Beers & Stewart, 1970). Flagellate and dinoflagellate biovolumes were converted into biomass with a conversion factor of 0.14 pgC μm^{-3} suggested by Lessard (1991) for dinoflagellates fixed with glutaraldehyde.

Biomass of total phytoplankton and phytoplankton < 10 µm was estimated from chlorophyll data (total and < 10 µm)assuming a average C/Chl a ratio of 35 proposed by Dehairs *et al.* (1992) for Antarctic phytoplankton.

Protozoa and phytoplankton were classified in size group, smaller (nanoplankton) and larger (microphytoplankton) than 10 µm (ESD, equivalent spherical diameter).

Biological activities

Protozoan feeding activity

Ingestion rates of bacteria and nanoplanktonic algae by protozooplankton were measured using the method based on the uptake of fluorescent prey (Sherr *et al.*, 1987; Rublee & Gallegos, 1989). Natural protozoan populations were incubated in the presence of added prey (bacteria and nanophytoplankton), previously stained with DTAF (5-(4,6-dichlorotriazin-2-yl) aminofluorescein). The number of prey ingested by protozoa per unit of time was kinetically measured during the incubation experiment through the microscopic identification of fluorescent prey within the protozoan vacuoles. Grazing rates (number of prey ingested by protozoa per hour) was deduced from the initial slope of the time-dependence curve.

Preparation of FLB and FLA:

Fluorescent labeled bacteria (FLB) were prepared from natural assemblages of bacterioplankton (equivalent spherical diameter of 0.44 µm +/- 0.12 µm; n=500) and mean biovolume of 0.06 μm^3) according to the procedure of Sherr *et al.* (1987). Fluorescent labeled algae (FLA) were obtained from cultures of Antarctic *Phaeocystis* cells (equivalent spherical diameter of 4.01 µm +/- 0.19 µm (n = 100)and mean biovolume of 33.5 μm^3) using the procedure of Rublee and Gallegos (1989). Stock solutions of FLB and FLA were kept at -4°C before feeding experiments.

Ingestion experiments:

Feeding experiments were carried out in 500 ml polycarbonate (Nalgene) bottles and run in the dark at *in situ* temperature under gently shaking. After an acclimation period of 30 min., natural assemblages of protozoa were inoculated with trace concentrations (10 %) of FLA and FLB. Sub-samples were removed every 15-60 minutes during the incubation periods (2 and 8 hours for FLB and FLA experiments, respectively). Biological activity was immediately stopped through the sequential addition of the following preservatives: alkaline lugol solution (0.5 % final concentration), borate buffered formalin (3% final concentration), and a drop of 3% sodium thiosulfate. According to Sherr *et al.* (1989), this fixative does not cause the egestion of prey.

Between 10 to 20 ml of the preserved samples were stained with DAPI (Porter & Feig, 1980). Protozoa were collected by filtration on 0.8 and 10 µm Nucleopore black polycarbonate membranes. Protozoan abundance and biomass, and average number of FLB or FLA ingested per protozoa were determined by epifluorescence microscopy. Ingestion rates of bacteria and phototrophic flagellates were then calculated for different groups of protozoa from the linear slope of the time dependent curve of average FLB and FLA number ingested per protozoa (Sherr *et al.* 1987). Integrated daily ingestion rate (mgC m^{-2} day^{-1}) were calculated by integration of protozoan ingestion rate up to the depth of the upper mixed layer water mass. Specific ingestion rates was defined as the ratio between the ingestion rate and the protozoan biomass.

Bacterial production

Bacterial production was estimated by measuring the incorporation of ^{3}H-Leucine according the Kirchman's protocol (1985). Data are described in extenso in Talbot (1995) and in Yoro (1997).

Surface layer daily bacterial production (mg C m^{-2} day^{-1}) was calculated by integration of bacterial production to the depth of the upper mixed layer water mass.

Phytoplankton production

Daily primary production was calculated from phytoplankton biomass, nutrient concentrations, light availability, ambient temperature using the AQUAPHY set of equations of Lancelot *et al.* (1991). Parameters of AQUAPHY were experimentally determined for natural micro- and nano-size population according to the protocol of Mathot *et al.* (1992). It involves on one hand short-term (1-3 hours) incubation of ^{14}C phytoplankton uptake at different light intensities (photosynthetic parameters) and on the other hand long-term (24 hours) kinetics of phytoplankton ^{14}C incorporation into cellular components (small metabolites, proteins, polysaccharides, lipids) during a natural day-night cycle. All experiments were conducted under "in situ" simulated conditions. AQUAPHY parameters were determined by mathematical fitting of experimental data. Daily rates were determined by integration of AQUAPHY equations on the variation of light at the surface and within depth. Incident surface PAR was continuously recorded by a cosine LiCor sensor set on the upper deck of the ship. Vertical light attenuation was measured by deploying the underwater sensor PNF (Biospherical Instruments).

RESULTS

Oceanographic conditions

In October 1995, the Indian sector was covered by ice up to latitude 59°30 S. The surface layer were characterized by low stability and low temperature (Descolas-Gros & Mayzaud 1997). The upper mixed layer was generally deep (> 100 m), excepted at the station A12 (Fig. 1). This station located at about 167 km north of the pack-ice (58°S) is submitted to melt water input from the pack ice as suggested by the lower salinities (33.7). Additionally, the presence of blocks of pack ice in this area reduced the wind stress and hence created a shallow and stable mixed layer of 25 m. As expected, nutrients concentrations were increasing along a North to South gradient. Silicate and nitrate at the southern stations were respectively 3.2 times (13.9 to 44.5 µmol $Si(OH)_4$ l^{-1}) and 1.1 times (26.0 to 29.5 µmol NO_3 l^{-1}) higher compared than northern concentrations (Floch *et al.* 1997). Ammonium was very low, < 0.05 µM in POOZ and between 0.05 and 1.5 µM in PFr. Chlorophyll a concentration varied between 0.37 and 0.21 µg l^{-1} in POOZ and PFr, respectively. At the station bordering the ice-edge, Chl a concentration reached 0.47 mg m^{-3}.

In February 1994, the ice retreating process was completed and much of the investigated area was ice free since one month. At the continental shelf stations, the depth of the upper mixed layer was around 50 m. On the contrary, strong wind was prevailing between latitudes 50° and 58 °S deepening the wind mixed layer to depths greater than 100 m. Like in early spring, North to South gradients were recorded for nitrate (23 to 29 µmol NO_3 l^{-1}), phosphate (1.55 to 1.95 µmol PO_4 l^{-1}) and silicate (5 to 55 µmol $Si(OH)_4$ l^{-1}) with northernmost concentrations being significantly lower than southernmost ones (Goeyens 1995). As expected ammonium concentrations during summer were an order of magnitude higher (0.23 to 0.82 µmol NH_4 l^{-1}) than in spring and its distribution pattern showed spots of high concentrations in the southern stations and in the PFr (Semeneh 1997). Chlorophyll a concentrations were very low between 0.1 and 0.5 mg m^{-3}.

Regional and seasonal distribution of microbial organism biomass

Protozooplankton

Protozooplankton biomass varied between 1.2 and 12.2 mg C m^{-3} (Fig. 3).

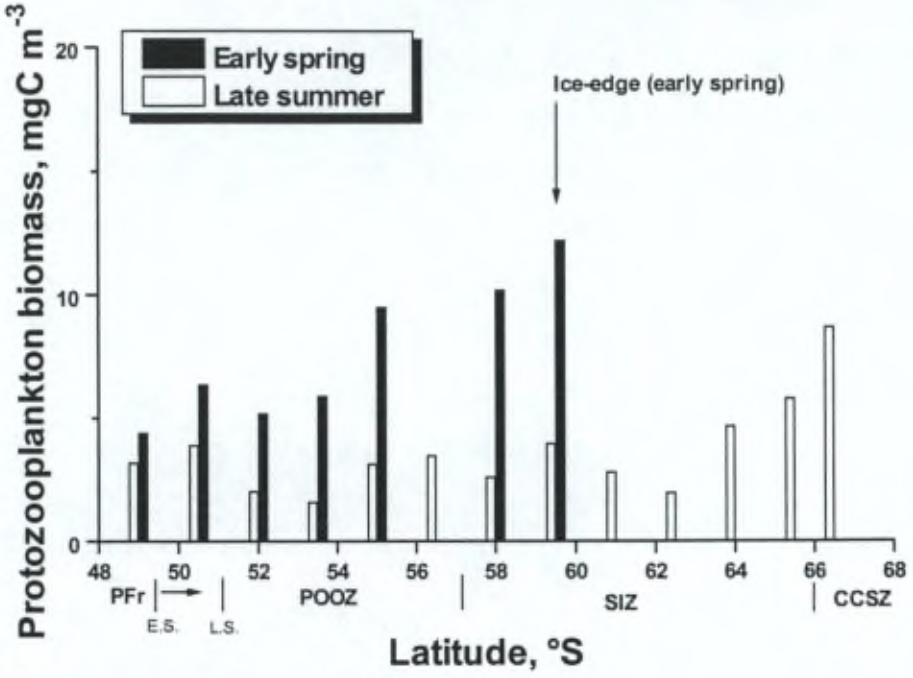


Figure 3. Geographical *distribution of protozooplankton biomass (mgC m^{-3}) in early spring (October 1995, ANTARES 3) and late summer (February 1994, ANTARES 2) along 62°W. The position of the PFr in early spring (E.S.) and late summer (L.S.), the POOZ, the SIZ and the CCSZ are indicated.*

Values recorded in early spring 1995 were significantly higher than those observed at the end of summer 1994. Maximum values were observed at the receding ice edge (SIZ) in early spring and at the most southern station (CCZS) at the end of summer. At these stations, micro sized organisms dominated the protozooplankton biomass. On the contrary, the protozooplankton of the POOZ and the PFr was dominated by nano sized organisms. Nanoprotozooplankton dominated in mean to 58 and 61 % of protozooplankton biomass respectively in early spring and late summer (Table 1 & 2).

Table 1. *Mean and extreme values of biomass (mgC m^{-3}) for main protozooplankton groups during early spring (October 1995, ANTARES 3) in the surface mixed layer.(-): negligible.*

Region **Station**	**PFr** **A18**	**POOZ** **A17 - A13**	**SIZ** **A12 - A11**	**%**
	Mean **(min.-max.)**	**Mean** **(min.-max.)**	**Mean** **(min.-max.)**	
Nanoprotozooplankton				
Choanoflagellates	0.1	0.4 (0.3 - 0.5)	0.3 (0.0 - 0.5)	6
Dinoflagellates	1.7	2.1 (1.3 - 3.6)	1.7 (1.5 - 1.8)	45
Other flagellates	1.2	2.2 (1.8 - 2.7)	1.8 (0.9 - 2.7)	41
Ciliates	0.2	0.7 (0.5 - 1.1)	0.3 (0.1 - 0.5)	8
Total	**3.2**	**5.5** **(3.8 - 7.4)**	**4.0** **(2.5 - 5.5)**	**58**
Microprotozooplankton				
Dinoflagellates	0.1	1.3 (1.0 - 2.1)	2.5 (2.1 - 2.9)	35
Ciliates	1.1	1.2 (1.0- 1.3)	1.4 (1.0 - 1.7)	33
Mixotrophic Ciliates	-	0.1 (0.1 - 0.1)	3.3 (3.0 - 3.6)	29
Sarcodines	-	0.1 (0.0 - 0.3)	0.2 (0.0 - 0.3)	3
Total	**1.2**	**2.7** **(2.0 - 3.5)**	**7.4** **(7 - 7.6)**	**42**
Protozooplankton	**4.4**	**8.2** **(6.1 - 9.5)**	**11.3** **(10.2 - 12.2)**	

Table 2. *Mean and extreme values of biomass (mgC m^{-3}) for main protozooplankton groups during late summer (February 1994, ANTARES 2) in the surface mixed layer.(-): negligible.*

Region Station	PFr A18 - A17	POOZ A16 - A14	SIZ A12 - A07	CCSZ A06	%
	Mean (min.-max.)	Mean (min.-max.)	Mean (min.-max.)	Mean (min.-max.)	
Nanoprotozooplankton					
Choanoflagellates	0.4 (0.1 - 0.6)	0.3 (0.0 - 0.7)	0.6 (0.0 - 1.2)	2.0	26
Dinoflagellates	-	-	0.03 (0.00 - 0.04)	0.0	0
Other flagellates	2.6 (2.4 - 2.8)	1.5 (0.9 - 2.3)	1.4 (0.7 - 2.1)	1.8	74
Ciliates	-	-	-	-	-
Total	**3.0** **(2.5 - 3.4)**	**1.8** **(0.9 - 3.1)**	**2.0** **(0.8 - 3.3)**	**3.8**	**61**
Microprotozooplankton					
Dinoflagellates	-	-	0.1 (0.0 - 0.2)	0.0	1
Ciliates	0.6 (0.5 - 0.7)	0.9 (0.1 - 2.4)	2.5 (0.9 - 3.7)	4.9	99
Mixotroph ciliates	-	-	-	-	-
Sarcodines	-	-	-	-	-
Total	**0.6** **(0.5 - 0.7)**	**0.9** **(0.1 - 2.4)**	**2.6** **(0.9 - 3.7)**	**4.9**	**39**
Protozooplankton	**3.5** **(3.2 - 3.9)**	**2.8** **(1.2 - 4.3)**	**4.6** **(2.5 - 6.1)**	**8.7**	

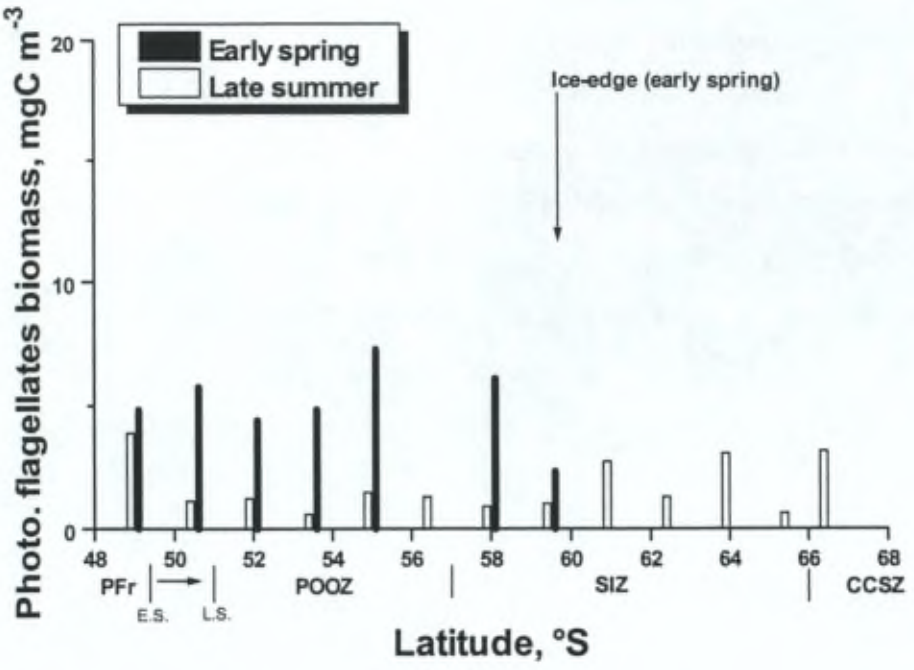
Among the nano-size community, these called other flagellates contributed to 41 % (early spring, Table 1) and 74 % (late summer, Table 2) of the nanoprotozooplankton biomass. Choanoflagellates biomass was always low, although absolute values were significantly higher, in particular in the CCSZ (26 % of total nanoprotozooplankton biomass, Table 2). As a general trend however little seasonal variability was recorded among choanoflagellate and other flagellated nanoprotozoa biomasses didn't show significant difference between both seasons. Contrasting, ciliates (8 % of the nanoprotozooplankton biomass) and heterotrophic dinoflagellate biomass (45 % of the nanoprotozooplankton biomass) were significant in the only spring 1995

(Table 1). The microprotozooplanktonic community was composed of dinoflagellates, heterotrophic and mixotrophic ciliates and sarcodines. In early spring (Table 1), dinoflagellates, heterotrophic ciliates and mixotrophic ciliates contributed, respectively, to 35, 33 and 29 % of the microprotozooplankton biomass . Mixotrophic species were only recorded in early spring, when they represented 45 % of the microprotozooplankton biomass in the SIZ (Table 1). The spring biomass of microdinoflagellates and microciliates was regionally different with the predominance of ciliates over dinoflagellates in the PFr and the opposite in the SIZ. In the POOZ microdinoflagellates and microciliates were equally distributed and represented the bulk of the microprotozoa biomass (Table 1). At the end of summer, dinoflagellate biomass became insignificant and ciliates dominated at 99 % of the microprotozoa biomass in the whole investigated area (Table 2).

Potential protozoan food

The concomitant distribution of bacteria and phototrophic flagellates distribution indicate that these microorganisms could largely contributed to the protozoan diet.

As a general trend, the average biomass of phototrophic flagellate was higher in early spring than in late summer (Fig. 4a). In early spring 1995, maximum biomass was typically observed at about latitude 55°S north of the receding ice edge (Fig. 4b) although very modest. At the end of summer 1994, the maximal nanophytoplanktonic biomass was observed at the PFr and in the vicinity of the continent when biomasses in the POOZ were extremely low (Fig. 4b). The maximum phototrophic flagellate biomass reached 7.6 mgC m^{-3} in early spring and 3.9 mgC m^{-3} in late summer (Fig. 4b). The phototrophic flagellate biomass ranged between 0.9 and 7.6 mgC m^{-3}, representing between 11 and 80 % of the total phytoplankton biomass (Fig. 4b, Table 3). In early spring, it represented 44 % as average of total phytoplankton biomass, with minimun (28 %) in the Sea Ice Zone. At the end of summer, it contributed to 39 % of total phytoplankton biomass, with low percent (31 %) in the SIZ.



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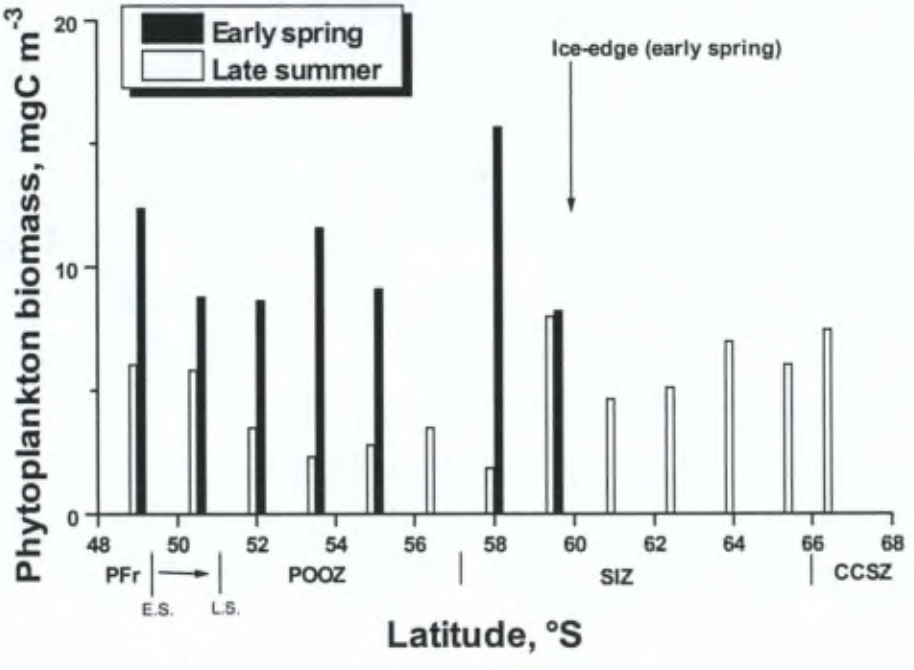


Figure 4. *Geographical distribution of phototrophic flagellates (A) and phytoplankton (b) biomass (mgC m^{-3}) in early spring (October 1995, ANTARES 3) and late summer (February 1994, ANTARES 2) along 62°E. The position of the PFr in early spring (E.S.) and late summer (L.S.), the POOZ, the SIZ and the CCSZ are indicated.*

Table 3. *Percentages of phototrophic flagellates in the total phytoplankton biomass in the Polar Frontal region, Permanently Open Ocean Zone, Sea Ice Zone and Coastal Continental Shelf Zone during October 1995 and February 1994.*

	Early spring (min - max) mean	Late summer (min - max) mean
PFr	(32- 65) **52**	(20 - 65) **42**
POOZ	(39 - 80) **53**	(26 - 54) **41**
SIZ	**28**	(11 - 59) **31**
CCSZ		**43**
Total	**44**	**39**

As a general trend, bacterioplankton biomass (Fig. 5) was the same order of magnitude than phototrophic flagellate biomass, with values ranging between 4.3 and 14.5 mgC m^{-3}. However, the seasonal variation was opposite with phytoplankton and protozooplankton biomasses, late summer bacterial biomass higher than that in early spring. Geographically, maximum values were observed in the CCSZ (early spring) and in the PFr although the range of variation was less compared to that of flagellates.

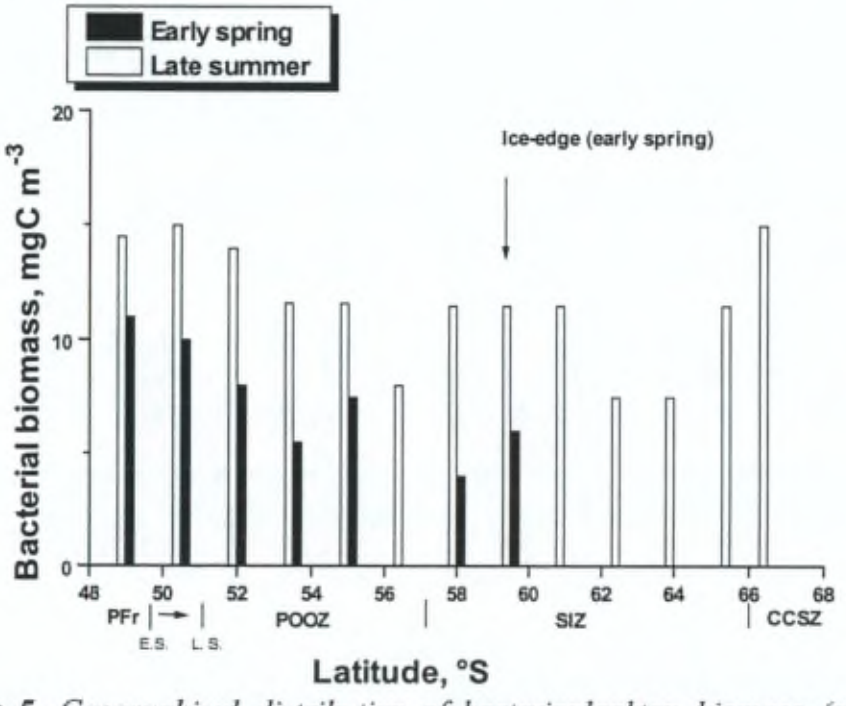


Figure 5. *Geographical distribution of bacterioplankton biomass (mgC m^{-3}) in early spring (October 1995, ANTARES 3) and late summer (February 1994, ANTARES 2) along 62°E. The position of the PFr in early spring (E.S.) and late summer (L.S.), the POOZ, the SIZ and the CCSZ are indicated.*

Protozoan feeding activities:

Specific ingestion rates of the different protozoan taxons on bacteria and phototrophic flagellates are reported in Table 4, 5. The examination of these table show a large variability was between different taxa but also within a same taxon.

Each protozoan taxon was feeding on bacteria (Table 4). However, the specific ingestion rates of nanoprotozooplankton and particularly those of choanoflagellates were extremely high (mean value of 0.0219 h^{-1}, Table 4). Therefore, bacteria were principally ingested (87 - 99 %, Table 6) by the nanoprotozooplankton, whatever the season was. respectively in early spring and late summer.

Table 4. *Specific ingestion rate (h^{-1}) of protozoa on bacteria during early spring (October 1995) and late summer (February 1994).*

	Early spring	**Late summer**
	(min - max) **mean**	**(min - max)** **mean**
Nanoprotozooplankton		
Choanoflagellates	(0.0008 - 0.1125) **0.0219**	(0.0006 - 0.1412) **0.0215**
Dinoflagellates	(0.0004 - 0.0112) **0.0033**	
Other flagellates	(0.0003 - 0.0408) **0.0081**	(0.0006 - 0.0225) **0.0089**
Ciliates	(0.0005 - 0.0198) **0.0082**	
Microprotozooplankton		
Dinoflagellates	(0.0001 - 0.0018) **0.0006**	
Ciliates	(0.0001 - 0.0041) **0.0010**	(0.0001 - 0.0003) **0.0002**
Mixotrophic ciliates	(0.0002 - 0.0004) **0.0003**	-

Table 5. *Specific ingestion rate (h^{-1}) of protozoa on nanoflagellates during early spring (October 1995)and late summer (February 1994).*

	Early spring (min. - max.) mean	**Late summer (min. - max.) mean**
Nanoprotozooplankton		
Dinoflagellates	(0.0001 - 0.1957) **0.0056**	
Other flagellates	(0.0001 - 0.0421) **0.0023**	
Ciliates	(0.0001 - 0.0280) **0.0023**	
Microprotozooplankton		
Dinoflagellates	(0.0006 - 0.0252) **0.0056**	
Ciliates	(0.0001 - 0.0789) **0.0128**	(0.0024 - 0.018) **0.0070**
Mixotrophic ciliates	(0.0003 - 0.0540) **0.0105**	-

All protozoa, excepted the choanoflagellates, were ingesting phototrophic flagellates (Table 5). Specific feeding rates of dinoflagellates in particular were similar for both nano- and microorganisms. Contrasting, specific feeding rate of microciliates were significantly higher than those of nanociliates. No difference was observed between the specific ingestion rates of heterotrophic and mixotrophic ciliates when occurring Early spring, 55, 37 and 8 % of phototrophic flagellates were ingested by nano-, micro-protozooplankton and mixotrophic ciliates, respectively. At one station (ice-edge), these mixotrophic organisms consumed up to 32 % of ingested phototrophic flagellates. In late summer, phototrophic flagellates were consumed by the only microprotozooplankton.

No significant difference for the specific ingestion rates was observed between the difference seasonal periods.

Table 6. *Mean and extreme percents of ingested bacteria and phototrophic flagellates by protozooplankton , and mixotrophic ciliates during early spring (October 1995) and late summer (February 1994).*

Protozoan taxon	% of bacteria (min.-max.), mean	% of phot. flagellates (min.-max.), mean
Nanoprotozooplankton		
Early spring	(71 - 99), **87**	(0 - 97), **55**
Late summer	(97 - 100), **99**	(0 - 1), **0**
Microprotozooplankton		
Early spring	(1 - 29), **11**	(1 - 99), **37**
Late summer	(0 - 3), **1**	(99-100), **100**
Mixotrophic ciliates		
Early spring	(0 - 8), **2**	(0 - 32), **8**

Protozoan daily ingestion rates in the upper wind mixed layer and particularly those on phototrophic flagellates, were significantly higher in early spring than in end- summer (Fig.6 and 7).

Bacterial ingestion rates displayed little seasonal variations ranging between 20.0 and 118.3 mg C m^{-2} d^{-1} (mean value of 48.5 mg C m^{-2} d^{-1}) and between 15.8 and 83.73 mg C m^{-2} d^{-1} (mean value of 33.75 mg C m^{-2} d^{-1}), respectively in early spring and late summer. Maximal values were observed in the PFr and in POOZ (south to the PFr) during early spring ,and close to the continent at the end of the summer.

High seasonality was recorded for nanoflagellates ingestion rates, ranging between 33.1 and 190.0 mg C m^{-2} d^{-1} (mean value of 105.7 mg C m^{-2} d^{-1}) in early spring and between 1.1 and 63.4 mg C m^{-2} d^{-1} (mean value of 16.5 mg C m^{-2} d^{-1}) in late summer. Maximal values were observed at about 100-150 km of the receding ice edge early spring and close to the continent at the end of the summer.

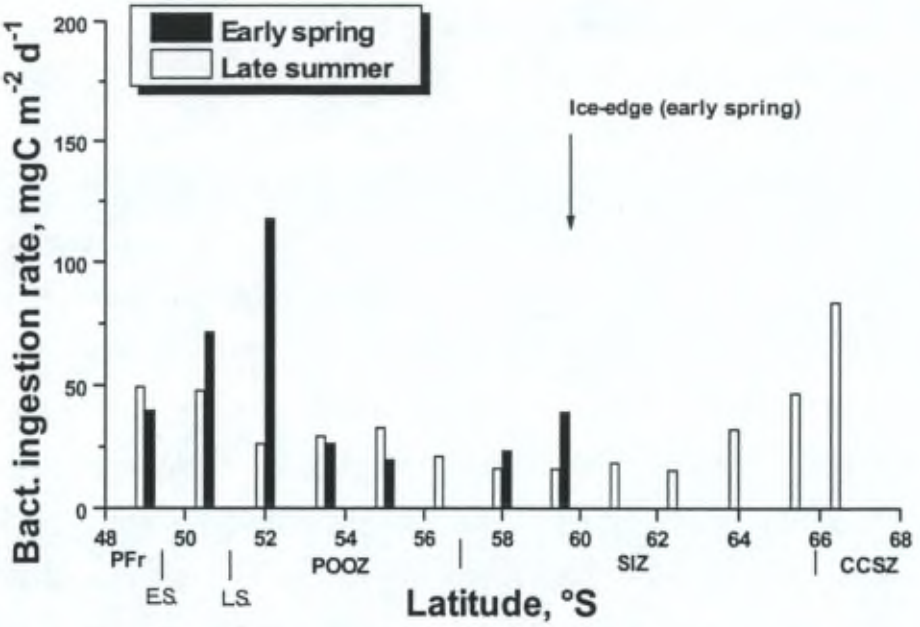


Figure 6. *Geographical distribution of bacterial ingestion rate along 62°E in early spring (October 1995 ,ANTARES 3) and late summer (February 1994 ANTARES 2).*

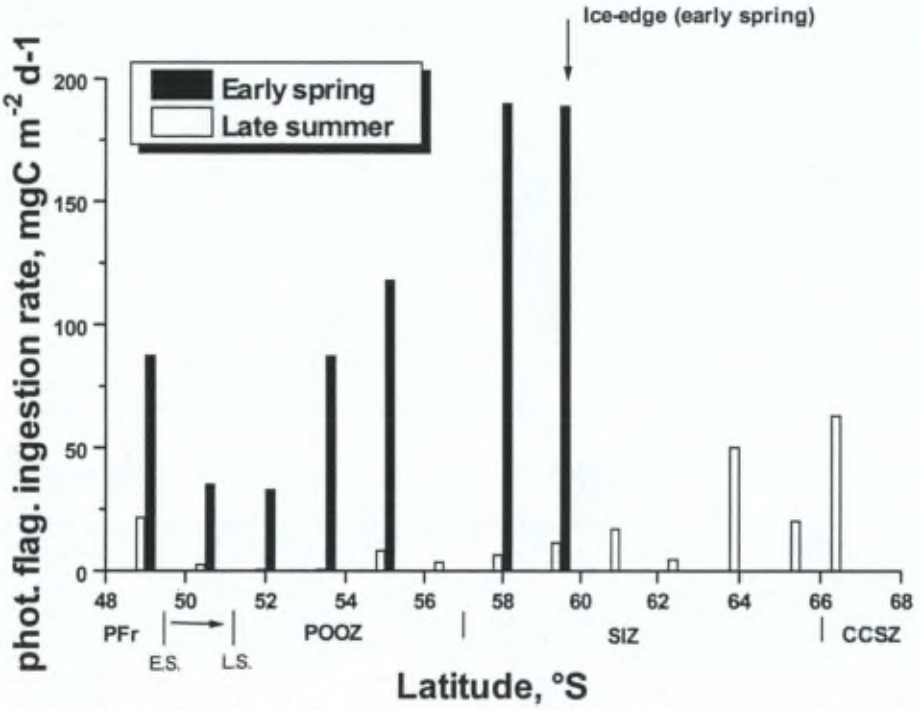


Figure 7. Geographical *distribution of phototrophic flagellate ingestion rate along 62°E in early spring (October 1995, ANTARES 3) and late summer (February 1994, ANTARES 2).*

DISCUSSION

Distribution of protozooplankton and potential food

Protozooplankton biomass measured in the Indian sector of the Southern Ocean in late summer 1994 and early spring 1995 was amongst the lowest recorded in the Southern Ocean (Becquevort *et al.* 1992, Becquevort 1997, Burkill *et al.* 1995, Garrison & Buck 1989, Garrison *et al.* 1991, 1993, Klaas 1996, Nöthig 1988 , Scharek *et al.* 1994). The maximum reached was 12 mgC m^{-3} and was observed in early spring in the marginal ice zone. This biomass is however low compared to those observed in spring in the marginal ice zone and which maximum recorded is 42 mgC m^{-3})(review by Becquevort, submitted). Despite its low level, protozoa biomass was relatively significant among the total microbial biomass. Indeed, it contributed to 30 % and 20 % of the total microbial biomass (bacterioplankton, total phytoplankton and protozooplankton) in early spring 1995 and late summer 1994, respectively (Table 7 & 8). As a general trend, the whole microbial community was low in this sector of the Southern Ocean at the investigated seasonal periods.

Table 7. *Mean biomass for each microbial groups and % of the total microbial biomass during October 1995 in the surface mixed layer.*

Region Station	PFZr A18 mgC m^{-3} %	POOZ A17 - A13 mgC m^{-3} %	SIZ A11 - A12 mgC m^{-3} %	Whole area mgC m^{-3} %
Phytoplankton	11.6	11.9	9.1	10.9
	44	47	34	41
Bacterioplankton	10.4	5.3	6.4	7.4
	40	21	24	28
Protozooplankton	4.4	8.2	11.3	7.6
	16	32	42	30

Table 8. *Mean biomass for each microbial groups and % of the total microbial biomass during February 1994 in the surface mixed layer.*

Region Station	PFZr A18 - A17 mgC m^{-3} %	POOZ A16 - A13 mgC m^{-3} %	SIZ A12 - A07 mgC m^{-3} %	CCSZ A06 mgC m^{-3} %	Whole area mgC m^{-3} %
Phytoplankton	5.9	3.0	5.3	7.5	5.4
	24	17	27	24	23
Bacterioplankton	14.8	11.4	10.1	15.0	12.8
	61	66	51	48	57
Protozooplankton	3.5	2.8	4.6	8.7	4.9
	15	17	22	28	20

This distribution is typical in the Southern Ocean in early spring (Becquevort *et al.* 1992, Becquevort 1997, Burkill *et al.* 1995, Garrison & Buck 1989, Garrison 1991b, Garrison &

Gowing 1993). Unexpected, however, the percentage of protozooplankton biomass did not increase in summer as reported by Garrison and Mathot (1996) who observed a significant increase of the relative contribution of protozoan in the total (nano and microplankton) biomass, along the season. On the contrary protozoan contribution reported here is very similar to the range of winter values calculated from the AMERIEZ (Antarctic Marine Ecosystem Research in the Ice Edge Zone) studies data in the Weddell and Scotia Seas (6-11, 8-19 and 48-76 % for the spring, autumn and winter studies, respectively) (Garrison & Mathot 1996).

Nanosize protozoa was dominating in the whole protozooplankton biomass, as reported for other studies in the Southern Ocean (Becquevort *et al.* 1992, Becquevort 1997, Burkill *et al.* 1995, Klaas 1997, Nöthig 1988, Nöthig *et al.* 1991, Scharek *et al.* 1994), excepted at the stations where maximum biomass were recorded. In the latter stations, micro size group was dominant. Nanoprotozooplankton was composed in majority of flagellates such as choanoflagellates, dinoflagellates and the so-called "other flagellates". Heterotroph dinoflagellates were not reported at the end of summer. This contrast with recent literature reporting that dinoflagellates are significant microorganisms in the Southern Ocean along the whole seasonal cycle (Nöthig *et al.* 1991, Bjornsen & Kuparinen 1991, Becquevort *et al.* 1992; Archer *et al.* 1996, Becquevort 1997) and particularly in spring and winter (Garrison & Gowing 1992). However, other observations, in the Weddell Sea, indicate that the contribution of heterotrophic dinoflagellates to the total protozooplankton biomass could be less significant in autumn too (Garrison & Mathot 1996). Mixotrophic ciliates as well weren't observed at the end of summer 1994 in the Indian sector of the Southern Ocean. However, mixotrophic ciliates were principally observed in the vicinity of the ice-edge in the Southern Ocean (Gowing & Garrison 1991, 1992), These mixotrophic organisms have not been reported in sufficient biomass to suggest a major contribution to primary production (Garrison *et al.* 1993), nevertheless, in this study, ingestion measurements show that they could be important grazers of the phototrophic flagellates.

The geographical and seasonal distributions of protozoan biomass was correlated with that of phototrophic nanoflagellates. On the other hand, bacterial and phototrophic flagellates biomasses were inversely correlated, phototrophic flagellates dominated in early spring in the SIZ although bacteria in end-summer in the PFr and CCSZ. Furthermore, bacteria were the most important component of the microbial community in late summer (Table 7). Indeed, a sharp increase of the relative importance of bacteria in the planktonic assemblage was observed, the fraction of bacterial biomass in the total microbial biomass shifted from 28 % in early spring to 57 % at the end of summer (Tables 7 and 8).

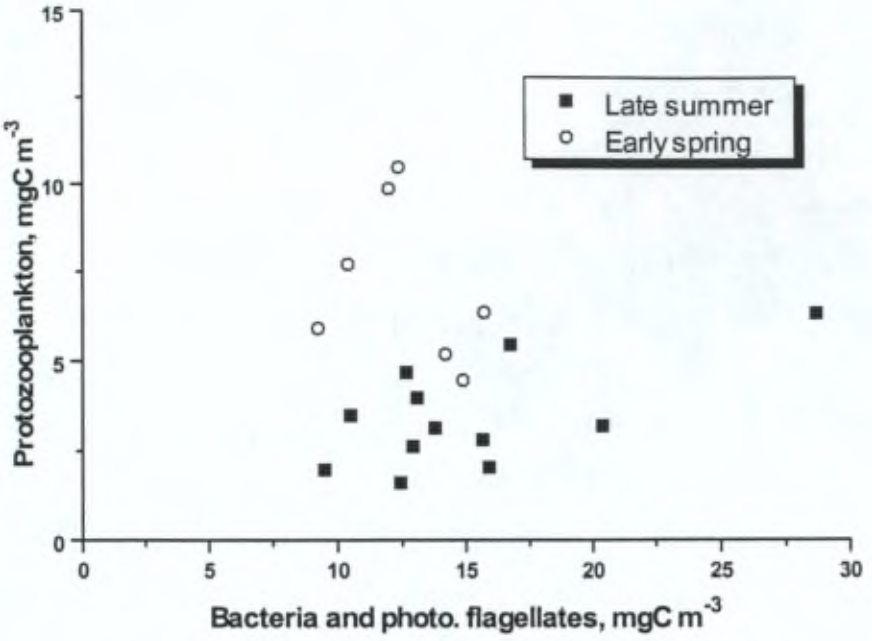


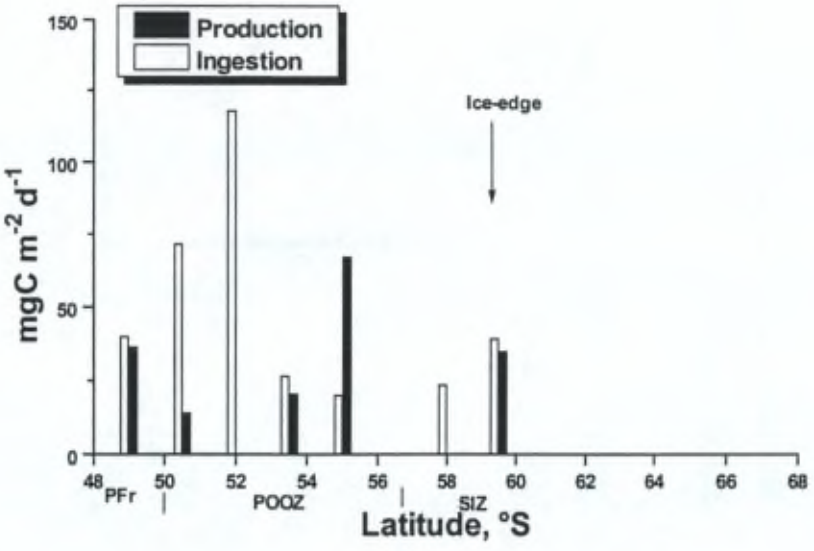
Figure 10. *Relationship between protozooplankton biomass and combined of bacterio-and phototrophic flagellates in early spring (ANTARES 3) and late summer (ANTARES 2). Early spring: no significant correlation. Late summer: Y= 0.80 + 0.17 X (R = 0.62)*

As shown in Fig.10, the ratio between protozoa and total potential food biomass (bacteria and phototrophic flagellates) was higher in early spring (27 - 84 %) than in late summer (13 - 46 %, mean 26 %). Interestingly, the qualitative composition (phototrophic flagellates and bacteria) of food available for the total protozoa community changed along the season. In early spring, the food available to protozooplankton was composed in majority of flagellates in early spring and bacteria in late summer.

Protozoan ingestion

Phototrophic flagellates were ingested by nanoprotozoa and microprotozoa. Among nanoprotozoa, the only dinoflagellates were actively grazing on phototrophic flagellates, due to their reported ability to feed on a large size spectrum of prey (Gaines & Elbrächter 1987, Hansen 1991). Bacteria were as expected ingested by protozoa < 10 µm, especially by choanoflagellates.

A.



B.

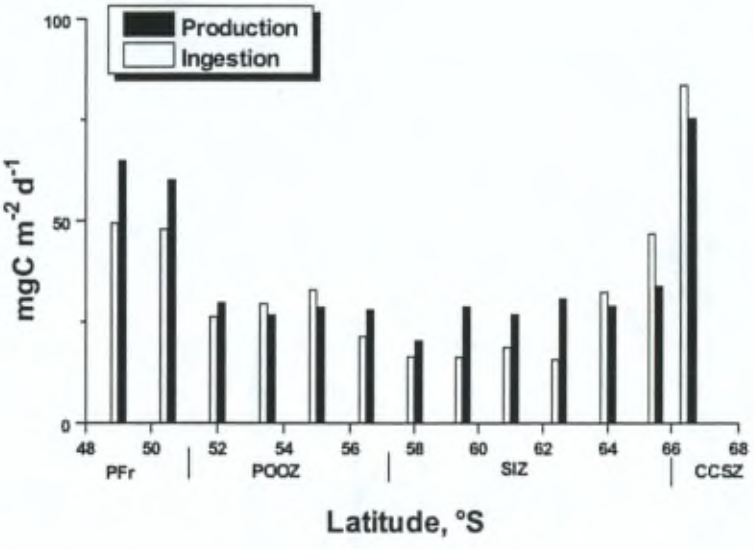
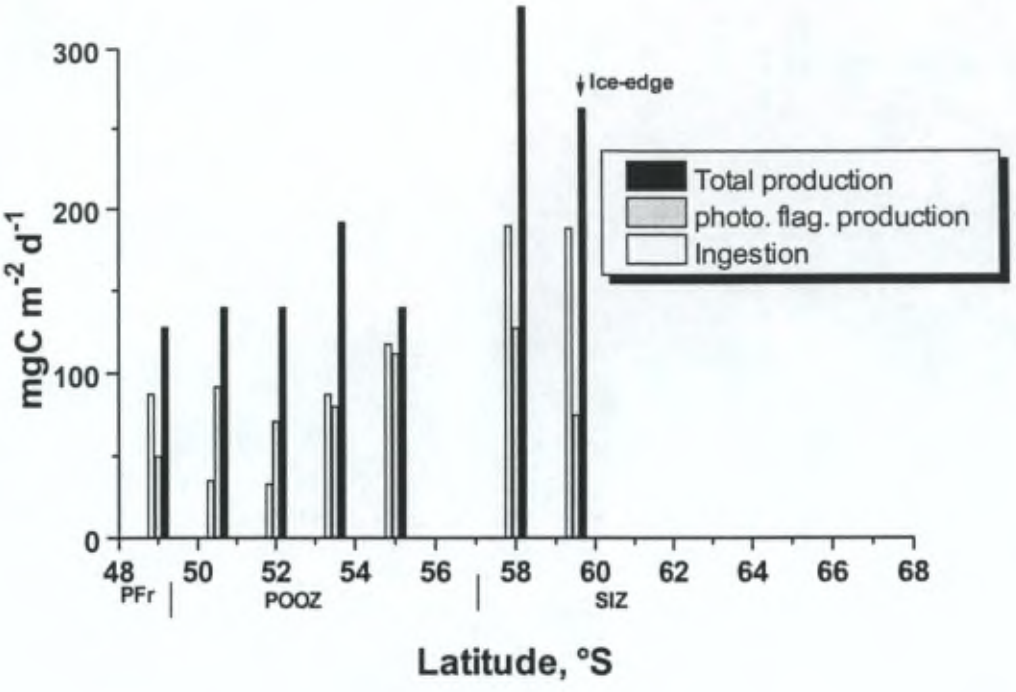


Figure 11. Geographical *distribution of daily ingestion rate of bacteria by protozooplankton and the daily bacterial production along the 62° E in October 1995 (ANTARES 3) and February 1994 (ANTARES 2).*

A.



B.

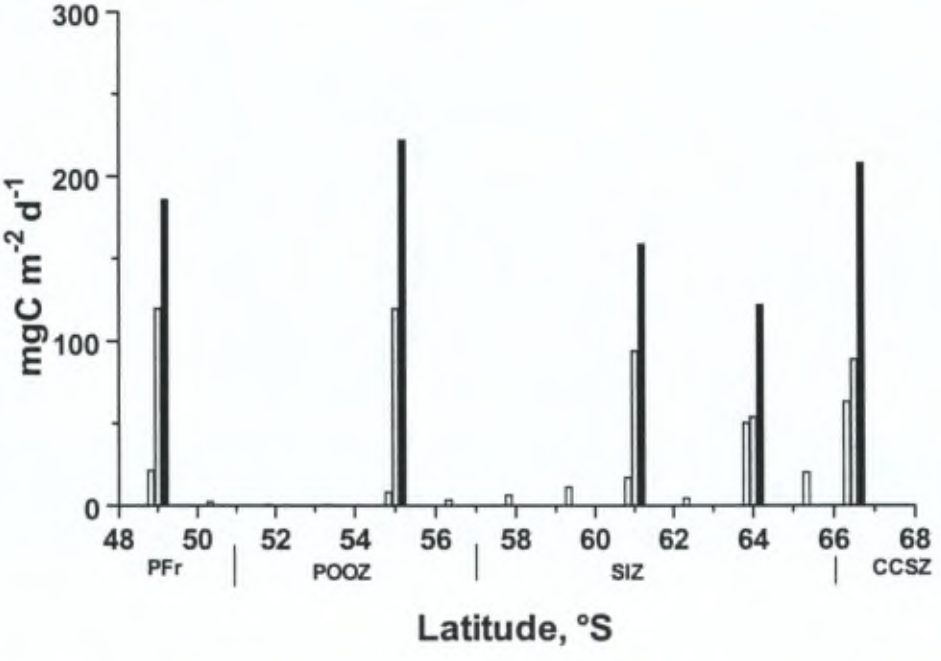


Figure 12. Geographical *distribution of daily ingestion rate of phototrophic flagellates by protozooplankton and the daily phytoplankton production (total and nanoflagellates) along the 62° E in October 1995 (ANTARES 3) and February 1994 (ANTARES 2).*

Daily protozoan ingestion on flagellates and bacteria (Fig. 11 and 12) were more higher in early spring than in late summer explained by the presence of higher protozoan biomass in spring compared to late summer. The daily protozoan ingestion rates on flagellates ranged between 23 and 182 mgC m^{-2} d^{-1}, with maximum values in early spring in SIZ. The daily protozoan ingestion rate on bacteria was maximum in early spring as well and reached 118 mgC m^{-2} d^{-1}. The total (nanoflagellates and bacteria) ingestion by protozoa was thus more important in early spring, but the relative proportion of ingested bacteria in the total protozoan ingestion was more important in summer (43 and 58% in early spring and late summer, respectively). In parallel, the relative proportion of choanoflagellates and other flagellates, potential consumers of bacteria (Sherr & Sherr 1989), in the nanoprotozoan biomass became higher in summer. As reported in Becquevort & Menon (submitted), the protozoan community was highly food selectivity, no significant competitive inhibition between bacteria and phototrophic flagellate prey could be evidenced in the Indian sector of the Southern Ocean. This suggested that protozoan organisms can be classified either as strict bacterivorous or flagellate consumers.

Trophic role of protozoa

The trophic role of protozooplankton in controlling the bacterial and primary production in the Indian sector of the Southern Ocean was estimated by comparing the ingestion by protozoa on phytoplankton and bacteria with their respective productions (Fig.11 and 12). In early spring 1995, the primary production was ranged between 128 and 327 mgC m^{-2} d^{-1} (mean 190 mgC m^{-2} d^{-1}) with maximal values near the ice-edge. 46 % was synthesised by phototrophic flagellates. The bacterial production (14- 67 mgC m^{-2}, mean 35 mgC m^{-2}) constituted 18 % of the primary production. In late summer 1994, the primary production was ranging between 122 and 222 mgC m^{-2} d^{-1} (mean 179 mgC m^{-2} d^{-1}), with 42 % by phototrophic flagellates. Bacterial production represented in mean 21 % of the primary production with maximal values of 35 and 37 % respectively in the PFZ and CCSZ.

Table 9. *Mean and extreme percents of bacterioplankton production ingested by protozoa in the Polar Frontal region, Permanently Open Ocean Zone, Sea Ice Zone and Coastal Continental Shelf Zone during early spring and late summer.*

	Early spring (min - max), mean	**Late summer (min - max), mean**
PFr	**110**	(76 - 80), **78**
POOZ	(30 - 510), **223**	(76 - 115), **94**
SIZ	**113**	(51 - 138), **86**
CCSZ		**111**
Total	**> 100**	**90**

Table 10. *Mean and extreme percents of phototrophic flagellates and total phytoplankton production ingested by protozoa in the Polar Frontal region, Permanently Open Ocean Zone, Sea Ice Zone and Coastal Continental Shelf Zone during early spring and late summer.*

	Early spring		**Late summer**	
	phot. flagellates (min - max), mean	**Total (min - max), mean**	**phot. flagellates (min - max), mean**	**Total (min - max), mean**
PFr	**175**	25 - 68, **47**	**18**	**13**
POOZ	38 - 109, **75**	25 - 84, **45**	**7**	**6**
SIZ	149 - 252, **200**	58 - 72, **65**	(18 - 93), **56**	(17 - 69), **43**
CCSZ	-	-	**71**	**34**
Total	**125**	**54**	**42**	**28**

Protozooplankton was controlling up to 90 % of the daily bacterioplankton production over the whole seasonal period (Table 9). On the contrary, protozoa didn't control totally the primary production (Table 10). In spring, it consumed 54 % of the total daily primary production but more than 100 % of phototrophic flagellate daily production. At the end of summer, protozoan grazing was controlling the primary production to a less extent, i.e. only 42 % of the phototrophic flagellates daily production. As a general trend, the grazing pressure of protozoa on phytoplankton was less significant at the end of summer than in spring.

CONCLUSION

In conclusion, , the protozoa trophic role in the carbon cycle in the Indian sector of the Southern Ocean was different during the different studied seasons. In early spring, protozooplankton controlled significantly the phototrophic flagellate production which represented as average 46 % of the primary production. Under such condition, the microbial food web (nanophytoplankton • protozoa) could constitute a significant carbon pathway to the traditional food chain. In late summer, the control by protozoa on phytoplankton became less significant. Only 18 % of the primary production was directly consumed by protozoa. Phytoplankton and protozoa would be controlled by metazooplankton following the traditional schema of linear food chain. On the other hand, bacterioplankton production in summer was more higher than early spring and was controlled significantly by protozoa, therefore the microbial loop (dissolved organic matter - bacteria - protozoa) didn't constitute a significant carbon pathway to metazooplankton due to intermediate trophic levels. Assuming a protozoa growth yield of 0.38 and two trophic steps before to be available for metazooplankton, only 3 % of the primary production became available to metazooplankton when it was channelled via the microbial loop.

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Chapitre 5

Modélisation mathématique: développement du module protozooplancton HBP et son intégration dans le modèle écologique SWAMCO

RESUME- Le modèle mathématique mécanistique constitue un outil intégrateur des connaissances acquises sur la cinétique des processus biologiques et permet de faire le lien entre l'observation phénomènologique et les mécanismes de fonctionnement de l'écosystème. Le modèle validé par confrontation des prédictions avec l'observation permet le calcul des flux de matières à l'échelle saisonnière ou annuelle de l'océan et constitue un outil scientifique performant d'exploration des facteurs physico-chimiques et biologiques qui régissent le fonctionnement de l'écosystème.

Les mécanismes qui déterminent la nature « HNLC » de l'écosystème antarctique ont ainsi été étudiés à l'aide du modèle mécanistique SWAMCO (SeaWAter Microbial COmmunities) construit progressivement sur base des connaissances acquises tout au long des programmes nationaux de recherche sur l'Antarctique ANTAR-I, -II, -III. Ce modèle décrit la circulation du carbone et des éléments biogéniques associés (N, P, Si) ainsi que du fer - en considération de son rôle déterminant dans la structuration de la chaîne planctonique - au travers des compartiments chimiques et biologiques-clef qui caractérisent le réseau planctonique microbien. Le modèle SWAMCO résulte du couplage direct de 3 modules décrivant respectivement la dynamique du phytoplancton (AQUAPHY; Lancelot et al., 1991), du bactérioplancton (HSB; Billen & Servais 1989, Billen & Becquevort 1992) et du protozooplancton (HBP; Becquevort, 1999). Le module AQUAPHY décrit les processus de photosynthèse, de croissance et d'assimilation de nutrients (NO_3, NH_4, PO_4, $Si(OH)_4$) associés à la communauté phytoplanctonique considérée comme formée de 2 groupes initiants des voies trophiques distinctes: le nanophytoplancton composé de nanoflagélés autotrophes et le microphytoplancton composé de diatomées. HSB décrit la dégradation de la matière organique dissoute par les bactéries et les flux de régénération de nutriments (NH_4, PO_4, Fe) associés à leur métabolisme. Le modèle HBP distincte 2 groupes de protozoaires qui se distinguent par la taille et les proies: les nanoprotozoaires brouteurs de bactéries et les microprotozoaires se développant à partir des nanoflagellés auto- et hétérotrophes. Les concepts physiologiques qui sous-tendent la formulation mathématique, la mise en équation et la paramétrisation du modèle HBP sont l'aboutissement de ce travail de doctorat et sont décrits in extenso dans la section 5.1. du présent chapitre.

Les performances du modèle assemblé SWAMCO peuvent être évaluées dans la section 5.2. qui présente l'application du modèle dans le secteur atlantique de l'océan Antarctique durant le printemps austral 1992. La capacité de prédiction du modèle SWAMCO est démontrée par confrontation des prédictions avec les observations récoltées durant la campagne ANTX/6 du navire de recherche océanographique "Polarstern". Pour cette application le code numérique du modèle mécanistique a été couplé 'off-line' à un modèle physique de mélange turbulent calculant la profondeur de la couche de surface en fonction des conditions météorologiques locales et de la couverture de glace. Les résultats du modèle montrent que les flux d'exportation de carbone organique de la couche de surface vers l'océan profond sont associés à des efflorescences de diatomées lesquelles sont co-gouvernées par la disponibilité de la lumière et du fer dissous.

Modèle HBP (Herbivorous & Bacterivorous Protozoa): concepts, formulation et paramétrisation

Formulation de la dynamique du protozooplancton

Dans ce travail, nous nous sommes attachés à formuler la dynamique des protozoaires consommant des bactéries et des flagellés autotrophes et hétérotrophes. Des expériences permettant de tester la sélectivité alimentaire des protozoaires réalisées dans différents sous-systèmes du secteur indien de l'océan Antarctique, ont suggéré que la communauté protozooplanctonique était hautement sélective dans son régime alimentaire (Lancelot *et al.* 1997). Certains ne consomment que des bactéries tandis que d'autres ne consomment que des flagellés hétérotrophes et autotrophes.

Ainsi la communauté protozooplanctonique a pu être représentée simplement par deux variables d'état. Les nanoflagellés hétérotrophes (HNF) consommant seulement des bactéries et les microprotozoaires (MCZ) consommant les nanoflagellés hétérotrophes (HNF) et autotrophes (NF). L'ensemble de la communauté protozooplanctonique étant consommé par le métazooplancton.

1. Les variations dans le temps des biomasses des nanoflagellés hétérotrophes (HNF) et des microprotozoaires (MCZ) dépendent de leurs croissances (μ) moins des processus de mortalité tel que la lyse cellulaire (lys) et le broutage (graz) par le zooplancton: les équations sont les suivantes:

$$\frac{dHNF}{dt} = \mu_{HNF} - lys_{HNF} - graz_{MC/HNF}$$

$$\frac{dMCZ}{dt} = \mu_{MCZ} - lys_{MCZ} - graz_{MS/MC}$$

- Le taux de croissance est proportionnel à leur rendement de croissance (Y_{zoo}) multiplié par leur taux d'ingestion (graz):

$$\mu_{HNF} = Y_{ZOO} graz_{HNF}$$

$$\mu_{MCZ} = Y_{ZOO} graz_{MCZ}$$

L'ingestion des protozoaire est fonction de la biomasse de ceux-ci (HNF, MCZ) multiplié par leurs taux d'ingestion spécifique. Le taux d'ingestion spécifique des protozoaires est lié à la concentration en particules alimentaires (f_{ut}) au dessus d'une valeur seuil (ths) en particules alimentaires (voir parametrisation) selon un réponse fonctionnelle Holling de type II analogue à une cinétique de type Michaelis-Menten caractérisée par un taux d'ingestion maximum ($graz_{max}$) et une constante de demi-saturation (k_g) :

$$graz_{HNF} = graz_{\max}^{HNF} \frac{f_{ut}}{f_{ut} + k_g} HNF$$

$$graz_{MCZ} = graz_{\max}^{MCZ} \frac{f_{ut}}{f_{ut} + k_g^{mcz}} MCZ$$

avec pour les nanoflagellés hétérotrophes consommant des bactéries:

$$f_{ut} = BAC - ths_{HNF}$$

où BAC: biomasse bactérienne

ths_{HNF}: valeur seuil de la biomasse bactérienne en dessous duquel les protozoaires n'ingèrent pas des bactéries.

et pour les microprotozoaires consommant des flagellés autotrophes et hétérotrophes:

$$f_{ut} = NF + HNF - ths_{MCZ}$$

où NF: biomasse des flagellés autotrophes

HNF: biomasse des flagellés hétérotrophes

ths_{MCZ}: valeur seuil de la biomasse en flagellés en dessous duquel les protozoaires n'ingèrent pas de flagellés.

- La lyse cellulaire du protozooplancton est décrite selon une cinétique de première ordre:

$$lys_{HNF} = k_d^{ZOO}\ HNF$$

$$lys_{MCZ} = k_d^{ZOO}\ MCZ$$

où

k_d^{zoo} est la constante de lyse de première ordre.

- La mortalité par broutage est pour les flagellés hétérotrophes réalisée par les microprotozoaires et pour ces derniers par le métazooplancton , selon la proportion relative de leurs particules alimentaires :

Donc pour les flagellés hétérotrophes (HNF) consommés par les microprotozoaires pouvant également consommer des flagellés autotrophes (NF), la mortalité par le broutage s'exprime de la façon suivante:

$$graz_{MC/HNF} = graz_{MCZ}\frac{HNF}{NF + HNF}$$

où $graz_{MCZ}$ est formulé ci dessus.

Pour les microprotozoaires consommés par le métazooplancton qui consomment également des diatomées (DA), la mortalité par le broutage s'exprime de la façon suivante:

$$graz_{MS/MC} = graz_{MSZ} \frac{MCZ}{MCZ + DA}$$

où $graz_{MSZ}$ est une fonction de forçage.

2. La régénération en nutriments (N, P, Fe) par les protozoaires est également formulée:

Ces nutriments sont régénérés par les protozoaires, ceci en fonction de leur besoin relatif (leur rapport C/N/P/Fe) et la composition relative (rapport C/N/P/Fe de leur particules alimentaires) de leurs particules alimentaires en ces éléments.

Ainsi la régénération par les flagellés hétérotrophes consommant des bactéries s'exprime de la façon suivante:

$$reg^{N}_{HNF} = graz_{HNF} / cn_{BAC} - \mu_{HNF} / cn_{ZOO}$$

$$reg^{P}_{HNF} = graz_{HNF} / cp_{BAC} - \mu_{HNF} / cp_{ZOO}$$

$$reg^{Fe}_{HNF} = graz_{HNF} fec_{BAC} - \mu_{HNF} fec_{ZOO}$$

où

cn_{ZOO}, cp_{ZOO}, fec_{ZOO} sont les rapports C/N, C/P et Fe/C des protozoaires

cn_{BAC}, cp_{BAC}, fec_{BAC} sont les rapports C/N, C/P et Fe/C des protozoaires

La régénération par les microprotozoaires consommant des flagellés autotrophes et hétérotrophes s'exprime de la manière suivante:

$$reg^{N}_{MCZ} = graz_{MCZ}\frac{NFF/cn_{phy} + HNF/cn_{ZOO}}{NF + HNF} - \mu_{MCZ}/cn_{ZOO}$$

$$reg^{P}_{MCZ} = graz_{MCZ}\frac{NFF/cp_{phy} + HNF/cp_{ZOO}}{NF + HNF} - \mu_{MCZ}/cp_{ZOO}$$

$$reg^{Fe}_{MCZ} = graz_{MCZ}\frac{NFF\ fec_{NF} + HNF\ fec_{ZOO}}{NF + HNF} - \mu_{MCZ}\ fec_{ZOO}$$

où

cn_{ZOO}, cp_{ZOO}, fec_{ZOO} sont les rapports C/N, C/P et Fe/C des protozoaires

cn_{PHY}, cp_{PHY}, fec_{PHY} sont les rapports C/N, C/P et Fe/C du phytoplancton

Valeurs des paramètres caractérisant la dynamique du protozooplancton

- L'ingestion des flagellés hétérotrophes consommant des bactéries ainsi que celle des microprotozoaies consommant des flagellés hétérotrophes et autotrophes ont été mesurés expérimentalement lors des campagnes océanographiques dans le secteur Atlantique et Indien de l'Océan Antarctique:

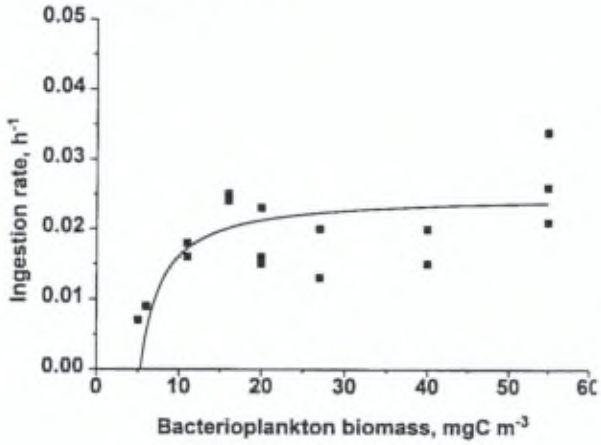

Figure 1. *Réponse fonctionelle des flagellés hétérotrophes consommant des bactéries.*

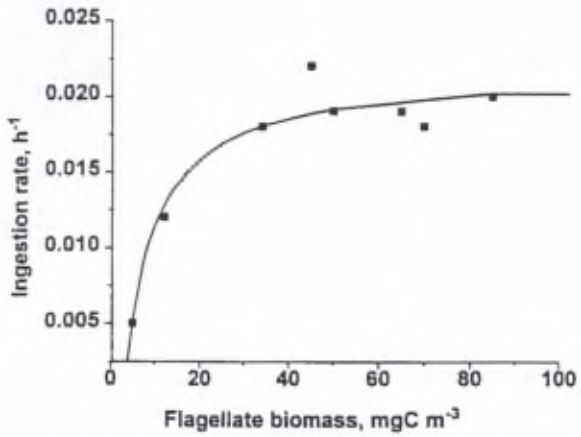

Figure 2. *Réponse fonctionelle des microprotozoaires consommant des flagellés hétérotrophes et autotrophes.*

Pour les deux groupes de protozoaires, il y a un seuil de concentration en particules alimentaires en dessous duquel les protozoaires ne consomment pas de nourriture (Fig. 1 & 2). Physiologiquement, cela s'explique très bien que lorsque la concentration en particules alimentaires devient trop faible, les protozoaires dépenserait trop d'énergie pour les capturer et dès lors il préfère faire la diète et éventuellement s'enkyster (Heinbockel 1978). Au dessus de ce seuil, la réponse fonctionnelle des deux groupes était une réponse fonctionnelle Holling de type II caractérisée par un taux maximum d'ingestion ($graz_{\max}^{HNF}$, $graz_{\max}^{MCZ}$) et une constante de demi-saturation (k_g^{HNF}, k_g^{MCZ}) (Fig 1 & 2)

- Un rendement de croissance de 0.38 était mesuré expérimentalement sur une communauté protozooplanctonique Antarctique par Björnsen & Kuparinen (1991). A ma connaissance, aucune autre valeur de rendement de croissance n'a été mesurée pour la communauté protozooplanctonique Antarctique. Les rendements de croissance pour les protozoaires reportés dans la littérature varient dans une très large gamme de 0.02 à 0.76 (Caron 1991) mais en général on estime que les protozoaires ont un rendement de croissance de l'ordre de 0.3 (Fenchel 1987).

- La constante de lyse cellulaire était estimée selon des valeurs mesurées sur des communautés phytoplanctoniques (Brussaard *et al.* 1995) .

- Les rapports C/N/P/Fe sont tirés de la littérature (Morel *et al.* 1990, Sunda & Huntsman 1997, Tortell *et al.* 1996).

Les valeurs des différents paramètres sont rassemblés dans les tables 1 et 2.

Table 1. *Valeurs des paramètres caractérisant la dynamique des flagellés hétérotrophes consommant des bactéries.*

Paramètres	Symboles	Valeurs	Unités
Seuil en bactéries	ths_{HNF}	0.33	mmolC. m^{-3}
Taux maximum d'ingestion	$graz_{\max}^{HNF}$	0.03	h-1
Constante de demi-saturation	k_g^{HNF}	0.25	mmolC. m^{-3}
Rendement de croissance	Y_{HNF}	0.38	-
Constante de lyse	lys_{HNF}	0.001	h^{-1}
HNF C/N ratio	cn_{ZOO}	5	mmolC/mmolN
HNF C/P ratio	cp_{ZOO}	80	mmolC/mmolP
HNF Fe/ C ratio	fec_{ZOO}	0.0024	µmolFe/mmolC

Table 2. *Valeurs des paramètres caractérisant la dynamique des microprotozoaires consommant des flagellés autotrophes et hétérotrophes.*

Paramètres	Symboles	Valeurs	Unités
Seuil en flagellés	ths_{MCZ}	0.083	mmolC. m^{-3}
Taux maximum d'ingestion	$graz_{\max}^{MCZ}$	0.02	h^{-1}
Constante de demi-saturation	k_g^{MCZ}	0.25	mmolC. m^{-3}
Rendement de croissance	Y_{MCZ}	0.38	-
Constante de lyse	lys_{MCZ}	0.001	h^{-1}
HNF C/N ratio	cn_{ZOO}	5	mmolC/mmolN
HNF C/P ratio	cp_{ZOO}	80	mmolC/mmolP
HNF Fe/ C ratio	fec_{ZOO}	0.0024	µmolFe/mmolC

Intégration de ce sous-modèle protozooplancton au modèle SWAMCO

Ce sous-modèle décrivant explicitement la dynamique du protozooplancton a été intégré au modèle mécanistique SWAMCO décrivant la circulation du carbone, de l'azote, du phosphore et du fer dans l'écosystème planctonique Antarctique. Il a été appliqué dans le secteur Atlantique de l'Océan Antarctique au printemps 1992 (voir chapitre 5.2.).

Modeling phytoplankton blooms and related carbon export production in the Southern Ocean : application to the Atlantic sector in Austral spring 1992

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ABSTRACT- The High Nutrient Low Chlorophyll (HNLC) conditions of the Southern Ocean have been explored with an ecological model (SWAMCO) describing C, N, P, Si and Fe cycling through different aggregated chemical and biological compartments of the plankton ecosystem. The structure of the model has been chosen in order to take explicitly into account biological processes of importance in carbon biomass formation and mineralisation in surface waters as well as in carbon export production. State variables include major inorganic nutrients (NO_3, NH_4, PO_4, $Si(OH)_4$), dissolved Fe, two groups of phytoplankton (diatoms and nanoflagellates), bacteria, heterotrophic nanoflagellates, microzooplankton, labile DOC and two classes of dissolved and particulate organic polymers with specific biodegradability. The model is closed by export production of particulate organic matter out of the surface layer and, when relevant, by metazooplanton, the grazing pressure of which is described as a forcing function. parametrisation was derived from the best current knowledge on the kinetics of biological processes in the Southern Ocean and in other 'HNLC' areas. For its application in the Atlantic sector in spring 1992, the SWAMCO model was coupled 'off-line' to a 1D physical model forced by in situ meteorological and sea-ice conditions. The predictions of the model were successfully compared with chemical and biological observations recorded in the Antarctic Circumpolar Current (ACC) during the 1992 cruise ANTX/6 of RV Polarstern. In particular the model simulates quite well the diatom bloom and carbon export event recorded in the iron-enriched Polar Frontal region as well as the lack of ice-edge phytoplankton blooms in the marginal zone (MIZ) of the ACC area. Model results analysis show that sufficient light and iron concentrations above 1 µmol m^{-3} are the necessary conditions for enhancing diatom blooms and particulate carbon export production in the Southern Ocean. Low iron availability prevents diatom growth but is still adequate for nanophytoplankton, the biomass of which is however kept to Chl *a* levels less than 1 mg m^{-3} due to the loss term by the ubiquitous micrograzers. Little carbon export is predicted under iron-limitation conditions. Sensitivity tests conducted on the parameters describing iron uptake by diatoms reveal the complex nature of Fe and Si limitation in regulating the magnitude and extent of diatom blooms and export production in the Southern Ocean.

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INTRODUCTION

The Southern Ocean is known to be a region with High Nutrient but Low Chlorophyll (HNLC) and the issue has been to understand this Antarctic Paradox. Once unraveled this would furthermore allow addressing the role played by the Southern Ocean in global carbon cycling and hence its influence on global climate regulation. Within this region, the combined effects of wind stress and thermohaline circulation result in circumpolar surface divergence and upwelling which maintain high concentrations of all major nutrients in the surface layer (nitrate : 20-30 mmol m^{-3}; phosphate : 1.6-2 mmol m^{-3}; silicate : 30-100 mmol m^{-3} see e.g. Gordon *et al.*, 1986). The light regime, while highly seasonal, reaches during summer daily integrated values as high as in the tropics (Campbell and Aarup, 1989). Despite the permanently high nutrient concentrations and seasonally high incident surface light, primary production is generally low (e.g. the review by Mathot *et al.*, 1992). Mesoscale events of high productivity do however occur in (i) the Polar Front between 47° and 50°S (e.g. Bathmann *et al.*, 1997); (ii) shallow, coastal embayments (e.g. Holm-Hansen and Mitchell, 1991) and (iii) the vicinity of the retreating ice-edge (e.g. Smith and Nelson, 1985). Yet recorded maximum phytoplankton biomasses seldom reach the 25 mg Chl *a* m^{-3} expected from the nutrients stocks (Mitchell and Holm-Hansen, 1991).

Several hypotheses have tempted to explain the paradox of high nutrients and low Chl *a* concentrations in the Southern Ocean. In a recent review, de Baar and Boyd (1998) suggest that phytoplankton growth in the Southern Ocean is under the triple control of (i) light availability driven by incident light, ice cover and wind stress; (ii) iron availability and (iii) micrograzing pressure. However, the degree to which physical, chemical and biological factors are co-limiting phytoplankton bloom events is not fully understood and their relative importance may vary with location, time and local meteorological conditions (Lancelot *et al.*, 1993).

The major role played by ice cover and the turbulence of the water column in controlling available light to phytoplankton and hence bloom initiation has been evidenced by numerous field data. It is now admitted that deep-mixed ice-free areas are not highly productive and are dominated by nanoplankton communities (El-Sayed, 1984; Smetacek *et al.*, 1990). On the other hand many observational evidences (e.g. Smith and Nelson 1985, 1986; Nelson *et al.* 1987; Sullivan *et al.* 1988; Lancelot *et al.* 1991a,b) indicate that the circumpolar marginal ice zone is a region of enhanced primary production owing to the formation, at the time of ice melting, of a shallow vertically stable upper layer as a result of the production of melt water. Provided the ice-edge is well-defined, these ice-edge related phytoplankton blooms trail the ice-edge as a narrow band 50 - 200 km wide (Smith and Nelson, 1985; Lancelot *et al.*, 1993a). Yet phytoplankton biomass reached in these hydrodynamically stable areas, either dominated by nanophytoplankton

(Hewes *et al.*, 1990; Lancelot *et al.*, 1993) or diatoms (Bianchi *et al.*, 1993), remains modest, less than 10 mg Chl *a* m^{-3}, significantly lower than expected from nutrients concentrations (Mitchell and Holm-Hansen, 1991). Furthermore non appearance of otherwise expected phytoplankton blooms has recently been reported at the receding ice-edge of the ACC in the Atlantic sector (Smetacek et al., 1997) and in the Bellingshausen Sea (Turner and Owens, 1995).

Iron limitation of phytoplankton growth in this remote area, already suggested in 1931 (Gran, 1931), has been investigated since 1988 in several regions of the Southern Ocean by running various Fe-enrichment experiments in shipboard microcosms: the Weddell and Scotia Sea (de Baar *et al.*, 1990; Buma et al., 1991), the Drake Passage (Helbling *et al.*, 1991), the Ross Sea (Martin *et al.*, 1990) and the Atlantic sector of the Antarctic Circumpolar Current (van Leeuwe *et al.*, 1997; Scharek *et al.*, 1997). Bioassay results show that the addition of Fe was consistently found to stimulate the growth of the large diatoms. This impact of added Fe on large diatoms was also observed in other HNLC areas like the equatorial Pacific Ocean (Chavez *et al.*, 1991; Fitzwater *et al.*, 1996; Zettler *et al.*, 1996) and the subarctic North Pacific Ocean (Boyd *et al.*, 1996). More recently, the repeated intentional in situ iron enrichment experiment in the equatorial Pacific Ocean (Coale *et al.*, 1996) also led to a diatom bloom. Apparently diatoms not only require light and all three major nutrients N, P and Si but also some iron as suggested before (Harvey, 1933, 1937). From the modern evidence it can be concluded that the general low availability of dissolved Fe in HNLC areas is not limiting phytoplankton growth rate per se. Rather Fe availability is structuring the phytoplankton community that drives in turn the structure of the dominant food web (carbon retention-microbial food-web versus carbon export-linear diatom-mesozooplankton food chain) and export production. Low Fe supply is indeed limiting the growth rate of large diatoms while still sufficient for the development of pico- and nano-sized cells, better competitors at low nutrient concentration due to their larger surface:volume ratio (Morel, 1990). The biomass of these minute organisms is kept at very low level, grazed by the ubiquitous fast-growing protozoa (Frost and Franzen, 1992; Lancelot *et al.*, 1993; Price *et al.*, 1994). Recent bioassay studies on Antarctic diatoms (Takeda, 1998) show that iron limitation leads to more silicified, hence faster-sinking, diatoms evidencing a more complex pattern of nutrient limitation interactions in HNLC ecosystems with consequences for the related biogeochemical cycles.

Considering the circumpolar variations in the distribution of dissolved iron (de Baar *et al.*, 1998) and the large variability of meteorological conditions (in particular wind stress and sea ice prevailing at these high latitudes), the contribution of physical, chemical and biological factors to the control of phytoplankton bloom development will greatly vary within the Southern Ocean,

both geographically and temporally. Phytoplankton will experience forcing between two extremes - low trace metal concentration and windy meteorological conditions or sufficient trace metal concentration and serene meteorological conditions - giving rise to quite different phytoplankton species dominance and biomass, food-web structures and carbon export production.

Towards addressing the role of the Southern Ocean in global carbon cycling and its response to or influence on climate change, stress then the need to implement ecological models that describe and predict the transfers of carbon, nitrogen, silicon and iron through appropriate biological and chemical compartments of the polar ocean over seasons and years, in response to the physical forcing. These biogeochemical models have to be based on the best available understanding of biological processes of importance in carbon biomass formation and mineralisation in the surface waters and carbon export production to deeper layers of the ocean. They have to take into consideration the dynamics of sea-ice retreat and formation as well as the different routes of Fe supply. As a first step in this direction, an 'off-line' coupled physical-biological 1D-model (Lancelot *et al.*, 1991,a,b; Lancelot *et al.*, 1993) had been developed for the simulation of ice-edge nanophytoplankton blooms in the marginal ice zone of the north-western Weddell Sea. The published model describes C and N circulation through aggregated biological components of the planktonic microbial food-web consisting explicitly in nanophytoplankton and bacteria, and relying on temperature-dependent first-order kinetics for describing micrograzing loss. Inorganic nitrogen includes ammonia (NH_4) and nitrate (NO_3). The preference of phytoplankton for uptake of ammonia was also considered. Although outstanding for describing C cycling in regions dominated by pico- and nanoplankton, the existing model was not applicable for estimating the carbon sequestration capability of the Southern Ocean and the trophic efficiency of the global marine ecosystem.

This paper presents and describes the SWAMCO (SeaWAter Microbial Community) model, an upgraded version of existing ecological model of Lancelot *et al.* (1991,a,b; 1993) for its application at the scale of the whole Southern Ocean. In order to take into consideration the key role of iron in driving the structure and functioning of the Southern Ocean ecosystem and the related biogeochemical cycles, the structure of the biogeochemical model has been extended by (i) adding to the nutrient pool dissolved Fe, silicic acid and phosphate as explicit state variables; (ii) considering two phytoplankton groups : nano-sized flagellates under control of micrograzer pressure and large diatoms feeding mesozooplankton and krill; and (iii) elaborating an explicit mathematical module of nano- (heterotrophic nanoflagellates) and micro-grazer (microzooplankton) feeding activities and related regeneration of both ammonia, phosphate and

dissolved Fe. Parametrization of the extended numerical code was derived from data on phytoplankton physiology (Jochem *et al.*, 1995; Scharek *et al.*, 1997; Mathot, unpublished data) and feeding activity of bactivorous and herbivorous protozoa (Becquevort, 1997) gained during the SO-JGOFS expedition ANT X/6 of RV Polarstern in the Atlantic sector of the Southern Ocean, in early spring 1992 as well as from literature data on HNLC areas. The capability of the model to properly simulate phytoplankton bloom and carbon export events in the Southern Ocean was assessed through its application in the Atlantic sector of the Southern Ocean covered by the ANT X/6 cruise of 1992. This well-documented cruise was chosen because it has been sampling repeatedly during 40 days along one section (6°W) crossing different water masses with contrasting ice coverage, physical stability, iron concentration, diatom bloom and particulate export production (Smetacek *et al.*, 1997). The synergistic effect of light and iron in stimulating phytoplankton blooms and carbon export production in the Southern Ocean were further investigated, based upon SWAMCO iron-enrichment scenarios runs at contrasting latitudes of the ANT X/6 section.

MODEL DESCRIPTION

General structure of the SWAMCO model

The model results from the off-line coupling of the ecological model SWAMCO with a one-dimensional hydrodynamical model. It consists of a two-layers 1-D model composed of a well-mixed upper layer and a stratified deeper layer up to the euphotic depth delineated at 100m (Lancelot *et al.*, 1993). The hydrodynamical model is an adaptation to polar seas of the wind-mixed layer model of Denman (1973). The current numerical code has been extended with terms describing freshwater fluxes from ice-melting and the effects of wind friction changes over ice-covered regions. Basic concepts, mathematical description and parametrization are described extensively by Veth (1991a,b). Performance and limits of the model are discussed by Veth *et al.* (1992).

The structure of the SWAMCO model - state variables and processes linking them -is schematically illustrated by Fig. 1 and Table 1.

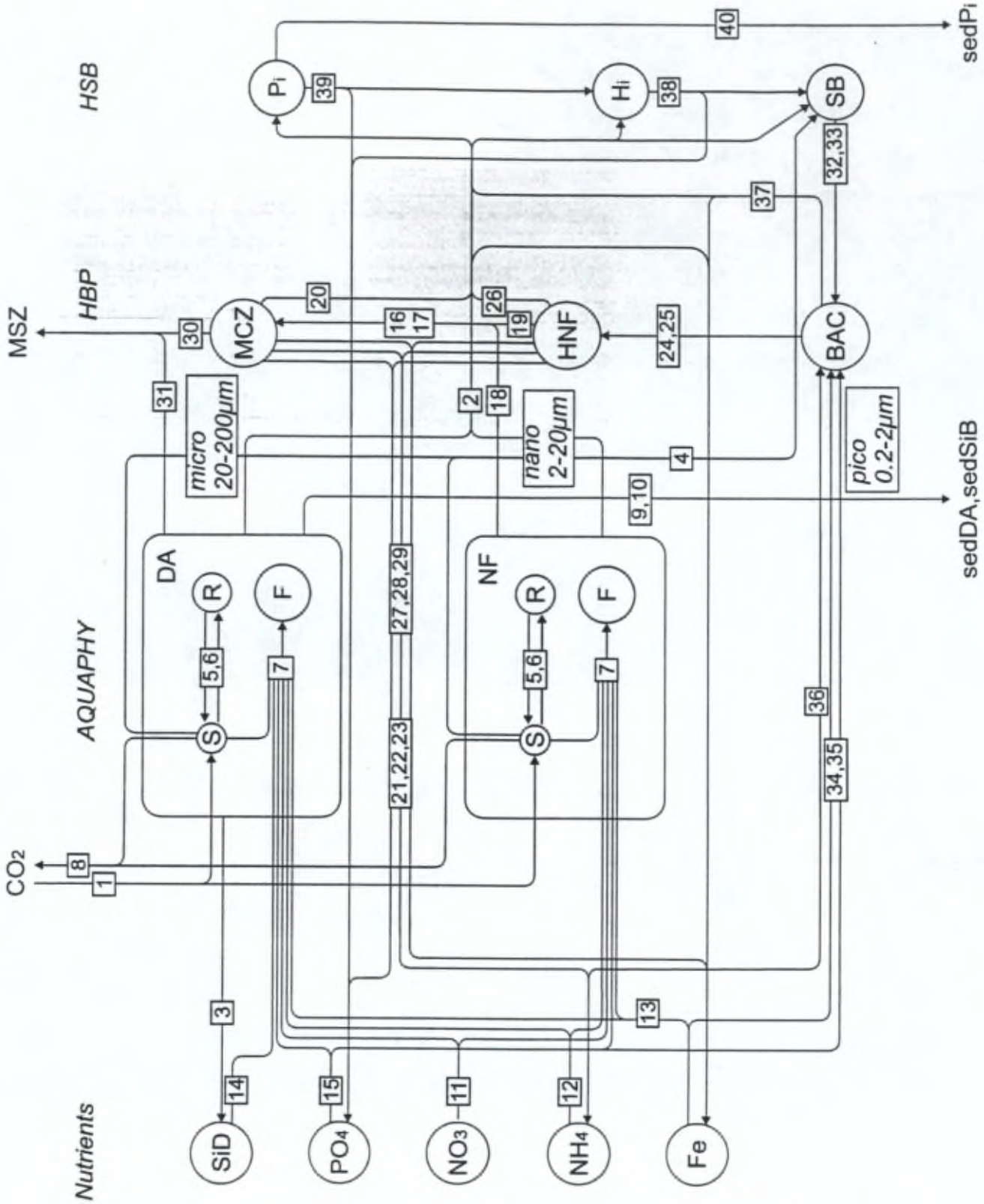

Figure 1. *Diagrammatic representation of structure of the biogeochemical SWAMCO model (state variables and processes linking them are defined in Table 1).*

Table 1a. *Nomenclature of the SWAMCO model: state variables*

DAF	functional and structural metabolites (diatoms)
DAS	monomers (diatoms)
DAR	reserve material (diatoms)
NFF	functional and structural metabolites (autotrophic nanoflagellates)
NFS	monomers (autotrophic nanoflagellates)
NFR	reserve material (autotrophic nanoflagellates)
MCZ	microzooplankton
HNF	heterotrophic nanoflagellates
BAC	bacteria
SBC	bacteria substrate (C monomers)
SBN	bacteria substrate (N monomers)
HC1	C dissolved organic matter (high biodegradability)
HC2	C dissolved organic matter (low biodegradability)
PC1	C particulate organic matter (high biodegradability)
PC2	C particulate organic matter (low biodegradability)
HN1	N dissolved organic matter (high biodegradability)
HN2	N dissolved organic matter (low biodegradability)
PN1	N particulate organic matter (high biodegradability)
PN2	N particulate organic matter (low biodegradability)
HP1	P dissolved organic matter (high biodegradability)
HP2	P dissolved organic matter (low biodegradability)
PP1	P particulate organic matter (high biodegradability)
PP2	P particulate organic matter (low biodegradability)
NO3	nitrate
NH4	ammonium
PO4	phosphate
SiD	silicic acid
SiB	particulate Si
Fe	dissolved iron

Table 1b. *Nomenclature of the SWAMCO model: biogeochemical processes (number are those reported on Fig.1).*

1	φ_i	photosynthesis (i=1 : diatoms ; i=2 : nanoflagellates)
2	lys_i^j	phytoplankton autolysis (i=1 : diatoms ; i=2 : nanoflagellates) (j=1 : F ; j=2 : S ; j=3 : R)
3	lys_{SiB}	biogenic silica lysis
4	e_i	phytoplankton exudation (i=1 : diatoms ; i=2 : nanoflagellates)
5	s_R^i	synthesis of reserve products (R) (i=1 : diatoms ; i=2 : nanoflagellates)
6	c_R^i	catabolism of reserve products (R) (i=1 : diatoms ; i=2 : nanoflagellates)
7	μ_i	phytoplankton growth (i=1 : diatoms ; i=2 : nanoflagellates)
8	$resp_i$	phytoplankton respiration (i=1 : diatoms ; i=2 : nanoflagellates)
9	sed_{DA}	diatoms sedimentation
10	sed_{SiB}	biogenic silica sedimentation
11	$upt_{PHY}^{NO_3}$	nitrate uptake by the phytoplankton
12	$upt_{PHY}^{NH_4}$	ammonium uptake by the phytoplankton
13	upt_{PHY}^{Fe}	dissolved iron uptake by the phytoplankton
14	upt_{PHY}^{Si}	silicic acid uptake by the phytoplankton
15	upt_{PHY}^{P}	phosphate uptake by the phytoplankton
16	μ_{MCZ}	microzooplankton growth
17	$graz_{MCZ}$	microzooplankton grazing
18	$graz_{MC/NF}$	microzooplankton grazing on autotrophic nanoflagellates
19	$graz_{MC/HNF}$	microzooplankton grazing on heterotrophic nanoflagellates
20	lys_{MCZ}	microzooplankton autolysis
21	reg_{MCZ}^{N}	nitrogen regeneration by the microzooplankton
22	reg_{MCZ}^{P}	phosphorus regeneration by the microzooplankton
23	reg_{MCZ}^{Fe}	iron regeneration by the microzooplankton
24	μ_{HNF}	heterotrophic nanoflagellates growth
25	$graz_{HNF}$	heterotrophic nanoflagellates grazing
26	lys_{HNF}	heterotrophic nanoflagellates autolysis
27	reg_{HNF}^{N}	nitrogen regeneration by the heterotrophic nanoflagellates
28	reg_{HNF}^{P}	phosphorus regeneration by the heterotrophic nanoflagellates
29	reg_{HNF}^{Fe}	iron regeneration by the heterotrophic nanoflagellates
30	$graz_{MS/MC}$	mesozooplankton grazing on microzooplankton
31	$graz_{MS/DA}$	mesozooplankton grazing on diatoms
32	μ_{BAC}	bacteria growth
33	upt_{BAC}	carbon uptake by bacteria
34	upt_{BAC}^{P}	phosphorus uptake by bacteria
35	upt_{BAC}^{Fe}	iron uptake by bacteria
36	α_{BAC}	ammonification
37	lys_{BAC}	bacteria autolysis
38	$elys_{H_i}$	H_i extra-cellular hydrolysis by bacteria
39	lys_{P_i}	P_i extra-cellular hydrolysis by bacteria
40	sed_{P_i}	particulate organic matter sedimentation

It results from the assemblage of 3 sub-models describing (i) the physiological growth of autotrophic nanoflagellates (NF) and diatoms (DA) according to the AQUAPHY conceptual model (Lancelot_*et al.*, 1991a); (ii) the dynamics of microbial organic matter degradation (the HSB model, Billen and Servais, 1988); and (iii) the dynamics of bactivorous (HNF) and herbivorous (MCZ) protozoa (the HBP model, Becquevort, in preparation).

Nitrate (NO_3), ammonia (NH_4), phosphate (PO_4) and iron (Fe) are assimilated by both phytoplankton groups whilst silicic acid (SiD) is taken up by the only diatoms (DA) which therefore also constitutes the pool of biogenic silica SiB. Phosphate and iron are always taken up by bacteria (BAC). On the other hand the bacterial uptake of ammonia is occasional and occurs at times when the chemical composition of the bacterial substrates (SB) is N-depleted. Ammonia is regenerated through metabolic activity of bacteria , as well as the bactivorous (HNF) and herbivorous (MCZ) protozoa. The iron is released after microbial lysis and also as the product of HNF and MCZ catabolism. Mesozooplankton grazing pressure on diatoms and herbivorous protozoa is described as a forcing function and no food preference is considered. C, N, Si and Fe export production into the deep ocean corresponds to the loss from the surface layer of particulate organic matter by sedimentation of diatoms as well as dead (detrital) particulate matter (P) including fecal pellets. Due to their low density, the sedimentation nanophytoplankton, bacteria and protozoa is neglected. All microorganisms undergo autolytic processes which release dissolved (D) and particulate (P) polymeric organic matter in the water column.

The differential equations describing the state variables conservation are listed in Table 2. The equations relative to the AQUAPHY, HBP and HSB modules are described in Table 3; process-related parameters are defined and listed in Table 4.

Table 2. *Conservation equations of the state variables of the SWAMCO model*

Phytoplankton

DA : diatoms, *NF* : autotrophic nanoflagellates
F : functional + structure metabolites, *S* : monomeric substrates, *R* : reserve material

$DA = DAF + DAS + DAR \quad ; \quad NF = NFF + NFS + NFR$

$$\frac{d\,DAF}{d\,t} = \mu_{DA} - lys_F^{DA} - (graz_{MS/DA} + sed_{DA})\frac{DAF}{DA} \qquad \textbf{Eq. V- 1}$$

$$\frac{d\,DAS}{d\,t} = \varphi_{DA} + c_{DAR} - s_{DAR} - \mu_{DA} - resp_{DA} - lys_S^{DA} - e_{DA} - (graz_{MS/DA} + sed_{DA})\frac{DAS}{DA} \qquad \textbf{Eq. V- 2}$$

$$\frac{d\,DAR}{d\,t} = s_{DAR} - c_{DAR} - lys_R^{DA} - (graz_{MS/DA} + sed_{DA})\frac{DAR}{DA} \qquad \textbf{Eq. V- 3}$$

$$\frac{d\,NFF}{d\,t} = \mu_{NF} - lys_F^{NF} - graz_{MC/NF}\frac{NFF}{NF} \qquad \textbf{Eq. V- 4}$$

$$\frac{d\,NFS}{d\,t} = \varphi_{NF} + c_{NFR} - s_{NFR} - \mu_{NF} - resp_{NF} - lys_S^{NF} - e_{NF} - graz_{MC/NF}\frac{NFS}{NF} \qquad \textbf{Eq. V- 5}$$

$$\frac{d\,NFR}{d\,t} = s_{NFR} - c_{NFR} - lys_R^{NF} - graz_{MC/NF}\frac{NFR}{NF} \qquad \textbf{Eq. V- 6}$$

Protozooplankton

Micro-zooplankton (MCZ)

$$\frac{d\,MCZ}{d\,t} = \mu_{MCZ} - lys_{MCZ} - graz_{MS/MC} \qquad \textbf{Eq. V- 7}$$

Heterotrophic nanoflagellates (HNF)

$$\frac{d\,HNF}{d\,t} = \mu_{HNF} - lys_{HNF} - graz_{MC/HNF} \qquad \textbf{Eq. V- 8}$$

Bacteria (BAC), C and N monomeric substrates for bacteria (SBC, SBN)

$$\frac{d\,BAC}{d\,t} = \mu_{BAC} - lys_{BAC} - graz_{HNF} \qquad \textbf{Eq. V- 9}$$

$$\frac{d\,SBC}{d\,t} = elys_{H_1} + elys_{H_2} + lys_S^{DA} + lys_S^{NF} + e_{DA} + e_{NF} - upt_{BAC} \qquad \textbf{Eq. V- 10}$$

$$\frac{d\,SBN}{d\,t} = elys_{H_1}\frac{HN_1}{HC_1} + elys_{H_2}\frac{HN_2}{HC_2} - upt_{BAC}\frac{SBN}{SBC}$$ **Eq. V- 11**

Organic matter (H = soluble, P = particular, *i* : 1. quickly- 2. slowly biodegradable substrates)

$$\frac{d\,HC_i}{d\,t} = \varepsilon_d^i\, lys_{bio} + lys_{PC_i} - elys_{H_i}$$ **Eq. V- 12**

$$\frac{d\,PC_i}{d\,t} = \varepsilon_p^i\, lys_{bio} - lys_{PC_i} - sed_{PC_i}$$ **Eq. V- 13**

with : $lys_{bio} = lys_F^{DA} + lys_R^{DA} + lys_F^{NF} + lys_R^{NF} + lys_{MCZ} + lys_{HNF} + lys_{BAC}$

$$\frac{d\,HN_i}{d\,t} = \varepsilon_d^i\, lysN_{bio} + lys_{PN_i} - elys_{HC_i}\frac{HN_i}{HC_i}$$ **Eq. V- 14**

$$\frac{d\,PN_i}{d\,t} = \varepsilon_p^i\, lysN_{bio} - lys_{PN_i} - sed_{PN_i}$$ **Eq. V- 15**

with : $lysN_{bio} = \frac{lys_F^{DA} + lys_F^{NF}}{cn_{PHY}} + \frac{lys_{MCZ} + lys_{HNF}}{cn_{ZOO}} + \frac{lys_{BAC}}{cn_{BAC}}$

$$\frac{d\,HP_i}{d\,t} = \varepsilon_d^i\, lysP_{bio} - elys_{HC_i}\frac{HP_i}{HC_i}$$ **Eq. V- 16**

$$\frac{d\,PP_i}{d\,t} = \varepsilon_p^i lysP_{bio} - lys_{PP_i} - sed_{PP_i}$$ **Eq. V- 17**

with : $lysP_{bio} = \frac{lys_F^{DA} + lys_F^{NF}}{cp_{PHY}} + \frac{lys_{MCZ} + lys_{HNF}}{cp_{ZOO}} + \frac{lys_{BAC}}{cp_{BAC}}$

Nutrients

$$\frac{d\,NO_3}{d\,t} = -upt_{PHY}^{NO_3}$$ **Eq. V- 18**

$$\frac{d\,NH_4}{d\,t} = \alpha_{BAC} + reg_{MCZ}^{N} + reg_{HNF}^{N} - upt_{PHY}^{NH_4}$$ **Eq. V- 19**

$$\frac{d\,PO_4}{d\,t} = elys_{H_1}\frac{HP_1}{HC_1} + lys_{PP_1} + elys_{H_2}\frac{HP_2}{HC_2} + lys_{PP_2} + reg_{MCZ}^{P} + reg_{HNF}^{P} - upt_{PHY}^{P} - upt_{BAC}^{P}$$ **Eq. V- 20**

$$\frac{d\,SiD}{d\,t} = lys_{SiB} - upt_{DA}^{Si}$$ **Eq. V- 21**

$$\frac{d\,SiB}{d\,t} = upt_{DA}^{Si} - lys_{SiB} - sed_{SiB}$$ **Eq. V- 22**

$$\frac{d\,Fe}{d\,t} = reg_{MCZ}^{Fe} + reg_{HNF}^{Fe} + lys_{bio}^{Fe} - upt_{PHY}^{Fe} - upt_{BAC}^{Fe}$$ **Eq. V- 23**

with : $lys_{bio}^{Fe} = lys_{F}^{DA}\,fec_{DA} + lys_{F}^{NF}\,fec_{NF} + \left(lys_{MCZ} + lys_{HNF}\right)fec_{ZOO} + lys_{BAC}\,fec_{BAC}$

Table 3. *Process equations of the SWAMCO model*

AQUAPHY (phytoplankton) *i* = 1,2 : *DA, NF*

photosynthesis

$$\varphi_i = k_{\max}^{i}\left(1 - e^{-\alpha_i I / k_{\max}^{i}}\right)\left(e^{-\beta I / k_{\max}^{i}}\right) F_i$$ **Eq. P- 1**

with : $I = I_0\left(\left(1 - a_{ice}\right)ice + \left(1 - a_{sea}\right)\left(1 - ice\right)\right)e^{-\eta z}$

$a_{ice} = 0.95$; $a_{sea} = 0.15$

I_0 : global radiation $\left[\mu E / m^2\,s\right]$; z : depth$[m]$; ice : ice cover$[\ ]$

$$\eta = 0.042 + 0.025 \cdot \chi \cdot \sum_{i:DA,NF} F_i$$

Lysis and exudation

$$lys_F^i = k_{lys}\,F_i \quad ; \quad lys_S^i = k_{lys}\,S_i \quad ; \quad lys_R^i = k_{lys}\,R_i$$ **Eq. P- 2**

$$lys_{SiB} = k_{lys}\,SiB$$ **Eq. P- 3**

$$e_i = \varepsilon \varphi_i$$ **Eq. P- 4**

Synthesis (s) and catabolism (c) of reserve products

$$s_R^i = \rho_{\max}^{i}\,\frac{S^{ut}}{S^{ut} + k_s}\,F_i \quad \text{with : } S^{ut} = S_i / F_i - Q_s$$ **Eq. P- 5**

$$c_R^i = k_c^R\,R_i$$ **Eq. P- 6**

growth and respiration

$$\mu_i = \mu_{\max}\,\frac{S^{ut}}{S^{ut} + k_s}\,\widetilde{N}\,F_i$$ **Eq. P- 7**

with : $\widetilde{N} = \min\left(\frac{N^{ut}}{N^{ut} + k_n}, \frac{P^{ut}}{P^{ut} + k_p}, \frac{Fe^{ut}}{Fe^{ut} + k_{fe}^{i}} \left[, \frac{Si^{ut}}{Si^{ut} + k_{si}} \right]^{(*)} \right)$

$N^{ut} = NO_3 + NH_4 - {}^{k_n}/_{10}$

$P^{ut} = PO_4 - {}^{k_p}/_{10}$

$Fe^{ut} = Fe - {}^{k_{fe}^{i}}/_{10}$

$Si^{ut} = SiD - {}^{k_{si}}/_{10}$ (*)diatoms only

$resp_i = K_F \; F_i + \xi \, \mu_i$ **Eq. P- 8**

with : $\xi = ecs_{NH_4} \; rpi + ecs_{NO_3} \left(1 - rpi\right)$ (metabolic cost)

sedimentation (diatoms, biogenic silica)

$sed_{DA} = k_{sed}(DAF + DAS + DAR)$ **Eq. P- 9**

$sed_{SiB} = k_{sed} \; SiB$ **Eq. P- 10**

nutrients uptake

$upt_{PHY}^{NO_3} = \frac{f_{NO_3}}{cn_{PHY}} \sum_{i:DA,NF} \mu_i$ **Eq. P- 11**

with : $f_{NO_3} = 1 - \frac{I_m \, NH_4}{NH_4 + K_i}$

$upt_{PHY}^{NH_4} = \frac{1 - f_{NO_3}}{cn_{PHY}} \sum_{i:DA,NF} \mu_i$ **Eq. P- 12**

$upt_{PHY}^{Fe} = \sum_{i:DA,NF} \left(\mu_i \; fec_i \right)$ **Eq. P- 13**

$upt_{DA}^{Si} = \mu_{DA} \; sic$ **Eq. P- 14**

with : $sic = [Si{:}C]_0 + \Phi \, Fe$

$upt_{PHY}^{P} = \frac{1}{cp} \sum_{i:DA,NF} \mu_i$ **Eq. P- 15**

HBP (protozooplankton)

microzooplankton

grazing on nano-flagellates

$$\mu_{MCZ} = y_{ZOO}\ graz_{MCZ}$$ **Eq. P- 16**

$$graz_{MCZ} = graz_{\max}^{MCZ} \frac{f_{ut}}{f_{ut} + k_g^{mcz}} MCZ$$ **Eq. P- 17**

with : $f_{ut} = (NFF + NFS + NFR) + HNF - ths_{MCZ}$

$$graz_{MC/NF} = graz_{MCZ} \frac{NF}{NF + HNF}$$ **Eq. P- 18**

$$graz_{MC/HNF} = graz_{MCZ} \frac{HNF}{NF + HNF}$$ **Eq. P- 19**

lysis

$$lys_{MCZ} = k_d^{ZOO}\ MCZ$$ **Eq. P- 20**

nutrient regeneration

$$reg_{MCZ}^{N} = graz_{MCZ} \frac{NFF/cn_{phy} + HNF/cn_{ZOO}}{NF + HNF} - \mu_{MCZ}/cn_{ZOO}$$ **Eq. P- 21**

$$reg_{MCZ}^{P} = graz_{MCZ} \frac{NFF/cp_{phy} + HNF/cp_{ZOO}}{NF + HNF} - \mu_{MCZ}/cp_{ZOO}$$ **Eq. P- 22**

$$reg_{MCZ}^{Fe} = graz_{MCZ} \frac{NFF\ fec_{NF} + HNF\ fec_{ZOO}}{NF + HNF} - \mu_{MCZ}\ fec_{ZOO}$$ **Eq. P- 23**

heterotrophic nano-flagellates

grazing on bacteria

$$\mu_{HNF} = y_{ZOO}\ graz_{HNF}$$ **Eq. P- 24**

$$graz_{HNF} = graz_{\max}^{HNF} \frac{f_{ut}}{f_{ut} + k_g} HNF$$ **Eq. P- 25**

with : $f_{ut} = BAC - ths_{HNF}$

lysis

$$lys_{HNF} = k_d^{ZOO}\ HNF$$ **Eq. P- 26**

nutrient regeneration

$$reg^{N}_{HNF} = graz_{HNF}/cn_{BAC} - \mu_{HNF}/cn_{ZOO}$$ **Eq. P- 27**

$$reg^{P}_{HNF} = graz_{HNF}/cp_{BAC} - \mu_{HNF}/cp_{ZOO}$$ **Eq. P- 28**

$$reg^{Fe}_{HNF} = graz_{HNF}\,fec_{BAC} - \mu_{HNF}\,fec_{ZOO}$$ **Eq. P- 29**

grazing by mesozooplankton on diatoms and microzooplankton

$$graz_{MS/MC} = graz_{MSZ}\frac{MCZ}{MCZ + DA}$$ **Eq. P- 30**

$$graz_{MS/DA} = graz_{MSZ}\frac{DA}{MCZ + DA}$$ **Eq. P- 31**

with : $DA = DAF + DAS + DAR$ $graz_{MSZ}$: forcing function

HSB (microbial loop)

bacteria

growth

$$\mu_{BAC} = upt_{BAC}\,y_{BAC}$$ **Eq. P- 32**

$$upt_{BAC} = b_{\max}\frac{S^{ut}}{S^{ut} + k_{SBC}}BAC$$ **Eq. P- 33**

with : $S^{ut} = SBC - k_{SBC}/10$

P and Fe uptake

$$upt^{P}_{BAC} = \frac{\mu_{BAc}}{cp_{BAC}}$$ **Eq. P- 34**

$$upt^{Fe}_{BAC} = \mu_{BAC}\,fec_{BAC}$$ **Eq. P- 35**

ammonification

$$\alpha_{BAC} = upt_{BAC}\frac{SBN}{SBC} - \frac{\mu_{BAC}}{cn_{BAC}}$$ **Eq. P- 36**

lysis

$$lys_{BAC} = k_d^{BAC}\ BAC$$ **Eq. P- 37**

Organic matter

i : (1) quickly biodegradable substrates ; (2) slowly biodegradable substrates

extra-cellular hydrolysis

$$elys_{H_i} = e^i_{\max} \frac{HC_i}{HC_i + k_h^i} BAC$$ **Eq. P- 38**

$$lys_{PC_i} = k_b^i\ PC_i \quad ; \quad lys_{PN_i} = k_b^i\ PN_i \quad ; \quad lys_{PP_i} = k_b^i\ PP_i$$ **Eq. P- 39**

sedimentation

$$sed_{PC_i} = k_{sed}\ PC_i \quad ; \quad sed_{PN_i} = k_{sed}\ PN_i \quad ; \quad sed_{PP_i} = k_{sed}\ PP_i$$ **Eq. P- 40**

Temperature dependence : $p = p'\left(0.1 + 0.9\, e^{\frac{(T - T^{Opt})^2}{\Delta T^2}}\right)$ **Eq. P- 41**

Table 4 a. *Process parameters of the SWAMCO model: AQUAPHY module*

Symbol	Units	Meaning	Diatoms	Nanoflagellates
k_{fe}^{SPP}	µmolFe.m^{-3}	half saturation cst. for Fe uptake	1.2	0.03
fec_{SPP}	µmolFe/mmolC	Fe : C(F) ratio	0.2	0.0025
			both groups	
$k_{\max}^{SPP}$	h^{-1}	photosynthesis optimal specific rate	0.06	
α_{SPP}	$m^2 s / \mu E\, h$	photosynthetic efficiency	0.0007	
β	$m^2 s / \mu E\, h$	photoinhibition index	0.0	
$\mu_{\max}$	h^{-1}	max. specific rate of F synthesis	0.035	
k_s	mmolC/mmolC	half sat. constant of S assimilation	0.07	
Q_s	mmolC/mmolC	monomers cellular quota	0.07	
$\rho_{\max}^{SPP}$	h^{-1}	optimal specific rate of R synthesis	0.06	
k_c^R	h^{-1}	specific rate of R catabolism	0.06	
K_F	h^{-1}	maintenance specific rate of basal metabolism	0.0005	
ecs_{NH4}	mmolC/mmolC	E cost of F synthesis (NH_4 source)	0.4	
ecs_{NO3}	mmolC/mmolC	E cost of F synthesis (NO_3 source)	0.8	
k_{lys}	h^{-1}	specific rate of cell autolysis	0.001	
ε	-	exudation constant	0.05	
k_{sed}	m.h^{-1}	sedimentation rate	0.08	
k_n	mmolN.m^{-3}	half saturation cst. for N uptake	1	
k_p	mmolP.m^{-3}	half saturation cst. for P uptake	0.2	
k_{si}	mmolSi.m^{-3}	half sat. cst. for diatoms Si uptake	4	
cn_{PHY}	mmolC/mmolN	C(F):N ratio	5	
cp_{PHY}	mmolC/mmolP	C(F):P ratio	80	
Φ	$mmolSi / mmolC\,\mu molFe$	Si:C(F) - Fe dependancy, coefficient	-0.39	
$[Si:C]_0$	mmolSi/mmolC	Si:C(F) - Fe dependancy, intercept	1.52	
I_m	-	NO_3 uptake inhibition by NH_4 : maximum rate	0.8	
K_i	mmolN.m^{-3}	NO_3 uptake inhibition by NH_4 : half saturation constant	0.45	
χ	mgChl/mmolC	Chla / C(F) ratio	0.5	

Table 4 b. *Process parameters of the SWAMCO model: HBP module*

Symbol	Units	Meaning	Micro-zooplankton	heterotrophic nanoflagellates
ths_{SPP}	mmolC.m^{-3}	prey threshold	0.083	0.33
$graz_{\max}^{SPP}$	h^{-1}	maximum specific ingestion rate	0.02	0.03
			both groups	
k_g	mmolC.m^{-3}	half-saturation constant of ingestion	0.25	
y_{ZOO}	-	growth efficiency	0.38	
k_d^{ZOO}	h^{-1}	autolysis specific rate	0.001	
cn_{ZOO}	mmolC/mmolN	C/N ratio	5	
cp_{ZOO}	mmolC/mmolP	C/P ratio	80	
fec_{ZOO}	µmolFe/mmolC	Fe/C ratio	0.0024	

Table 4 c. *Process parameters of the SWAMCO model: HSB module*

Symbol	Units	Meaning	Value
ε_d^1	-	H1 fraction in lysis products	0.3
ε_d^2	-	H2 fraction in lysis products	0.2
ε_p^1	-	P1 fraction in lysis products	0.1
ε_p^2	-	P2 fraction in lysis products	0.4
$k_b^{1\,'}$	h^{-1}	PC1 hydrolysis rate	0.005
k_b^2	h^{-1}	PC2 hydrolysis rate	0.00025
$e_{\max}^{1\,'}$	h-1	max. specific rate of H1 exoenzymatic hydrolysis	0.75
$e_{\max}^{2\,'}$	h-1	max. specific rate of H2 exoenzymatic hydrolysis	0.25
k_h^1	mmolC.m^{-3}	half sat. constant for H1 exoenzymatic hydrolysis	8.3
k_h^2	mmolC.m^{-3}	half sat. constant for H2 exoenzymatic hydrolysis	83
$b_{\max}^{\,'}$	h^{-1}	max. specific rate of S uptake	0.18
k_{SBC}	mmolC.m^{-3}	half-saturation constant for S uptake	0.83
y_{BAC}	-	growth efficiency	0.25
$k_d^{BAC\,'}$	h^{-1}	autolysis specific rate	0.01
cn_{BAC}	mmolC/mmolN	c:n ratio	5
cp_{BAC}	mmolC/mmolP	c:p ratio	80
fec_{BAC}	µmolFe/mmolC	fe:c ratio	0.0024
T^{opt}	°C	optimal temperature	12
ΔT	°C	Temperature dependance	7

parameters with temperature dependence are identified by a '

Equations and parametrization of the AQUAPHY module

Each phytoplankton group (DA : diatoms; NF : nanoflagellates) is described by 3 state variables (functional cellular constituents F, reserve products R, monomers S) in order to distinguish between photosynthesis and growth processes (Lancelot *et al.*, 1991a). Conceptually this model is based on the notion of reserve products storage by phytoplankton cells, according to the future requirements of their growth. This was theoretically developed by Cohen and Parnas (1976) and experimentally demonstrated by Cuhel et al. (1984) and Lancelot *et al.* (1986). Basically, the photosynthetic process directly, and the catabolism of storage products indirectly provide the energy and reductants required for the biosynthesis of new cellular material as well as for the maintenance of basal metabolism (Shuter, 1979). The production and loss processes are listed in Eq. V -1-6 (Table 2) and are described explicitly by Eq. P -1-15 (Table 3).

The rate of phytoplankton growth μ (Eq. P-7, Table 3) is governed by the availability of intracellular monomers (S) and ambient inorganic nutrient (N) according to a multiplicative Michaelis-Menten kinetics characterized by 3 constants: the maximum specific growth rate μ_{max} and the half-saturation constants for the assimilation of S (k_s) and nutrient. One single nutrient is considered as limiting phytoplankton growth. It corresponds to the nutrient which displays the lowest ambient concentration compared to the half-saturation constant for phytoplankton uptake. Conceptually it can be either inorganic N (NO_3+NH_4), Si, PO_4 or Fe and the selection is determined at each time step by the minimum function described in Eq. P-7 (Table 3).

The photosynthetic process φ (Eq. P-1, Table 3) is governed by the photosynthetically available irradiance (PAR) or I according to the relationship of Platt *et al.* (1980). It is characterized by three parameters normalized to the functional cellular constituents, (i) the maximal photosynthetic capacity K_{max} , (ii) the photosynthetic efficiency α and a description of the photoinhibition β . The ambient light I is calculated from (i) the incident PAR I_0 in combination with (ii) ice cover assuming an albedo of sea-ice and water of 0.95 and 0.15 respectively, while I decreases in depth according to (iii) the Beer-Lambert equation parametrized by the coefficient of vertical light attenuation η (Eq. P-1, Table 3). The latter is calculated from phytoplankton biomass according to the empirical relationship determined by Lancelot *et al.* (1991a) for Antarctic waters.

The synthesis of reserve products s_R (Eq. P-5, Table 3) is governed by the availability of the intracellular monomers S following a Michaelis-Menten kinetics characterized by the constants ρ_{max} (the maximum specific rate of reserve products R) and k_S the half-saturation constant for the assimilation of S. The catabolism of the reserve products c_R is postulated to obey a first order kinetics characterized by the constant k_c^R (EQ. P-6, Table 3).

The metabolic costs, in terms of a demand for ATP and reductants, are primarily met by cellular respiration *resp*. This process is expressed by the sum of two terms (Eq. P-8, Table 3), associated with maintenance processes, and the synthesis of new cellular material (Shuter, 1979). Maintenance is related to the functional cellular biomass according to a first-order kinetics parametrized by the constant k_F. Metabolic costs for the synthesis of new cellular material are dependent on the form of the inorganic nitrogen source expressed by the dimensionless constant ξ assumed to vary linearly according to the inorganic nitrogen source (Shuter, 1979; Eq. P-8, Table 3).

The phytoplankton physiological losses include exudation (*e*) and cell autolysis (*lys*). The latter process affecting the whole cell operates on all phytoplankton state variables including the biogenic silica (*SiB)* and is described by a firs-order kinetics parametrized by the constant K_{lys} (Eq. P-2-3,Table 3). The exudation *e* is a constant fraction ε of photosynthesis φ (Eq. P-4,Table 3).

Sedimentation affects only the diatoms (Eq. P-9,Table 3) and biogenic silica (Eq. P-10, Table 3) and is described by first order kinetics parametrized by the constant k_{sed}.

The physiological parameters relative to phytoplankton growth were determined experimentally by mathematical fitting of experimental field ^{14}C data describing the photosynthesis-light relationship and time-course C assimilation in phytoplankton cellular constituents along a 24 hours cycle, making use of the AQUAPHY set of equations (Lancelot *et al.*, 1991; 1997; Mathot *et al.*, 1992). When conducted at iron-replete concentration, no significant difference in either photosynthetic or growth parameters of the nanophytoplankton-dominant or diatom-dominant communities could be evidenced (Lancelot *et al.*, 1997). Furthermore, no significant difference in the biochemical composition of controls and iron-enriched field populations has been recorded in iron enrichment bioassay experiments (van Leeuw *et al.*, 1997). Combining these results allow us to choose just one set of parameters to characterize the carbon metabolism (photosynthesis, growth, respiration, catabolism, exudation) of both phytoplankton groups (Table 4). Furthermore this set of parameters holds for the whole Southern Ocean due to the lack of significant temperature dependence to be observed in the range -1.8 and +3.5°C (Lancelot *et al.*, 1991a; 1997). Consequently, the physiological growth of diatoms (DA) and nanophytoplankton (NF) in the Southern Ocean differentiates only by the physiology of Fe assimilation , i.e. the differences in cellular Fe requirements and kinetics parameters of Fe uptake. The observed better ability of nanophytoplankton (NF) to outcompete large diatoms in the low-iron waters of the Southern Ocean (Sunda and Huntsman, 1995; Hutchins, 1995) has been designated by their higher affinity for dissolved iron uptake (low K_{Fe})

and their lower biochemical iron requirements. Half-saturation constant for uptake of dissolved Fe by nanophytoplankton and diatoms were chosen at 0.03 nM (Price *et al.*, 1994) and 1.2 nM respectively (Table 4) . The latter concentration was calculated from Fe-enrichment experiments conducted in the Atlantic sector of the Southern Ocean (Scharek *et al.*, 1997; van Leeuw *et al.*, 1997) when assuming that Fe supply in a low Fe environment stimulates only the diatom component of the phytoplankton community. The half-saturation constants are expressed as dissolved Fe to be consistent with measured dissolved Fe in the ambient seawater during the 1992 campaign (de Baar *et al.*, 1995; Loscher *et al.*, 1997). The role of chemical speciation of the Fe in solution is being ignored because in 1992 this had not yet been investigated. In a subsequent 1995 expedition in the remote Pacific sector the organic complexation of Fe was studied for the first time in the Southern Ocean (Nolting *et al.*, 1998). The about 98% organic complexation there observed leaves only 2 % for Fe' which is the sum of all inorganic Fe(III) species when ignoring reduced Fe(II) forms. When applied to the above K_{Fe} values for the large diatoms this would correspond to a half-saturation value $K_{Fe'}$ of 0.024 nM. This concentration corresponds well with $K_{Fe'}$ values in the order of 0.05 to 0.08 nM for a large neritic diatom Chaetoceros calcitrans grown in the laboratory in EDTA manipulated cultures (Timmermans et al., unpublished results). This agreement supports the suggestion (de Baar et al., 1997; de Baar and Boyd, 1998) that the large chain-forming diatoms observed in 1992 in the Polar Front were neritic in character. In due course more assessments are desirable of large chain-forming Antarctic diatoms which however are very fragile and notoriously difficult to maintain in culture

The cellular Fe requirement (Fe:C) was derived from literature (Morel, 1990; Brand, 1991; Sunda, 1991, Muggli *et al.*, 1996) and fixed at 0.2 and 0.0025 nM:µM for diatoms (DA) and nanophytoplankton (NF) respectively (Table 4). The model further considers the negative regulation by ambient Fe of the silification (Si:C), by diatoms as recently evidenced by Takeda (1998) and Hutchins and Bruland (1998). The empirical equation described in Eq. P-19 (Table 3) is derived from the bioassay experiments of Takeda (1998) on Antarctic diatoms. Here the term $[Si{:}C]_0$ is the silicification level at depleted Fe and ϕ is the slope of the negative correlation.

The sedimentation parameter k_{sed} was fixed at 0.08 $m.h^{-1}$ in order to take into consideration an average forcing of Fe stress (Muggli et al., 1996) and aggregation.

Equations and parametrization of the HBP module

The marine protozoan community includes a large range of microorganisms able to ingest bacteria and/or auto- and heterotrophic flagellates. Food competitive experiments run on several field communities (Lancelot *et al.*, 1997; Becquevort and Menon, in preparation) show that the

Antarctic protozoan community is highly food selective. The protozoan community can then safely be represented by two state variables. These are the bactivorous nanoflagellates HNF feeding on the only bacteria B and the microzooplankton MCZ grazing on autotrophic (NF) and heterotrophic (HNF) nanoflagellates. The whole community undergoes grazing pressure by metazoans and krill (Eq. V-7,8, Table 2).

The protozoan ingestion rate *graz* (Eq. P-17,25, Table 3) is governed by food availability and obeys a Michaelis-Menten kinetics above a threshold value (THS) below which no grazing is likely (Becquevort, 1997). In the absence of food selectivity, the fraction of microzooplankton grazing activity on nanophytoplankton (NF) corresponds to the relative abundance of the latter over the total nanoflagellates community (Eq. P-17-19). A constant fraction y_{zoo} of the ingested food by respectively microzooplankton (MCZ) and bactivorous nanoflagellates (HNF) is converted into biomass (Eq. P-16,24, Table 3), the remaining being respired. The rate of cell autolysis for both groups (lys_{MCZ} and lys_{HNF} in Eq. P-20,26) is described by first order kinetics, in which k_d^{zoo} is a first-order constant. Microzooplankton mortality by grazing losses corresponds to the part of metazoan grazing pressure (considered here as a biological constraint) on microzooplankton (MCZ) with respect to diatoms (DA), in the assumed absence of food selectivity (Eq. P-30, Table 3).

Protozoan feeding parameters (Table 4) were determined by mathematical fitting of kinetic experiments describing the ingestion rate of natural assemblages of protozoa in the presence of various concentrations of preys (Lancelot *et al.*, 1997; Becquevort and Menon, in preparation). Half-saturation constants for prey ingestion were remarkably similar for bactivorous nanoflagellates and microzooplankton, around 0.25 mmol C m^{-3} (Table 4). Unexpectedly, the threshold food concentration below which no grazing was occurring was significantly lower for microzooplankton (MCZ) than for bactivorous nanoflagellates (HNF) emphasizing a strong coupling between microzooplankton and their preys consisting of both auto- and heterotrophic nanoflagellates (NF and HNF). The common value of 0.3 was considered as typical for the growth efficiency of Antarctic protozoa (Bjornsen and Kuparinen, 1991).

Equations and parametrization of the HSB module

The model of microbial loop dynamics (HSB model, Billen and Servais, 1988) considers one single bacterioplankton group BAC (including both free-living and attached bacteria on particles and aggregates) and five pools of organic substrates (the monomers SB; the rapidly biodegradable dissolved and particulate organic matter H_1 and P_1 ; the slowly biodegradable dissolved and particulate organic matter H_2 and P_2). Basically, bacterial growth is directly dependent on the concentration of monomers (SB), the only organic molecules able to be transferred inside bacteria. These monomers are supplied either directly by phytoplankton exudation or indirectly after bacterial ectoenzymatic hydrolysis of the dissolved and particulate polymers (H_i, P_i). The elemental composition of organic polymers includes carbon (HC_i; PC_i), nitrogen (HN_i; PN_i) and phosphorus (HP_i; PP_i), That of the monomers includes carbon (SBC) and nitrogen (SBN). Conservation equations rates are listed in Table1 (Eq.V-9 to 17).

The dissolved and particulate polymers (H_i and P_i) are supplied by phytoplankton, bacteria and protozoa lysis. The model defines as ε_d^i and ε_p^i the fractions to Hi and Pi of the bulk of organic matter released by lysis (Eq.V-12-17, Table 2). The hydrolysis rate of particulate polymers lys_{Pi} (Eq. P-39, Table 3) is described by a first-order kinetics characterized by 2 constants k_b^1 and k_b^2. The involvement of attached bacteria in this process is indirectly considered by assuming a temperature-dependence for the hydrolysis constant k_b^1 such as described in Eq. P-41 (Table 3). The ectoenzymatic hydrolysis of dissolved organic polymers $elys_{Hi}$ (Eq. P-38, Table 3) obeys a Michaelis-Menten kinetics (Somville and Billen, 1983) characterized by two sets of two specific parameters (the maximum specific rate of ectoenzymatic hydrolysis e_{max}^i and the half-saturation constant for Hi hydrolysis k_H^i), owing to the different susceptibilities to enzymatic hydrolysis of the two classes of dissolved polymers (Billen, 1990).

The bacterial uptake of monomeric substrates (SB) upt_{BAC} is assumed to obey a Michealis-Menten kinetics (Eq. P-33, Table 3) where b_{max} and k_{SBC} are the maximum specific rate and half-saturation constant of substrate uptake by bacteria. A constant fraction y_{BAC} of the amount of substrates taken up is used for biomass production (Eq. P-32, Table 3), the remaining part being respired and remineralised.

Most parameters were determined experimentally and were described by Billen and Becquevort (1991); Lancelot *et al.* (1991b); Servais et al. (1987). Values are reported in Table 4. Contrasting with eukaryotic cells, bacterial activity in the Southern Ocean was found to be governed by ambient temperature according to the sigmoid relationship (Eq. P-41, Table 3) described in Billen and Becquevort (1991).

Equations and parametrization of the inorganic loop module

Nitrate, ammonium, phosphate, iron and silicate (NO_3, NH_4, PO_4, Fe and Si) are the inorganic nutrients considered by the model (Eq. V-18 to 23, Table 2). Both algal groups, the diatoms and the nanoflagellates are taking up nitrate, preferably ammonia, phosphate and iron, all to be assimilated into the only functional constituents F (Lancelot *et al.*, 1986). The ratio of phytoplankton nitrate uptake to the total inorganic N uptake (f_{NO3}; Eq. P-11 in Table 3) is governed by ammonia according to the non-competitive inhibition equation suggested by Harrison *et al.* (1996) and parametrized by Elskens *et al.* (1997; Table 4). Silicate is used only by the diatoms and is released in the surrounding medium after diatom autolysis. Uptake rates of N, P, Si and Fe (Eq. P-11-15, Table 3) are deduced from the computed phytoplankton growth rate (Eq. P-7, Table 3) and the cellular stoichiometry of diatoms and nanophytoplankton (Table 4). Iron and phosphorus requirements of the bacteria are met by direct uptake of both constituents. Contrasting, NH_4 can either be taken up or released by bacteria according to the N:C ratio of their substrates and their own biochemical requirements (Eq. P-36, Table 3). The ammonia, phosphate and iron are released by protozoa as product of their metabolism (Hutchins *et al.*, 1995). Regenerating processes are computed by comparing the N, P and Fe content of food resources with their biochemical requirements (Eq. P-21-23, Table 3). Micro-organism autolysis further releases Fe in the surrounding medium (Eq. V-23, Table 2).

Stoichiometric ratios (Fe:N:Si:C) were derived from literature values (Morel, 1990; Sunda and Huntsman, 1997 and Tortell *et al.*, 1996) and are reported in Table 4 for phytoplankton, protozooplankton and bacterioplankton.

MODEL RESULTS

The 1992 spring bloom in the Atlantic sector of the Southern Ocean

The ANTX/6 sampling site, at 6°W in the Atlantic sector of the Southern Ocean in October-November 1992, has been chosen for a first application of the SWAMCO coupled physical-biogeochemical model. The section is crossing by two eastward flowing but contrasting water masses (de Baar *et al.*, 1995; Veth *et al.*, 1997). These are the iron-depleted (~0.4nM) but sea-ice-associated southern branch of the Antarctic Circumpolar Current ACC (~ 51-56°S) and the iron-enriched (1.8nM) Polar Frontal jet (~ 47-50°S,). Transects extending from the ice edge of the eastern Weddell Sea, across the southern branch of the ACC into the Polar Front had repeatedly

been sampled over more than a one-month period (Fig. 2), at the early beginning of the growth season.

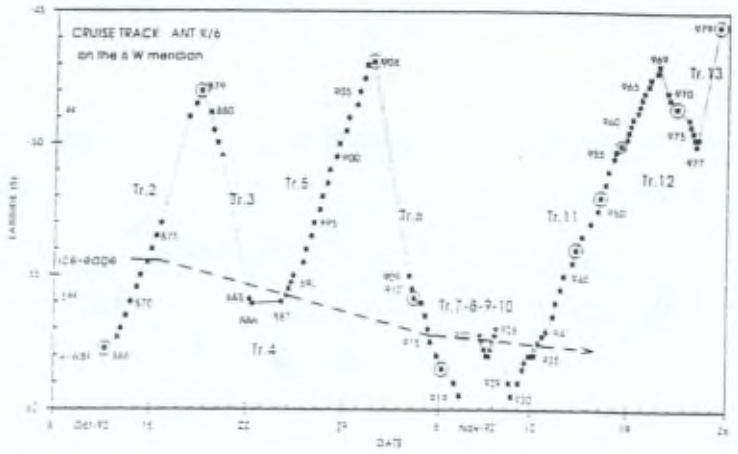

Figure 2. *Latitude vs time cruise track on the 6°W meridian of ANT X/6 aboard R.V. Polarstern. Transect number and the change in ice-edge position are indicated.*

Meteorological conditions were severe in particular during the first half of the cruise when storm events with wind velocities higher than 20 m s^{-1} were frequent. Results are well documented [see the special issue of DSR Part II, 44(1-2) edited by Smetacek *et al.*, 1997] and include a large data set (Rommets *et al.*, 1997) of spatio-temporal distributions of inorganic nutrients and dissolved iron (Loscher *et al.*, 1997), Chl *a* (Bathmann *et al.*, 1997), biogenic silica (Queguiner *et al.*, 1997), diatoms and nanophytoplankton (Scharek *et al.*, 1997b), bacteria (Lochte *et al.*, 1997), microzooplankton (Becquevort, 1997) and metazooplankton (Franz and Gonzales, 1997; Dubischar and Bathmann, 1997) that can be used for model results comparison.

One of the major finding of this cruise was the negligible build-up of phytoplankton biomass at the retreating ice-edge. Chl *a* concentrations were significantly less than 1 mg m^{-3} (Bathmann *et al.*, 1997). The spring microbial community was organized in a complex microbial network composed of autotrophic nanoflagellates, bacteria, bactivorous (heterotrophic flagellates) and protistovorous protozoa (microprotozoa) of low and relatively stable biomass (Becquevort, 1997). This was in contrast with the Polar Frontal Jet where concentrations of Chl *a* as high as 3 mg m^{-3} were observed at the end of the sampling period when meteorological conditions were improving (Bathmann *et al.*, 1997). At this Polar Front the Chl *a* had increased from 0.6-1.6 to 1.2-2.4 mg m^{-3} within about three weeks, while dissolved iron exhibited a concomitant seasonal decrease of almost 1nM (de Baar *et al.*, 1995). Elevated rates of primary production between 1000 and 3000 mg C m^{-2} d^{-1} , mostly synthesized by the largest (>20 μm) phytoplankton were measured (Jochem *et al.*, 1995) and the phytoplankton community was dominated by neurotic diatoms such as Corethron criophilum and Fragilariopsis kerguelensis (Veth *et al.*, 1997). Accordingly significant

export production of particulate carbon had been estimated in this area from ^{234}Th deficiencies (Rutgers van der Loeff *et al.*, 1997).

SWAMCO model implementation

The SWAMCO model was run at each half-degree of latitude between 47°S and 58°S, over a 40-day period (20th October-30th November 1992). The sea ice conditions, irradiance and meteorological data reconstructed from continuous shipboard measurements and satellite information were used as physical forcing functions. As a first application, and for a better assessment of the performance of the ecological model, advection by currents or wind drift has been neglected. This reduction of physical processes makes sense due to the larger scale of horizontal eastward advection of the overall ACC compared with the scale of vertical and biogeochemical terms of the mathematical model. Also, the stabilizing mechanisms occurring at the Polar Front i.e. the admixture of warmer subpolar waters from the North were not considered by the physical model. Metazoan grazing pressure was neglected for this application due to its negligible contribution at this period of the year (Dubischar and Bathmann, 1997). The temporal variation of the state variables was calculated by integrating the differential equations of the model (Table1, Eq. V-1 to 23) according to the Runge-Kutta 4th order procedure, with a step of 30 minutes and up to a depth of 100 m. The vertical resolution is one meter. The state variables were averaged at each time step over the total depth of the upper mixed layer, latter value having be provided by the off-line coupling with the hydrodynamical model. Initial values of chemical and biological state variables were those recorded at the first cross-section (Transect 2, Fig. 2) and are extracted from Rommets *et al.* (1997) database.

SWAMCO model validation

Despite the ANTX/6 database being the most comprehensive and extensive currently available for the Southern Ocean, there is still a major discrepancy in resolution of time and space with the half-degree latitude and 30 minutes time steps of the modelling. This is a general problem for calibration and validation of ecological models. Nevertheless the overall performance of the SWAMCO model was assessed by reconstructing transects 3, 5, 6, 11 of the cruise track (Fig. 2) and comparing model predictions of dissolved inorganic nutrients and Chl *a* averaged within the upper mixed layer with corresponding field observations (Figs 3-6).

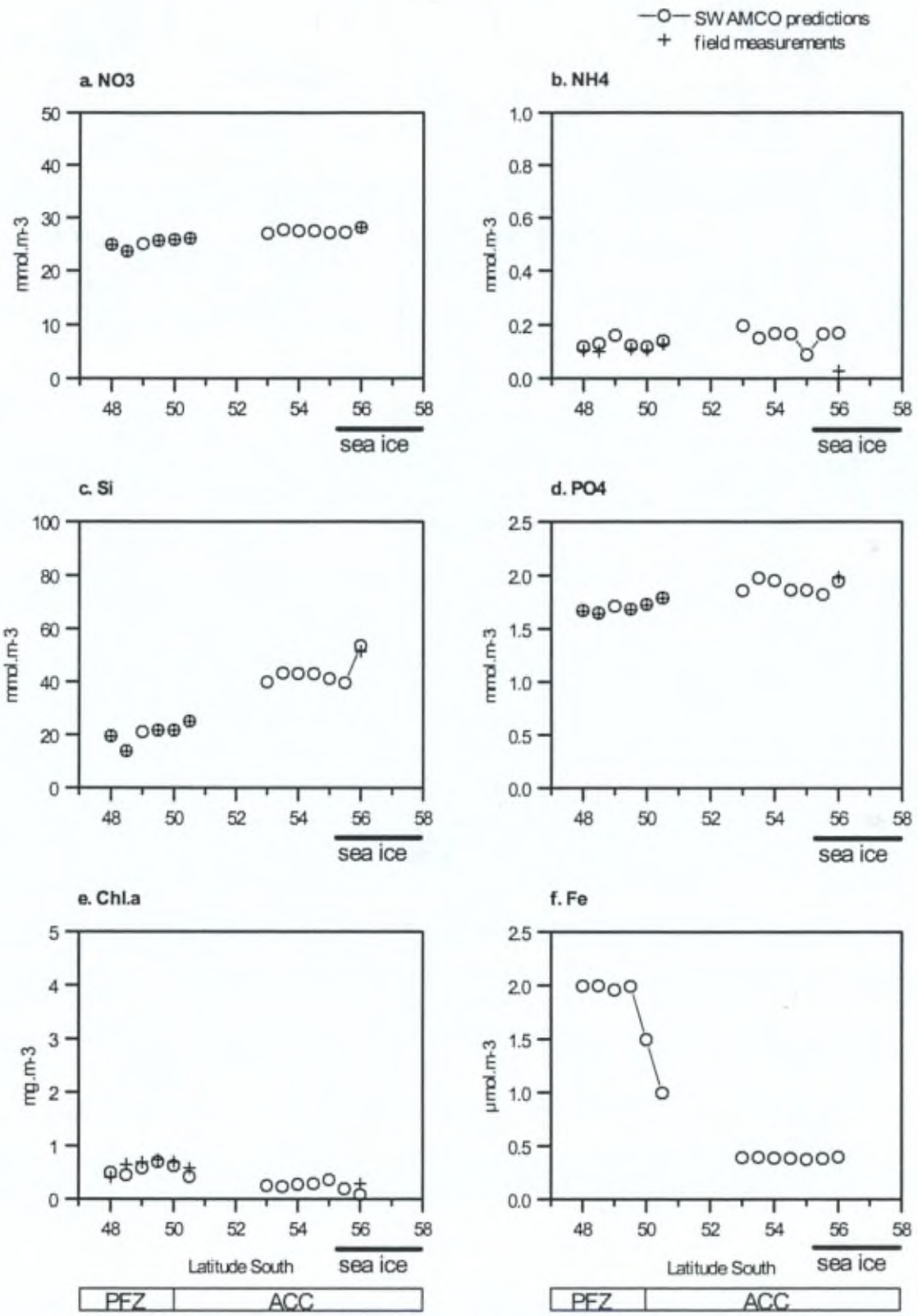

Figure 3. *SWAMCO model predictions (open circle) and field observations (cross) along transect 3 of the ANT X/6 cruise of the R.V. Polarstern: NO3(a), NH4 (b), Si (c), PO4 (d), Chla (e), dissolved fe (f).*

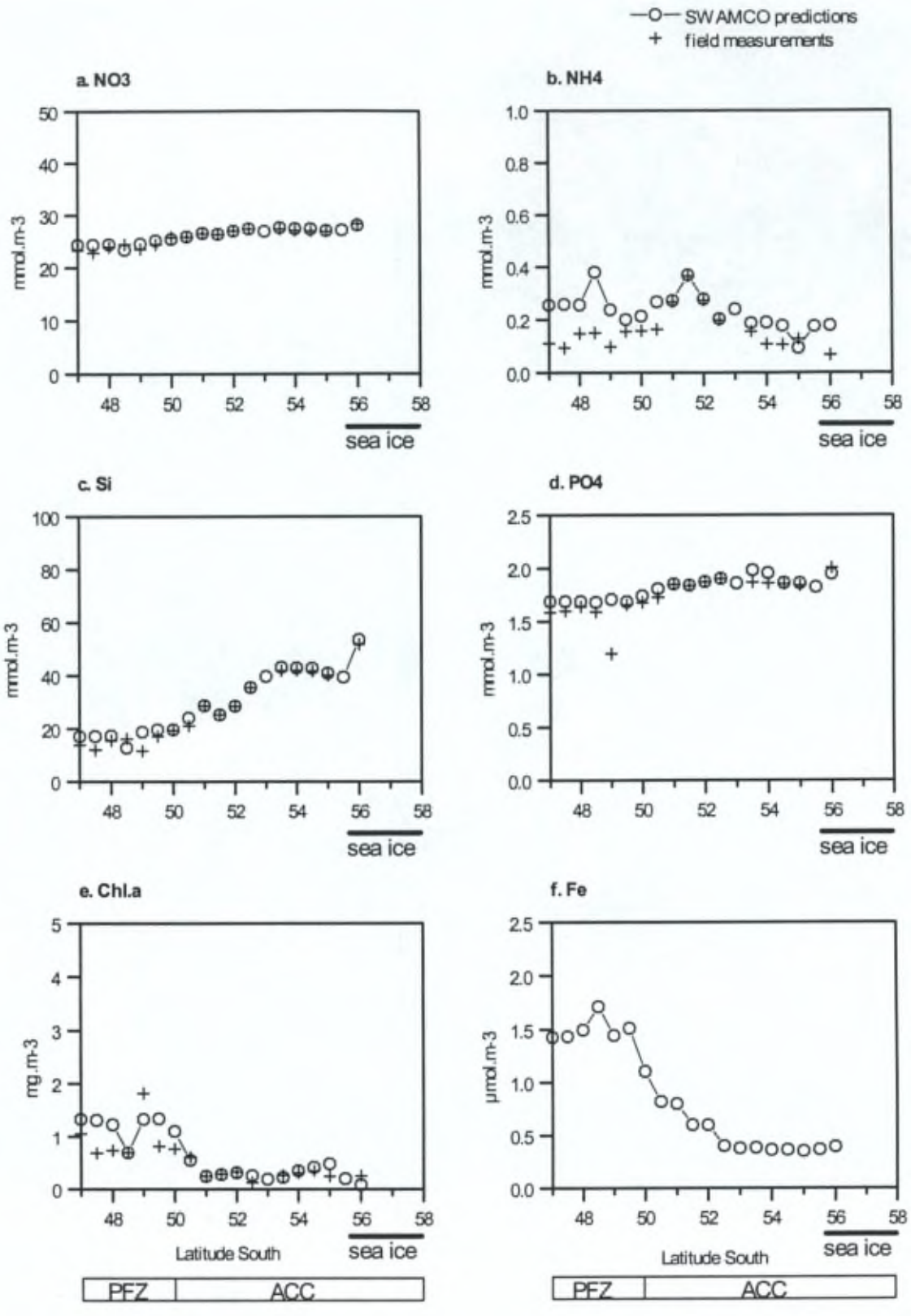

Figure 4. *SWAMCO model predictions (open circle) and field observations (cross) along transect 5 of the ANT X/6 cruise of the R.V. Polarstern: NO3(a), NH4 (b), Si (c), PO4 (d), Chla (e), dissolved fe (f).*

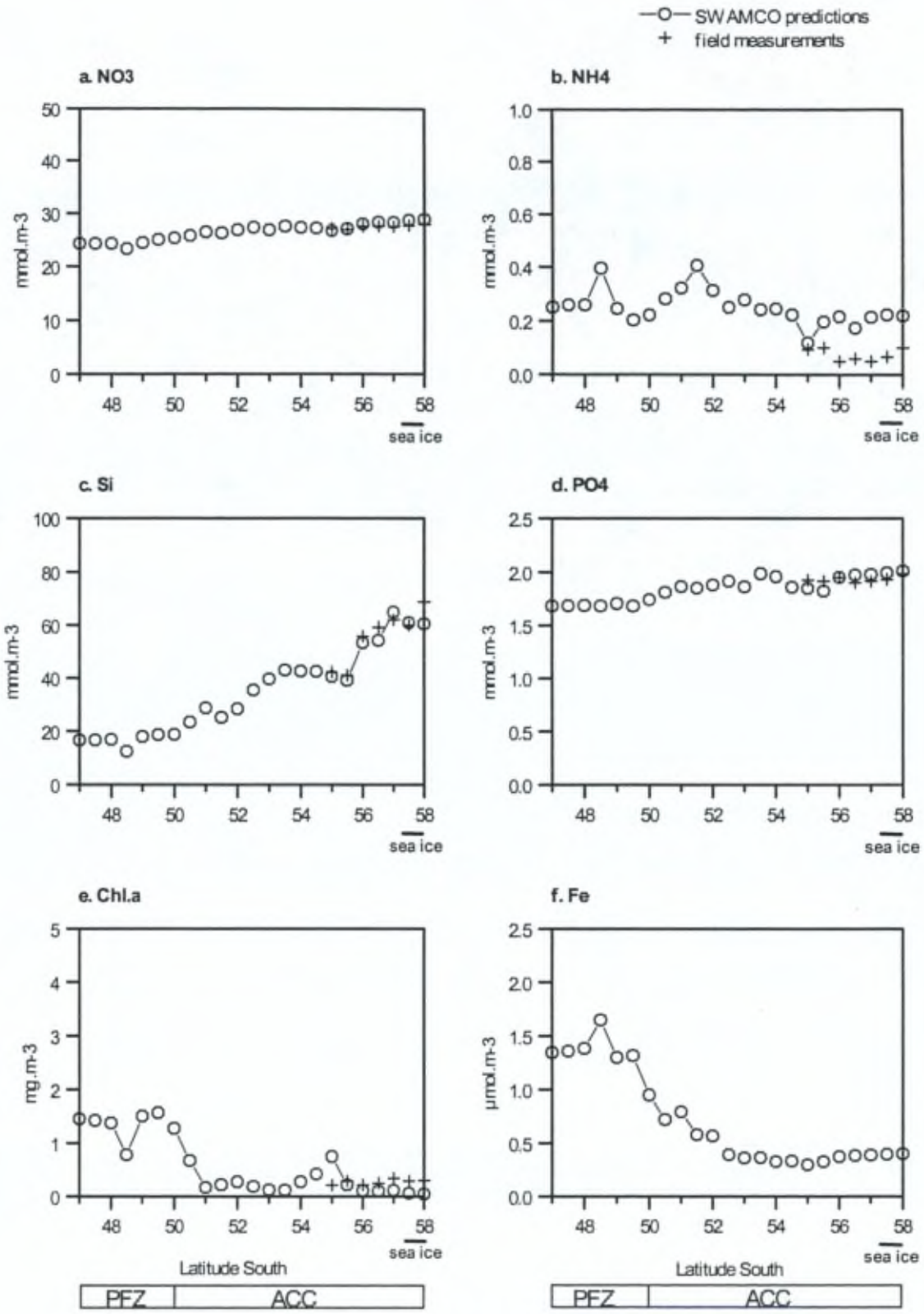

Figure 5. *SWAMCO model predictions (open circle) and field observations (cross) along transect 6 of the ANT X/6 cruise of the R.V. Polarstern: NO3(a), NH4 (b), Si (c), PO4 (d), Chla (e), dissolved fe (f).*

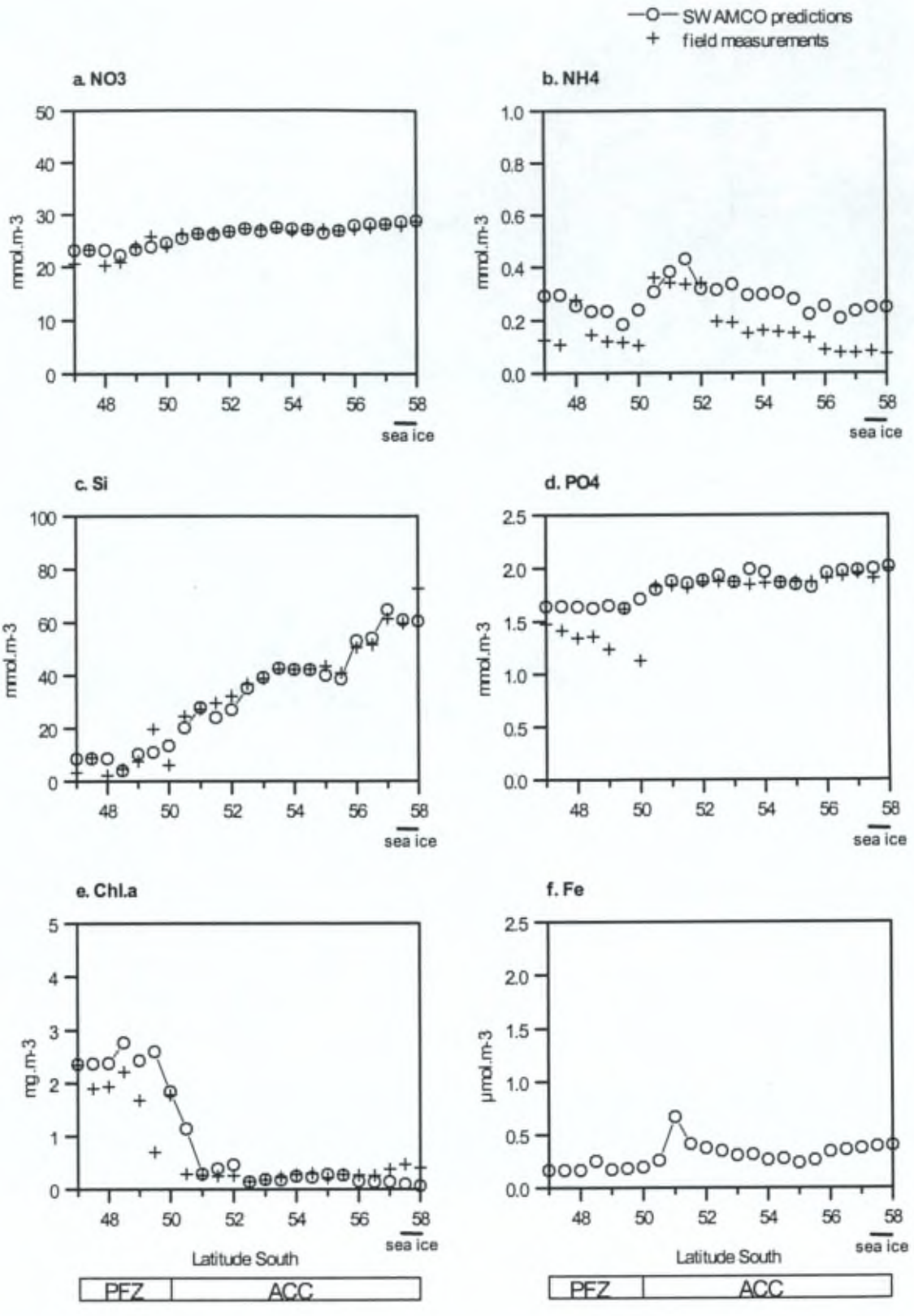

Figure 6. *SWAMCO model predictions (open circle) and field observations (cross) along transect 11 of the ANT X/6 cruise of the R.V. Polarstern: NO3(a), NH4 (b), Si(c), PO4 (d), Chla (e), dissolved fe (f).*

As a general trend, a fairly good agreement is reached between predictions and available observations (Figs 3-6), especially for nitrate (Figs 3a-6a), silicate (Figs 3c-6c) and Chl *a* (Figs 3e-6e). Less accuracy between model predictions and field data is however observed for regenerated forms of nutrients (ammonia Figs 3b-6b and phosphate, Figs 3d-6d). This is tentatively ascribed to their involvement in many uptake/loss microbiological processes. Unfortunately, direct comparison between model predictions and observations could not be Unfortunately, direct comparison between model predictions and observations could not be performed for dissolved iron due to the low reliability of most measurements at depths shallower than 40 m (de Baar *et al.*, 1995). Furthermore the model simulates remarkably well both the observed progressive growth of the phytoplankton spring bloom at the Polar Front and the lack of phytoplankton build up at the receding ice-edge (Figs 3e-6e). In good agreement with the field observations (Bathmann *et al.*, 1997), the model predicts at transect 11 (Fig. 6e) elevated Chl *a* concentrations of 2-2.8 mg m^{-3} in the Polar Frontal Jet, while phytoplankton of the southern ACC area is monotonously maintained at low Chl *a* concentration below 0.5 mg m^{-3}.

Conditions prevailing to the contrasting phytoplankton bloom situations observed at the ANTX/6 site were further considered, based on the detailed analysis of the SWAMCO predictions of biological biomasses and activities at transect 11 (Fig. 7). At this period, the phytoplankton bloom was more pronounced (Fig. 6e) and the biological data set is the best documented (Smetacek *et al.*, 1997; Rommets *et al.*, 1997).

In the iron-depleted s-ACC area (Fig. 6f), the predicted phytoplankton community is dominated by nanophytoplankton (Figs 7a,d), in accordance with the field data (Becquevort, 1997). Although increasing at the receding ice-edge, the nanophytoplankton biomass is clearly kept in check by microzooplankton (Fig. 7e) which grazing pressure is of the same order of magnitude as nanophytoplankton production (Figs 7f,g). In close agreement with the observations (de Baar *et al.*, 1995), the model predicts a little decrease of average dissolved iron within the s-ACC from 0.5 to 0.4 µmol m^{-3} over the one-month bloom period (Figs 3f-6f). Such a low apparent Fe utilization results from the strong coupling between phytoplankton iron uptake and iron regeneration associated with micrograzer activity (Fig. 7g). Low Fe availability in HNLC marine systems would then play a similar remineralization role as phosphate and ammonium in non Fe-limiting oligotrophic waters as for instances the temperate Central Gyre.

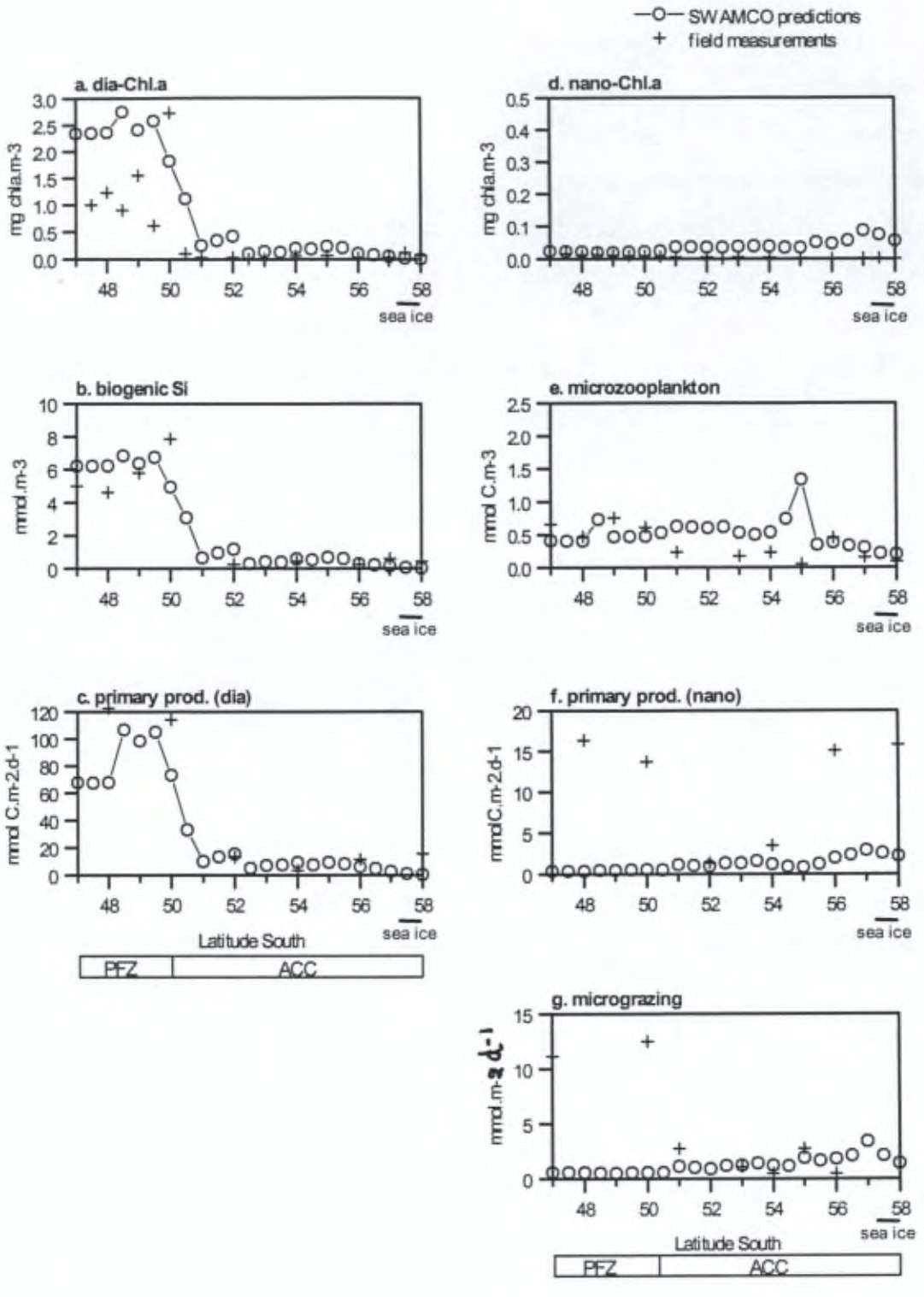

Figure 7. *SWAMCO model predictions (open circle) and field observations (cross) along transect 11 of the ANT X/6 cruise of the R.V. Polarstern: diatom-Chl a (a), biogenic silica (b), diatom primary production ©, nanophytoplankton-Chl a (d), microzooplankton carbon biomass (e), nanophytoplankton primary production (f), micrograzing (g).*

In the Polar Front, more than 90% of the predicted phytoplankton biomass is produced by diatoms (Figs 7a,c,d,f) with little contribution of nanophytoplankton. The model predicts an increase of diatomaceous Chl *a* of 1.8 mg m^{-3} over the one-month simulated period. This corresponds to a predicted accumulation of biogenic silica of about 7 mmol m^{-3} (Fig. 7b) which compares very well with field measurements (Queguiner *et al.*, 1997). Decreases of dissolved iron, silicate and nitrate of 1.7 µmol m^{-3}, 10 mmol m^{-3} and 2 mmol m^{-3} respectively were simulated for the same period. This is in perfect agreement with field data recorded in the Polar Front (de Baar *et al.*, 1995; Loscher *et al.*, 1997). Clearly at the end of the simulated period, diatom growth at the Polar Frontal zone was limited by the availability of dissolved Fe and Si (Figs 6c,f). Nanophytoplankton does not display much spatio-temporal variations in either the Polar Front or the s-ACC, being always present and maintained at low biomass (<1 mmol m^{-3}, Fig. 7d) by the heavy grazing pressure of the ubiquitous microzooplankton (Fig. 7g). Because of the latter, little phytoplankton biomass was accumulated at the ice edge in spite of the favorable meteorological conditions.

DISCUSSION

Diatom blooms and particulate export production

Particulate carbon export production in the upper 100 m was calculated from SWAMCO model runs for period between sampled transects. The predictions compare reasonably well with the estimates derived from deficiencies of the inventories of the natural tracer ^{234}Th (Rutgers van der Loeff *et al.*, 1997) within the Polar Front and the southern branch of the ACC (Table 5).

Latter estimates in units of carbon depend strongly on the adopted conversion factor for ^{234}Th versus C which has considerable uncertainty (Rutgers van der Loeff *et al.*, 1997) giving rise to the reported ranges of field values (Table 5).

Table 5. *Predicted and observed carbon export production, predicted available food ressources for metazoan and predicted opal export production in the upper 100 m as a function of latitude and for the periods between transects crossed during ANTX/6.*

Region period	PFz tr. 2-5	PFz tr. 5-11	S- ACC tr. 2-5	S- ACC tr. 5-11
primary production	0.23	1.5	0.1	0.23
diatom:	0.2	1.5	0.04	0.165
nanoflagellates	0.025	0.01	0.05	0.06
microzooplankton				
grazing	0.075	0.014	0.048	0.09
growth	0.03	0.011	0.021	0.035
Food resource for metazoa	0.15	0.9	0.045	0.14
C-export				
SWAMCO	0.083	0.63	0.041	0.1
^{234}Th	0.1-0.2	0.3-0.8	0.01-0.02	0.15-0.3
Opal-export mol. Si m^{-2}				
SWAMCO	0.055	0.36	0.011	0.034
Si:C	0.66	0.57	0.27	0.34

Otherwise the SWAMCO predictions are within or near these ranges and thus confirm that events of high particulate export production are associated with diatom production which occurred in the Polar Front during the second half of the cruise (Table 5) when meteorological conditions were favorable. As calculated by Rutgers van der Loeff *et al.* (1997), the predicted carbon export production is significantly higher at the iron-enriched Polar Frontal region than in the s-ACC. When compared to the level of primary production, however, the percentage of particulate C export is about 40% and does not differ much between areas. This would suggest that, under conditions of negligible metazoan grazing pressure, the exported percentage is not higher in a bloom situation than in a situation of modest continuous growth. Accordingly, the model predicts that more than 50% of primary production is accumulated and is available for mesozooplankton and krill (Table 5).

Opal export production in the upper 100 m, calculated similarly from model runs provides additional evidence of the role of diatom blooms in driving particulate export production. Predicted opal export production in the Polar Front region is one order of magnitude higher than in the s-ACC (Table 5). Furthermore, the computed Si:C ratios show that the particulate export production is more silicified in the Polar Front region compared to the s-ACC (Table 5). Such

mechanism is expected to enhance within the Polar Front region the transfer of heavy diatom-derived material from the surface layer into the deep ocean and the sediment. Such more rapid settling would help to minimize bacterial degradation and mineralisation that occur during this transfer. This agrees with the reported high rates of net opal sedimentation in this region (De Master, 1981).

Sensitivity testing based on SWAMCO model scenarios

Iron, light, sea-ice and wind stress are determining phytoplankton bloom events in the Southern Ocean

The successful application of the SWAMCO model to the sampling section of the cruise ANTX/6 of R/V Polarstern in the Atlantic sector of the Southern Ocean suggests that such a model based on biological principles, is generic and can be applied to the whole Southern Ocean to address its role in global carbon cycling, provided meteorological and sea-ice conditions as well as distributions of dissolved iron and silicate are known. Current knowledge of the structure and functioning of the Antarctic food chain (de Baar and Boyd, 1998; Lancelot *et al.*, 1993; 1997) suggests that both the timing, the amplitude and the extent of Antarctic phytoplankton blooms are determined by the combined action of the light environment - under control of sea ice and wind stress -, grazing pressure by micro-, mesozooplankton and krill and iron availability. The interplay between these factors is however not unique over the whole Southern Ocean, either temporally or geographically. To which extent the SWAMCO model is able to properly integrate the complex interaction between physical, chemical and biological factors as co-limiting agents of phytoplankton bloom developments and food-web structures has been appraised by analyzing diatom and nanophytoplankton spring blooms at two latitudes - 47°S in the iron-enriched and ice-free Polar Front region (Fig. 8) and 56°S in the iron-depleted marginal ice zone of the ACC (Fig. 9) - and by testing the response of the SWAMCO model to several iron-enrichment scenarios.

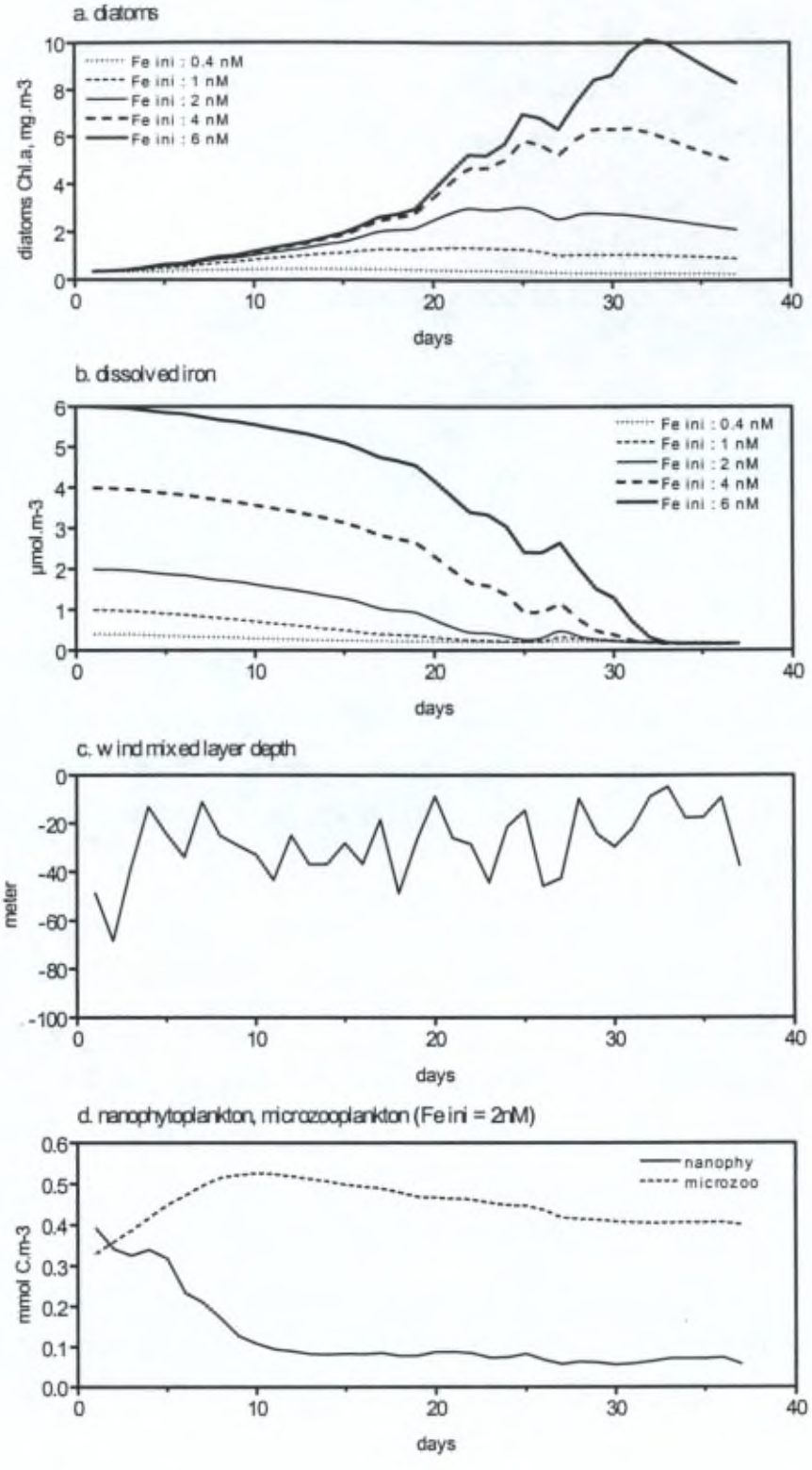

Figure 8. *SWAMCO model predictions of diatom-Chl a (a), dissolved Fe (b), nanoplankton carbon biomass (d) at the Polar Front (47°S) for different scenarios of Fe enrichment at zero time of the 40 day-simulation. Model runs are carried aut at in situ meteorological conditions which are driving the simulated change in the depth of the upper mixed layer (c).*

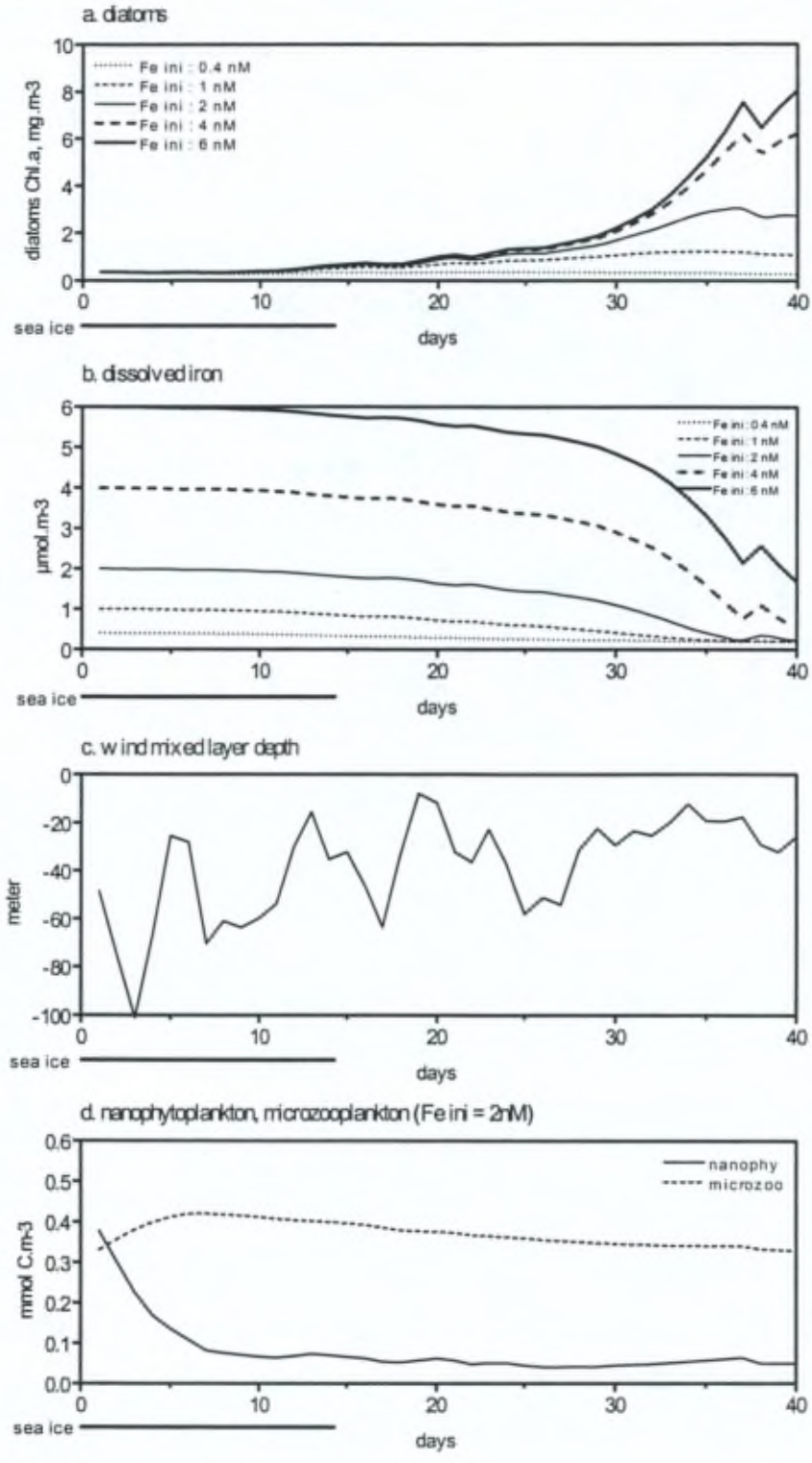

Figure 9. *SWAMCO model predictions of diatom-Chl a (a), dissolved Fe (b), nanoplankton carbon biomass (d) in the s-ACC (56°S) for different scenarios of Fe enrichment at zero time of the 40 day-simulation. Model runs are carried out at in situ meteorological conditions which are driving the simulated change in the depth of the upper mixed layer (c).*

Model simulations over the 40-day period clearly evidence the key role of Fe availability and meteorological conditions in driving phytoplankton bloom events and structuring the phytoplankton community (Figs 8,9). Diatom-dominant phytoplankton biomass is simulated in the Fe-rich Polar Frontal jet (Figs 8a,b). Exponential diatom growth is however observed during the second half of the simulated period i.e. when a surface layer of less than 40 m is reached and maintained for several days (Fig. 8c) due to persisting favorable meteorological conditions (wind speed less than 10 m s^{-1}). Under such conditions of enhanced vertical stability, Fe enrichment SWAMCO scenarios show that both the position in time of and the maximum biomass reached by the diatom bloom is determined by Fe concentration above 1 µmol m^{-3} (Figs 8a,b). Below this concentration, no real diatom bloom is predicted and the phytoplankton community is dominated by nanoflagellates (Fig. 8d). Interestingly enough, predicted nanophytoplankton biomass is maintained at low level by protozoan grazing pressure, independently of Fe concentration (Fig. 8d).

Contrasting, no diatom bloom and extremely low biomass of nanophytoplankton (however similar to that simulated in the Polar Front region) are predicted in the iron-deficient surface layer of the s-ACC (Figs 9a,b). No ice-edge related phytoplankton bloom is simulated. To which extent the lack of phytoplankton bloom at the receding ice-edge could be attributed to Fe deficiency or light limitation owing to the severe meteorological conditions met at this latitude was investigated with SWAMCO runs at different Fe enrichments. As predicted for the Polar Front, model simulations show a positive response of diatoms to increasing Fe concentrations but only when the upper mixed layer is stabilized at about 20m (Figs 9a,b,c). Ice cover and the frequent storm events prevailing during the first 25 days of the simulation were preventing any bloom to develop at the receding ice-edge, no matter how much iron was added. These drastic meteorological conditions were further slowing down the build up of diatom biomass, although the diatom biomass predicted in the s-ACC and the Polar Front at the end of the simulated period are similar (Figs 8a,9a). As simulated in the Polar Frontal jet, nanophytoplankton biomass varies independently of iron availability and is maintained at low level by the ubiquitous micrograzer community (Fig. 9d).

From these scenarios, it can be safely concluded that light limitation due to repetitive storm events, was the major factor limiting phytoplankton bloom at the beginning of the investigated period. During the favorable meteorological conditions met at the end of the cruise, iron limitation was the main factor regulating diatom bloom magnitude.

Sensitivity of the SWAMCO prediction of diatom blooms to iron parametrization

Considering the key role of Fe in driving diatom blooms, several SWAMCO runs were conducted at the Polar Frontal region to explore the model response to changing values of the parameters describing the diatom Fe uptake. These are the half-saturation constant for Fe uptake K_{FeDIA} and the cellular Fe content Fe:C. The range of tested values were those reported for diatoms by Sunda and Huntsman (1997). Results of these scenarios show that the magnitude and extent of the diatom blooms is not much dependent on the half-saturation constant for Fe uptake in the range 0.5-1.8 μmol Fe m^{-3} (Fig. 10). In contrast, both the magnitude and extent of the diatom bloom are strongly driven by the diatom iron stoichiometry (Fig. 11). In the absence of grazing pressure, decreasing the Fe requirement of diatom cells allows blooms to maintain longer and accumulate higher biomass (Fig. 11a). A major result of these scenarios is the predicted shift from Fe to Si control of a diatom bloom when a diatom Fe:C ratio of less than 100 μm:M is assumed (Figs 11b,c). These results reveal the complex interplay of Si and Fe limitation in regulating diatom blooms and the associated biogeochemical cycles in the Southern Ocean as already suggested by laboratory and field observations (Takeda et al., 1998; Hutchins and Bruland, 1998). These SWAMCO scenarios strongly indicate that more process-level investigations on the nutrient dynamics of phytoplankton are needed to understand mechanisms driving export production events in the Southern Ocean. Furthermore any modelling attempt to further address the source/sink role of the Southern Ocean in controlling atmospheric CO_2 clearly should involve not only several biological compartments in similar detail but also the explicit description of all inorganic nutrients cycling as already considered in the SWAMCO model.

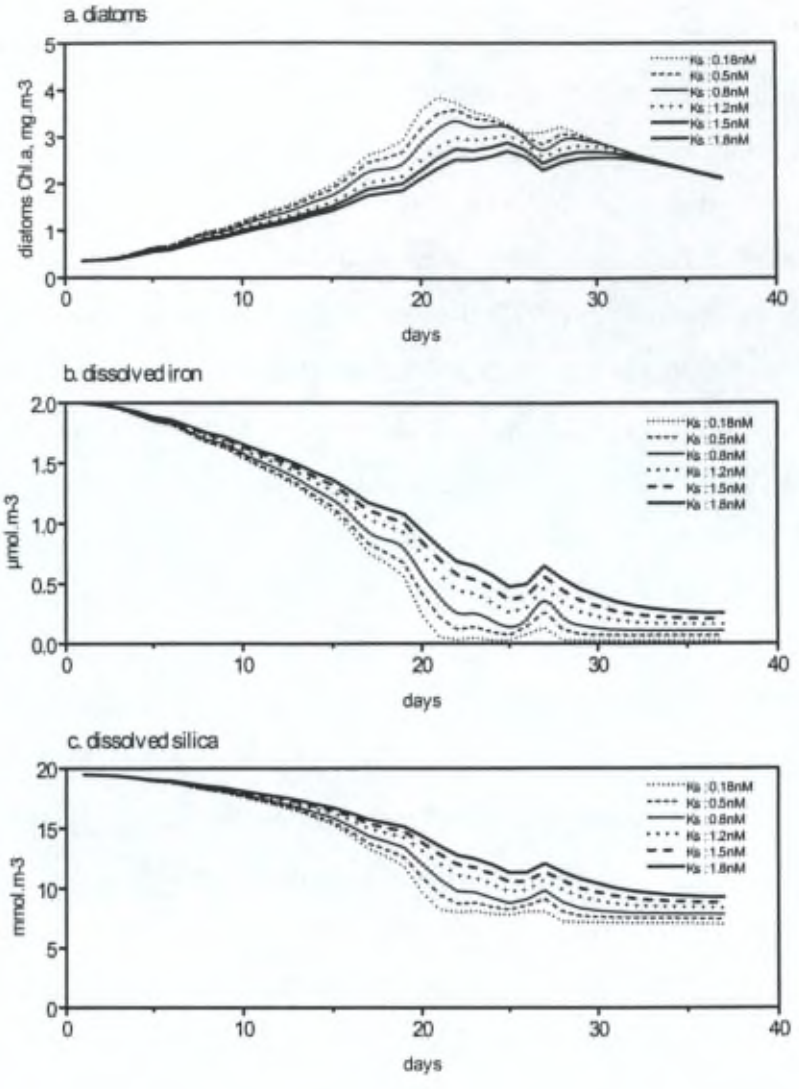

Figure 10. *SWAMCO model predictions of diatom-Chl a (a), dissolved Fe (b), silicic acid (c) at the Polar Front (47°S) for different scenarios of Fe enrichment at zero time of the 40 day-simulation. The model run is run for 40 days at in situ initial conditions and meteorological forcing.*

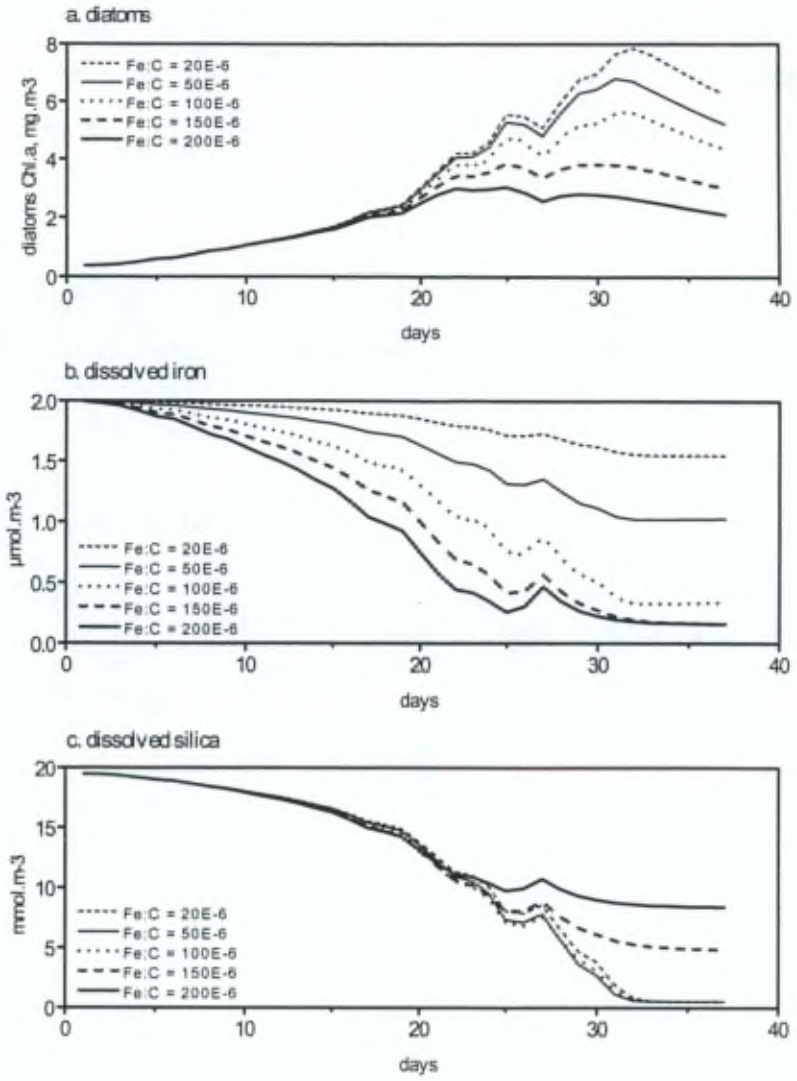

Figure 11. *SWAMCO model predictions of diatom-Chl a (a), dissolved Fe (b), silicic acid (c) at the Polar Front (47°S) for different diatom Fe:C ratios. The model run is run for 40 days at in situ initial conditions and meteorological forcing.*

CONCLUDING REMARKS

Ever since Brandt (1899) the paradigm of a single limiting factor for phytoplankton blooms has repeatedly been invoked in plankton ecology. For the Southern Ocean singular limitation by either light, grazing losses or Fe limitation has now and then been advocated (Tranter, 1982; Martin and Fitzwater, 1988; Mitchell *et al.*, 1991; Dugdale and Wilkerson *et al.*, 1991). The paradigm of a single controlling factor has been argued against (de Baar, 1994), as being an inappropriate extrapolation of the Law of the Minimum (von Liebig, 1840) beyond its validity for harvested crops, and having to give way to a realistic concept of ever-changing complex interactions of multiple growth and loss factors. Latter concept now appears confirmed by the complex interplay of rate and state variables in the SWAMCO model being required to be able to simulate the austral spring 1992 observations in the Antarctic Ocean.

Clearly one is beginning to understand some first basic principles of plankton dynamics of the Southern Ocean, but more is to be learned. The generic design of the model appears robust but will have to be further verified with new observational data sets of similar extent and coherence as SO-JGOFS ANT X/6 but in other regions and seasons of the Southern Ocean in particular to address the role of metazooplankton in food-web export. Also the model, while complicated, is modest when one reflects on the very intricate and diverse plankton community in real oceanic waters. Ongoing research on the speciation of different chemical forms of Fe in seawater affecting uptake of Fe by the cell will provide the basis for further refinements in the model. Several physical forcing functions known to exist have inadequate (e.g. meandering of Polar Front) or virtually non-existing (stabilizing mechanisms at Polar Front in 1992) observational data sets for validation, hence cannot yet become incorporated in the model.

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Chapitre 6

Synthèse: Structure et Fonctionnement du réseau trophique microbien dans l'océan Antarctique

RESUME- La structure et le fonctionnement du réseau trophique microbien dans l'océan Antarctique sont étudiés par une analyse étendue des données existantes sur les biomasses et les activités du phytoplancton, du bactérioplancton et du protozooplancton. Cette analyse est réalisée dans les 5 provinces biogéochimiques interdépendantes caractérisants l'océan Antarctique; la zone frontale, la zone océanique ouverte, la zone marginale de fonte de glace, la zone recouverte de manière permanente par la glace et la zone côtière et continentale. Il a été conclu que les conditions générales - concentrations en nutriments majeurs élevées mais concentrations faibles en chl-a - prévalant dans l'océan Antarctique résulteraient de l'avantage compétitif des communautés pico- et nanophytoplanctoniques dans un environnement pauvre en fer (< 1 nM) et souvent limité par la lumière. Ce phytoplancton de petite taille est par contre rapidement contrôlé par le protozooplancton. A ce système se surimpose des efflorescences de diatomées de grande taille ainsi que de colonies de *Phaeocystis* dans des régions riches en fer lors de conditions météorologiques favorables. Ces régions sont les eaux côtières et continentales alimentées en fer par les sédiments côtiers et le continent Antarctique (mer de Ross, baie de Prydz), les eaux du "Polar Frontal Jet " qui mémorise un signal significatif en fer provenant des sources côtières et de manière moins importante les régions influencées par la retraite de la banquise ayant accumulée des apports éoliens en fer.

Le rôle trophique du protozooplancton est évalué dans chaque province en intégrant durant un cycle annuel les taux journaliers de production primaire, de production bactérienne et d'ingestion des bactéries et du nanophytoplancton par le protozooplancton. Une production phytoplanctonique annuelle net entre 43 et 312 mgC m^{-2} est estimée. 52 à 65 % de cette production est incorporée directement ou indirectement par le réseau trophique microbien, soit par les bactéries soit par les protozoaires. La demande en carbone annuelle des bactéries représentait 12 à 21 % de la production primaire net annuelle. Les protozoaires bactérivores contrôlaient 46 à 98 % de la production bactérienne annuelle tandis que les protozoaires nanoplanctivores contrôlaient entre 31 et 98 % de la production primaire nette annuelle. L'efficience trophique du réseau microbien varie entre 25 et 33 %. Ces budgets en carbone montrent d'autre part que la production secondaire du réseau trophique microbien représente de l'ordre de 50 % de la demande alimentaire du krill. Ceci suggère que le protozooplancton joue un rôle clef dans le transfert d'énergie et de matières vers le métazooplancton et le krill dans l'océan Antarctique.

Structure and Functioning of the Microbial Food Web in the Antarctic Ocean

S. Becquevort, C. Lancelot,...

ABSTRACT- The structure and functioning of the microbial food web in the Antarctic Ocean are studied on the comprehensive analysis of existing data on phytoplankton, bacterioplankton and protozooplankton biomass and activity. This analysis is conducted in the five interdependent biogeochemical provinces which characterize the Antarctic Ocean; the Frontal Zone (FZ), the Open Ocean Zone (OOZ), the Marginal Ice Zone (MIZ), the Closed Pack Ice Zone (CPIZ) and the Coastal and Continental Shelf Zone (CCSZ). It is concluded that the general High Nutrient Low Chlorophyll (HNLC) conditions of the Southern Ocean are resulting from the successful development of protozoan grazer-controlled pico- and nanophytoplanktonic communities in a low-iron (<1nM) environment. Superimposing this active microbial food web, episodic blooms of diatoms or *Phaeocystis* colonies are well developing in iron-enriched areas that experience favorable meteorological conditions. Such areas are the near-shore neritic areas supplied with iron from the shelf sediments and the Antarctic continent (Ross Sea, Prydz Bay), the rapidly eastward flowing Polar Frontal Jet which retains a significant iron signal from the shelf sources and to a lesser extent some sea-ice covered areas having accumulated minor aerosol inputs.

The trophic role of protozooplankton in each biogeochemical province is evaluated from the integration over the seasonal cycle of the daily rates of primary production, bacterial production and bacterial and nanoplankton ingestion by protozoa. Net annual primary production in the Antarctic Ocean varies between 43 and 312 gC m^{-2}. From 52 to 65 % of the annual net primary production is directly and indirectly assimilated in the microbial food web, composed of bacterioplankton, bacterivorous and nanoplanktivorous protozoa. Bacterial carbon demand amounts to 12 - 21 % of the net primary production. Bacterivorous protozoa are controlling 46 - 98 % of the annual bacterial production while nanoplanktivorous protozoa are controlling 31 - 98 % of the annual phytoplanktonic production. The trophic efficiency of the microbial food web is ranging between 25 and 33 %. Interestingly, the microbial food web secondary production represents as much as 50 % of the annual krill food demand. This suggests that protozoa can play a key role in the transfer of energy and materials to krill and large zooplankton in the Antarctic Ocean.

to be submitted to other authors

INTRODUCTION

Antarctic waters are commonly dominated by pico- and nanophytoplankton communities which are superimposed by episodic "exceptional" bloom pulses of large phytoplankton such as large diatoms and *Phaeocystis* colonies (Smetacek *et al.* 1990). It has been suggested that iron deficiency (Martin *et al.* 1990, de Baar *et al.* 1990, van Leeuwe *et al.* 1997, Scharek *et al.* 1997), the silicate shortage (Nelson and Tréguer 1992, Quéguiner *et al.* 1997) and the high grazing pressure by the krill (Graneli *et al.*, 1993) are mainly repressing larger phytoplankters, explaining the predominance of smaller cells in the Southern Ocean (Lancelot *et al.* 1993, 1997). These minute cells are indeed competitive at low nutrient concentration, but they very seldom form blooms being heavily grazed by the ubiquitous protozooplankton. In spite of the widespread distribution of protozooplankton in Antarctic waters (Garrison 1991, Garrison and Gowing 1991), its ecological role as an energy link to higher trophic levels or as nutrients regenerators are still lively debated. Such important questions as well as their contribution to the food demand of metazoan and their role in maintaining the functioning of the microbial food web through the release of nutrients, iron in particular, as catabolic products are still unresolved.

This review examines the trophic role of protozooplankton in the Southern Ocean based on the comprehensive analysis of existing data on phytoplankton, bacterioplankton and protozooplankton biomass and activity. This analysis is conducted in the five distinct but interdependent biogeochemical provinces which characterise the Antarctic Ocean (Tréguer & Jacques 1992): (i) the Frontal Zone (FZ, are) which is mainly represented by the Polar Front (3 10^6 km^2, 9 % of the total surface of the Antarctic Ocean), (ii) the permanently ice-free Open Ocean Zone (OOZ, 14 10^6 km^2 , 41 % of the total surface of the Antarctic Ocean), north of ice covered areas which comprises mainly the large oceanic Antarctic Circumpolar Current located between the Polar Front and the northern limit of the pack ice zone; and (iii) the sea ice zone (16 10^6 km^2, 47.5 % of the total surface of the Antarctic Ocean), including the Marginal Ice Zone (MIZ) which is defined as the transition area between the ice-free OOZ and the heavy ice-covered area (>85 % of sea surface), the Closed Pack Ice Zone (CPIZ) which is the part of the sea ice associated area characterised by a marked ice cover (higher than 85 % of sea surface) and the Coastal and Continental Shelf Zone (CCSZ, 0.9 10^6 km^2 , 2.5 % of the total surface of the Antarctic Ocean) characterised by inshore and shallow waters.

In the first part, the paper discusses the role of the physico-chemical and biological factors as structuring agents of the food web based on the analysis of spatio-temporal distributions of

phytoplankton, bacterioplankton and protozooplankton biomass and activity. In the second part, the trophic role of protozooplankton in each biogeochemical province of the Antarctic Ocean is evaluated from carbon budgets estimated by integrating over the whole season phytoplankton, bacterioplankton and protozooplankton activities in the wind mixed layer.

1. Spatio-temporal distribution of microbial organisms biomass and activities

1.a. Phytoplankton

In order to increase the data set, we choose to use chlorophyll *a* as an indicator of phytoplankton biomass. Results expressed as mg Chla m^{-3} are gathered in Table 1. Primary production are summarized in Table 2. Additional information on the size (< and > 20 µm) dominance are indicated when available.

The resulting composite of chlorophyll *a* and primary production seasonal variation is illustrated by Fig. 1 and 2. A marked seasonnality of chlorophyll *a* and primary production is observed in the whole Southern Ocean as can be expected from the typical seasonal cycle of solar radiation prevailing in polar regions. In all biogeochemical provinces, autumn and winter chlorophyll *a* concentration and primary production are at their minimum level. The onset, duration and magnitude of the phytoplankton production (Fig. 2) greatly vary between the biogeochemical provinces. A one-month delay in the onset of phytoplankton production is observed from north to south (Fig. 2). Except in the CCSZ area (Fig.1e), phytoplankton bloom never reaches the expected 25 mg Chl-a m^{-3} as can be calculated from the nutrient bulk concentrations. Extremely, low phytoplankton (< 0.1 mg Chla m^{-3}) and low daily primary production (< 500 mg C m^{-2} d^{-1}) are typical of OOZ and CPIZ (Fig. 1d & 2d). In these areas, the phytoplankton community is almost exclusively composed of pico- and nano-size species (Table 1, 2). Mesoscale events of high biomass and productivity do however occur (i) in the FZ (Fig. 1a & 2a); (ii) in the MIZ (Fig. 1c & 2c) and (iii) in CCSZ (Fig. 1e & 2e). In these biogeochemical provinces, the time position of the maximum development varies from one province to another (Fig. 2). In the FZ, blooms of large diatoms (Table 1) are recorded in mid-spring. The maximum *chlorophyll a* and primary production reached are 3 mg m^{-3} and 3 gC m^{-2} d^{-1}, respectively (Fig. 1a & 2a). In the MIZ, both chlorophyll *a* and primary production are highly variable (Fig. 1c & 2c). Occasionally substantial blooms dominated by pico- and nanophytoplankton (Table 1) are recorded in late spring- early summer. The maximum *chlorophyll a* and primary production reached are 7 mg m^{-3} and 1400 mgC m^{-2} d^{-1} , respectively. The coastal and continental shelf zone is shown to be the most productive area with blooms of microphytoplanktonic species (diatoms and *Phaeocystis* colonies) reaching in full summer 20 mg Chl-a m^{-3} and of 3620 mgC m^{-2} d^{-1} of primary production. In the Ross Sea polynya, however, the phytoplanktonic production maxima (6222 mgC m^{-2} d^{-1}) is recorded in spring (Fig.1e & 2e, Table 1 & 2).

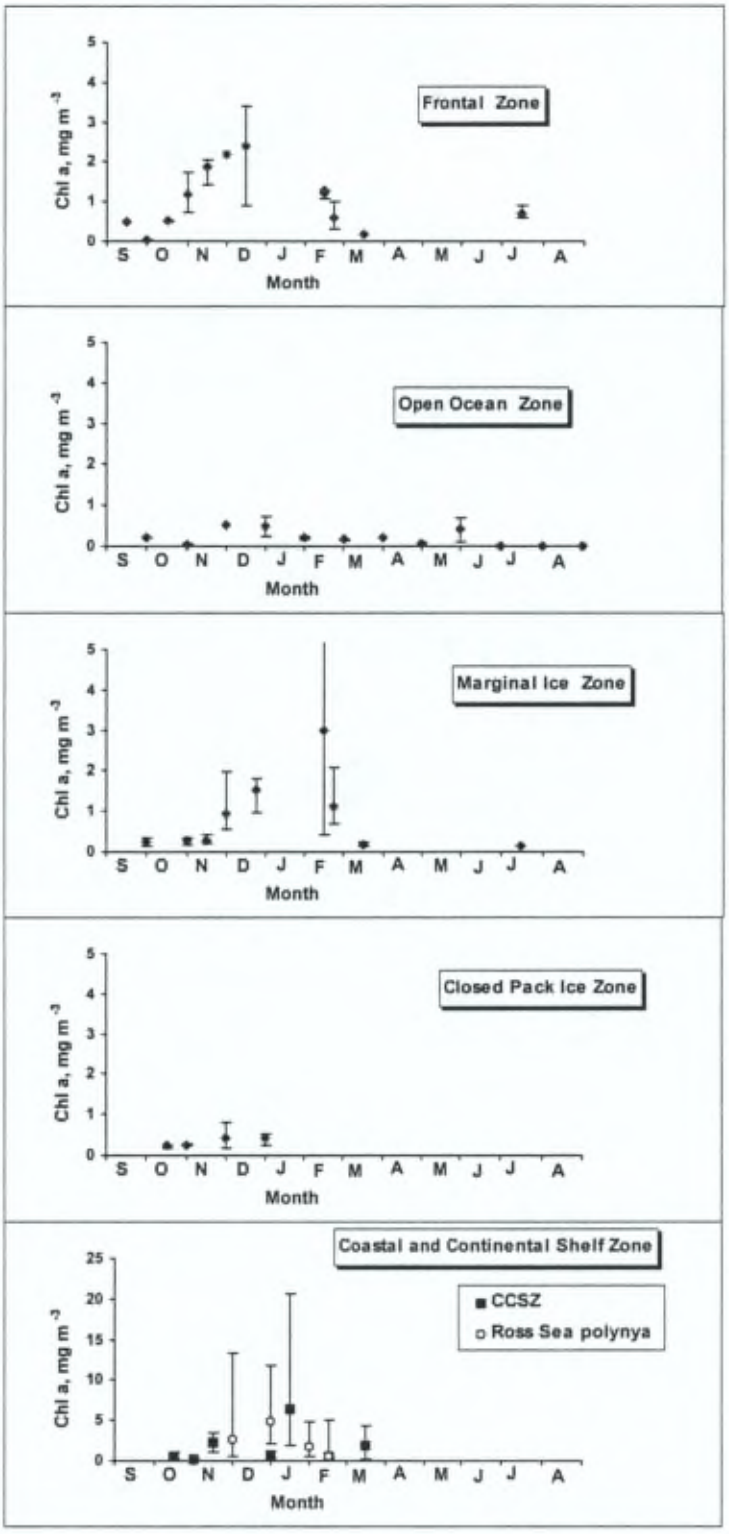

Figure 1. *Reconstructed seasonal cycle of the chlorophyll a concentration in the FZ, the OOZ, the MIZ, the CPIZ and the CCSZ. Min., max. and mean values are indicated.*

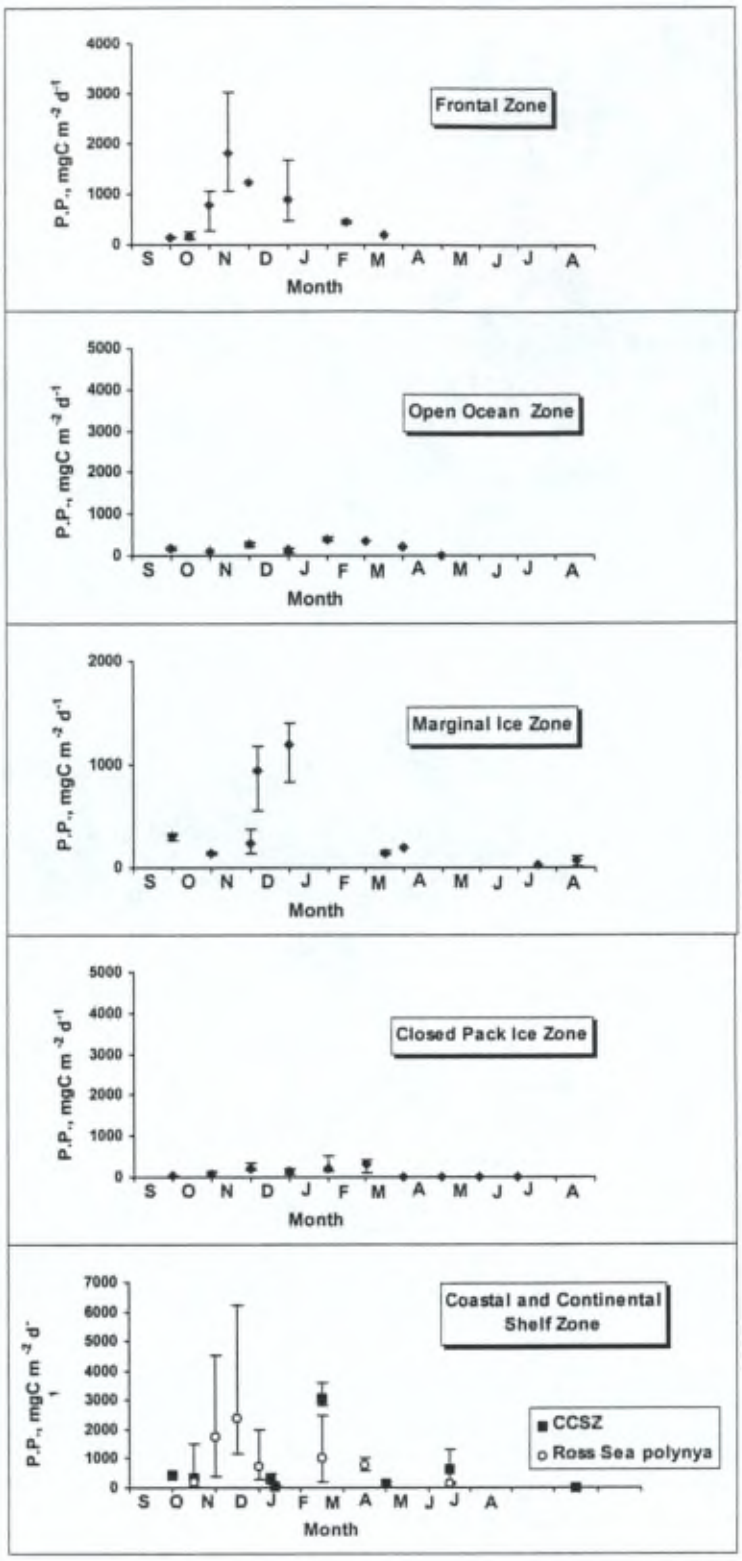

Figure 2. *Reconstructed seasonal cycle of the net primary production in the FZ, the OOZ, the MIZ, the CPIZ and the CCSZ. Min., max. and mean values are indicated.*

Table 1. (Part 1) *Compilation of the size-fractionated chlorophyll a data in the Antarctic Ocean*

Geographical location	Season	Chl.a mg m^{-3}	Methods	% of phytoplankton < 20 µm	Reference
Frontal zones					
Polar front (Atlantic sector)	Winter	0.6 - 0.9 , 0.7	Sequential filtration	80 - > 90	Froneman& Perissinotto, 1996a
Polar front (Atlantic sector)	Spring	0.5 - 2.1, 1.1	Microscopic observations	dominance of microphytoplankton	Bathmann *et al.*, 1997
Polar Front (Atlantic sector)	Early summer	0.9 - 3.4, 2.4	Sequential filtration	23 - 51, 37	Laubscher *et al.*, 1993
Polar Front (Atlantic sector)	late summer	1.1 - 1.3, 1.2	Sequential filtration	46 - 51, 49	Laubscher *et al.*, 1993
Polar Front (Atlantic sector)	Late summer	0.3 - 1.0, 0.6	Sequential filtration	Dominance of nanophytoplankton	Froneman & Perissinotto, 1996b
Polar Front (Atlantic sector)	Autumn		Sequential filtration	53	Weber & El-Sayed,1987
Weddell-Scotia confluence	Early spring	0.5	Sequential filtration	25 -60 (< 8 µm)	Gieskes & Elbrächter, 1986
Weddell-Scotia confluence	Spring-summer	1.2 - 3.3, 2.5	Sequential filtration	0 - 93, 36	Jacques & Panouse, 1991
Weddell-Scotia confluence	Late summer	1.3	Sequential filtration	32	Laubscher *et al.*, 1993
Polar front (Indian sector)	Early spring	0.3 - 0.4, 0.3	Sequential filtration	87 - 92, 90	Semeneh, 1997
Polar front (Indian sector)	Spring	0.6 ± 0.7			Fukuchi, 1980
Polar front (Indian sector)	Late summer	0.6 ± 0.7			Fukuchi, 1980
Polar Front (Indian sector)	Late summer	0.3 - 0.3, 0.3	Sequential filtration	83 - 92, 88	Fiala & Oriol, 1995; Semeneh, 1997
Antarctic Divergence	Autumn	0.2 - 1.7, 0.5			Mathot, 1993
Open Ocean					
Scotia Sea	Early spring	0.2	filtration through 8 µm Wathman GF/C)	> 75 (< 8 µm)	Gieskes & Elbrächter , 1986
Atlantic sector	Spring	0.1 0.8, 0.3	microscopic observations	dominance of nanophytoplankton	Bathmann *et al.*, 1997
Atlantic sector	Late summer	0.1 - 0.7, 0.4	Sequential filtration	Dominance of microphytoplankton	Froneman & Perissinotto, 1996b
Weddell Sea	Spring-summer	0.2 - 0. 8, 0.3	Sequential filtration	44 - 88, 68	Jacques & Panouse, 1991
Indian sector	Early spring	0.3 - 0.4, 0.3	Sequential filtration	80 - 83, 82	Semeneh, 1997
Indian sector	Spring	0.5 ± 0.3			Fukuchi, 1980
Indian sector	Late summer	0.1 - 0.1, 0.1	Sequential filtration	58 - 70, 68	Fiala & Oriol, 1995

Table 1. (Part 2) *Compilation of the size-fractionated chlorophyll a data in the Antarctic Ocean*

Sea Ice associated area					
A. MIZ					
Indian sector	Early spring	0.2 - 0.5, 0.4	Sequential filtration	45 - 47, 46	Semeneh, 1997
Weddell Sea	Early spring	1.1 - 1.3, 1.3	Sequential filtration	26 - 29, 27	Jacques & Panouse, 1991
Atlantic sector	Spring	0.2 - 0.3,0.3	microscopic observations	dominance of nanophytoplankton	Bathmann *et al.*, 1997
Weddell Sea	Spring-summer	0.6 - 3.6, 1.3	Sequential filtration	29 - 97, 91	Jacques & Panouse, 1991
Weddell Sea	Late summer	0.4 - 7.0, 3.0	Sequential filtration	dominance of phytoplankton < 20 µm	Laubscher *et al.*, 1993
Indian sector	Late summer	0.2 - 0.3, 0.2	Sequential filtration	60 - 80, 73	Fiala & Oriol, 1995
Atlantic sector	Late summer	0.7 - 2.1, 1.1	Sequential filtration	dominance of nanophytoplankton	Froneman & Perissinotto, 1996b
Weddell sea	Winter	0.1		dominance of nanophytoplankton	Garrison & Mathot, 1996
B. CPIZ					
Atlantic sector	Spring	0.2 - 0.4, 0.3	microscopic observations	dominance of nanophytoplankton	Bathmann *et al.*, 1997
Weddell Sea	Spring-summer	0.2 - 0.8, 0.4	Sequential filtration	84 - 95, 88	Jacques & Panouse, 1991
Lazarev Sea	Summer		Sequential filtration	38- 34, 36	Froneman *et al.*, 1997
C.CCSZ					
Antarctic Peninsula & Bransfield strait area					
West Bransfield Strait	Summer	1.1	Microscopic observations	59	Kopczynska, 1992
Bransfield Strait	Summer	0.6	Microscopic observations	82	Kopczynska, 1992
East Bransfield strait	Summer	0.4	Microscopic observations	80	Kopczynska, 1992
Western Bransfield Strait	Late summer	1 - 5	Sequential filtration	90 - 92	Holm-Hansen & Mitchell, 1991
Bransfield Strait	Late summer	0.1	Microscopic observations	96	Kopczynska, 1992
Drake passage	Spring	0.1 - 1.0	Sequential filtration	39 - 97, 64	Weber & El-Sayed, 1987
Drake Passage	Summer	0.6	Microscopic observations	49	Kopczynska, 1992
Drake Passage	Late summer	0.1	Microscopic observations	45	Kopczynska, 1992
Bellighausen Sea	Spring	0.1 - 0.3, 0.2	Sequential filtration	78 - 83, 81	Boyd *et al.*, 1995

Table 1. (Part 3) *Compilation of the size-fractionated chlorophyll a data in the Antarctic Ocean*

Prydz Bay					
Prydz Bay	Summer	1.9 - 20.7	microscopic observation	large diatom-dominated bloom	Archer *et al.* (1996)
Prydz Bay	Autumn	0.2 - 4.3, 1.9	microscopic observations	2 - 38, 21	Mathot, 1993
Indian sector	Late summer	0.4 - 0.5, 0.5	Sequential filtration	65	Fiala & Oriol, 1995
Ross Sea					
Ross Sea	Spring	0.5 - 13.3, 2.7			Smith *et al.*, pers.com.
Ross Sea	Early summer (January)	2.0 - 11.8, 4.9	microscopic observations	Dominance of microphytoplankton; Phaeocystis (Southeast), diatoms (Southwest	Smith *et al.*, 1996
Ross Sea	Summer (early february)	0.5 - 4.8 ,1.8			Smith *et al.*, 1996
Ross Sea	late summer	0.2 - 2.6, 0.6			Ditullio & Smith, 1996

Table 2. (Part 1) *Compilation of the primary production data in the Antarctic Ocean.*

Geographical location	Season	Phyto. production, mgC m^{-2} d^{-1}	Phytoplankton dominance	Reference
Frontal zones				
Polar Front (Indian sector)	Early spring	128 - 140, 134	< 20 µm	Lancelot, pers.com.
Polar Front (Atlantic sector)	Early spring	105 - 237, 171	< 20 µm	Mathot *et al.*, 1994
Polar Front (Atlantic sector)	Mid-Spring	277 - 1052, 772	> and < 20 µm	Mathot *et al.*, 1994
Polar Front (Atlantic sector)	Late Spring	1052 - 3041, 1831	> 20 µm	Mathot *et al.*, 1994
Weddell-Scotia Confluence	Spring	1040 - 1330, 1210	> 20 µm	Mathot, 1993
Polar Front (Atlantic sector)	Early summer	470 - 1680, 900	Phytoplankton > 20 µm	Laubscher *et al.*, 1993
Polar Front (Atlantic sector)	Late summer	420 - 460, 440	Phytoplankton < 20 µm	Laubscher *et al.*, 1993
Polar Front (Indian sector)	Late summer	186	< 20 µm	Lancelot, pers. com.
Antarctic Divergence (Indian sector)	Late summer	70	< 20 µm	Lancelot, pers. com.
Antarctic Divergence (Indian sector)	Autumn	30 - 380, 160	> 20 µm	Mathot, 1993
Open ocean				
ACC (Indian sector)	Early spring	140 - 192, 157	< 20 µm	Lancelot
ACC (Atlantic sector)	Early spring	118	< 20 µm	Mathot *et al.*, 1993
ACC (Atlantic sector)	Mid spring	210 - 315, 263	< 20 µm	Mathot *et al.*, 1993
ACC (Atlantic sector)	Late spring	79 - 184, 145	< 20 µm	Mathot *et al.*, 1993
Weddell- Scotia Seas	Early summer	330 - 436, 393	> 20 µm	Mathot *et al.*, 1993
Weddell- Scotia Seas	Summer	351	< 20 µm	Mathot *et al.*, 1993
ACC (Indian sector)	Late summer	222	< 20 µm	Lancelot, pers. com.
Sea ice associated area				
A. MIZ				
ACC (Indian sector)	Early spring	264 - 327, 296	< 20 µm	Lancelot
ACC (Atlantic sector)	Early spring	129 - 145, 136	< 20 µm	Mathot *et al.*, 1993
ACC (Atlantic sector)	Mid spring	142 - 374, 243	< 20 µm	Mathot *et al.*, 1993
Weddell Sea	Spring	240	< 20 µm	Garrison & Mathot, 1996
Weddell Sea	Spring	640	> 20 µm	Garrison & Mathot, 1996
Weddell Sea	Early summer	558 - 1179, 945	< 20 µm	Mathot *et al.*, 1992
Weddell Sea	Late summer	839 - 1402, 1200	< 20 µm	Mathot *et al.*, 1992
ACC (Indian sector)	Late summer	122 - 159, 141		Lancelot, pers. com.
Weddell Sea	Autumn	190	< 20 µm	Garrison & Mathot, 1996
Weddell Sea	Winter	30	< 20 µm	Garrison & Mathot, 1996
Scotia Sea	Late winter	20 - 110, 70		El-Sayed & Weber, 1982

Table 2. (Part 2) *Compilation of the primary production data in the Antarctic Ocean.*

B. CPIZ				
ACC (Atlantic sector)	Start-Spring	13 - 32, 19	< 20 µm	Mathot *et al.*, 1993
ACC (Atlantic sector)	Mid-Spring	6 - 140, 72	< 20 µm	Mathot *et al.*, 1993
Weddell Sea	Spring	180 - 350, 270	< 20 µm	Cota *et al.*, 1990
Weddell Sea	Start-Summer	139 -535, 196	< 20 µm	Mathot *et al.*, 1993
Weddell Sea	Mid-Summer	106 - 417, 314	< 20 µm	Mathot *et al.*, 1992
Weddell Sea	Autumn	80 - 200, 140	< 20 µm	Cota *et al.*, 1990
C. CCSZ				
South Georgia Island	Early spring	460		El-Sayed & Weber, 1982
South Georgia Island	Autumn	340		El-Sayed & Weber, 1982
South Sandwich Island	Early spring	340		El-Sayed & Weber, 1982
South Sandwich Island	Autumn	250		El-Sayed & Weber, 1982
Deception Island	Summer	2800 - 3620, 3073		Mandelli & Burkholer, 1966
Signy Island	Summer	2800		Horne *et al.*, 1969
Bellingshausen Sea	Spring	230 - 490, 300	> 20 µm	Savidge *et al.*, 1995
Bellingshausen Sea	Spring	40 - 80, 60	< 20 µm and > 20 µm	Savidge *et al.*, 1995
Gerlache Strait	Summer	3200		El-Sayed, 1967
Antarctica Peninsula	Late Winter	n. m. - 1100, 290		Kottmeier & Sullivan, 1987
Western Bransfield Strait	Late summer	70 - 210	< 20 µm	Holm-Hansen & Mitchell, 1991
Bransfield Strait	Winter	n.m. - 7, 2		Brightman & Smith, 1989
Indian sector	Late summer	208	< 20 µm	Lancelot, pers. com.
Prydz Bay	Autumn	140 - 1290, 610		Mathot, 1993
Ross Sea	Early spring	15 - 30, 20		El-Sayed *et al.* 1983, Wilson *et al.* 1986, Demaster *et al.* 1992
Ross Sea	Mid-spring	30 - 1500, 200	> 20 µm	DeMaster *et al.* 1992, Ducklow *et al.*1998
Ross Sea	Late spring	400 - 6220, 1750	>20 µm	Arrigo & McClain 1994, Lancelot *et al.* 1998, Ducklow *et al.* 1998
Ross Sea	summer	200 - 2500, 1000	>20 µm	Arrigo & Mc Clain 1994, Lancelot *et al.* 1998, Ducklow *et al.* 1998
Ross Sea	Late summer	600 - 1000, 800	>20 µm	Lancelot *et al.*, 1998, Ducklow *et al.* 1998
Ross Sea	Autumn	100 - 200, 150		Lancelot *et al.*, 1998, Ducklow *et al.* 1998

As a general trend, large phytoplankton biomass generally corresponds to the development of large species i.e. large diatoms and *Phaeocystis* colonies. As reported in Table 1 and in Fig. 3, the few stations characterised by high *chlorophyll a* concentration (> 10 mg m^{-3}) are dominated by microplankton. Phytoplankton assemblages with intermediate *chlorophyll a* (>1.5 < 10 mg m^{-3}) are mainly dominated by microplankton. Although moderate nanophytoplankton blooms of 3 - 6 mg Chl-a m^{-3} are observed in the MIZ. Pico- and nanoplanktonic cells are dominant as well as at biomass less than 1.5 mg Chla m^{-3} although some microphytoplankton cells are still present (Fig. 3).

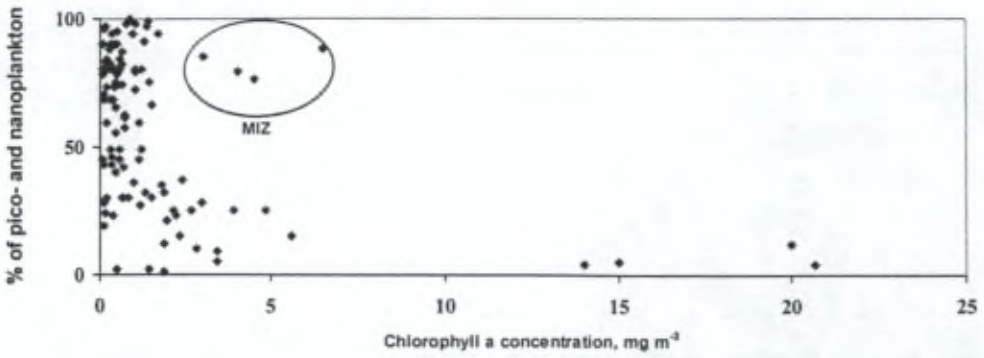

Figure 3. *Relationship between the relative proportion of pico- and nanophytoplankton into the total chlorophyll a concentration and the chlorophyll a concentration.*

The contrasted phytoplankton bloom conditions observed in the different biogeochemical provinces (Fig. 1 & 2) are clearly resulting from the contrasted meteorological and chemical conditions prevailing in each area. Limitation by irradiance and iron deficiency are the main factors controlling the phytoplankton size spectrum and productivity.

Indeed, the development of phytoplankton blooms in polar regions is a function of the light supply which depend on the sea-ice cover, solar radiation and the depth of vertical mixing itself driven by wind stress. Light availability controls all phytoplankton size classes, but especially the larger microplankton cells which have less quantum absorption efficiency (Morel & Bricaud 1981). The intense ice-albedo in the CPIZ, is thus strongly limiting the primary production in this area. This explains the near-complete dominance of pico- and nanophytoplankton. Accordingly, a negative correlation between the net primary production and the ice cover percentage has been shown by Mathot (1993). High limitation, driven by wind stress is likely responsible of the low production rates recorded in the OOZ area as well as of the dominance of pico- and nanoplanktonic species. The OOZ is frequently subjected to strong westerly winds inducing low water column stability and deep mixing (> 100 m). The high frequency of storm events occurring in the OOZ area are preventing phytoplankton cells from growing, being swept below the euphotic depth. On the other hand, shallow upper mixed layers have been observed in the MIZ, the FZ and the CCSZ, regions where phytoplankton blooms are indeed recorded (Fig. 1). In the sea-ice covered regions (MIZ, CCSZ), a shallow vertically stable upper layer of less than 50 m can be observed at the time of ice melting as the result of the melt water production. Moreover, the seeding of this marginal ice-edge zone by sea ice microalgae is likely to contribute to the developing planktonic population (Garrison *et al.*, 1987) although the extent to which this occurs has been questioned (Riebesell *et al.* 1991, Mathot *et al.* 1991).

However, events of high vertical stability are not always associated with the ice melting when the later is driven by wind. It has been shown that the frequent storm events of high intensity were

preventing the formation of shallow mixed layer in the MIZ in the Atlantic sector in spring 1992 (Lancelot *et al.* 1996). In the frontal system of the Polar Front, the admixture of warmer sub-Antarctic waters from the north causes the upper water column to be more stable and so retain the phytoplankton in the euphotic zone (Veth *et al.* 1997).

Phytoplankton biomass reached in the above hydrodynamically stable areas (MIZ and FZ) remains modest (less than 10 mg Chl a m^{-3}) and significantly lower than expected from the concentrations of major nutrients (Hayes *et al.* 1984). As controlling factor of phytoplankton production and size spectrum, trace metal limitation, in particular iron (Martin and Fitswater, 1988), has been investigated since 1988 in several regions of the Southern Ocean : the Weddell and Scotia Sea (de Baar *et al.*, 1990), the Drake Passage (Helbling *et al.*, 1991, Martin *et al.*, 1990), the Ross Sea (Martin *et al.*, 1990) and the Atlantic and Pacific sectors of the Antarctic Circumpolar Current (de Baar *et al.*, 1995). Results indicate that Fe availability is structuring the phytoplankton community. Low Fe supply is indeed limiting the growth rate of large diatoms while non affecting the development of pico- and nano-sized cells which are better competitors at low nutrient concentration due to their large surface:volume ratio (Morel, 1990). The biomass of these minute organisms is kept at very low level, grazed by the ubiquitous fast-growing protozoa. Supporting this, Fe-rich areas like the neritic waters e.g. the continental shelf and the proximity of islands-, the Frontal zone like the Polar Frontal Jet (de Baar *et al.* 1996, de Baar *et al.* 1998) and the Weddell-Scotia Confluence (Nolting *et al.* 1991) as well as some-ice covered regions having accumulated aeolian Fe, are spporting microphytoplankton-dominated blooms. However, microphytoplanktonic dominance is not always observed in Fe- and light- non limiting regions of the Southern Ocean. For instance the summer phytoplankton bloom recorded in the north-western Weddell Sea in 1988 was typically dominated by nanoflagellates, mainly *cryptomonas* (Becquevort *et al.* 1992). The dominance of nano-sized microbes in that region was shown to be the consequence of a krill swarm passage (Jacques and Panouse, 1992; Lancelot *et al.*, 1993b). Krill by selectively eliminating micro-sized microbes and mesozooplankton from the water column seems to have enhanced the development of nano-sized phytoplankton and of herbivorous protozoa (Lancelot *et al.*, 1993b). In this area of krill occurrence, the dominating food-web is mainly driven by random top predator control.

1.b. Bacterioplankton

As reported in Fig. 4 and 5, bacterioplankton biomass ranges between 0.7 and 145.5 mgC m^{-3} and production between 10.8 and 372 mgC m^{-2} d^{-1}.

As for phytoplankton, the maximal bacterial biomass is observed in the FZ (18 mgC m^{-3}), in the MIZ (18 mgC m^{-3}) and in the CCSZ (145 mgC m^{-3}), however the range of variations is less

important than that recorded for phytoplankton. On the contrary, bacterial production displays significant variations between the different sub-systems but specially between the different seasons. As for primary production, the maximum bacterial production is recorded in the CCSZ and the lowest in the OOZ and CPIZ (Fig.5, Table3). Elevated values are reported in end-summer-early autumn, particularly in FZ (up to 92 mgC m^{-2} d^{-1}), in the MIZ (up to 200 mgC m^{-2} d^{-1}) and in the CCSZ (up to 372 mgC m^{-2} d^{-1}). Unexcepted for the CCSZ, the bacterioplankton production and biomass in the Ross Sea are very low (< 13 mgC m^{-3} and < 32 mgC m^{-2} d^{-1} for the bacterial biomass and production, respectively, Fig. 4 & 5).

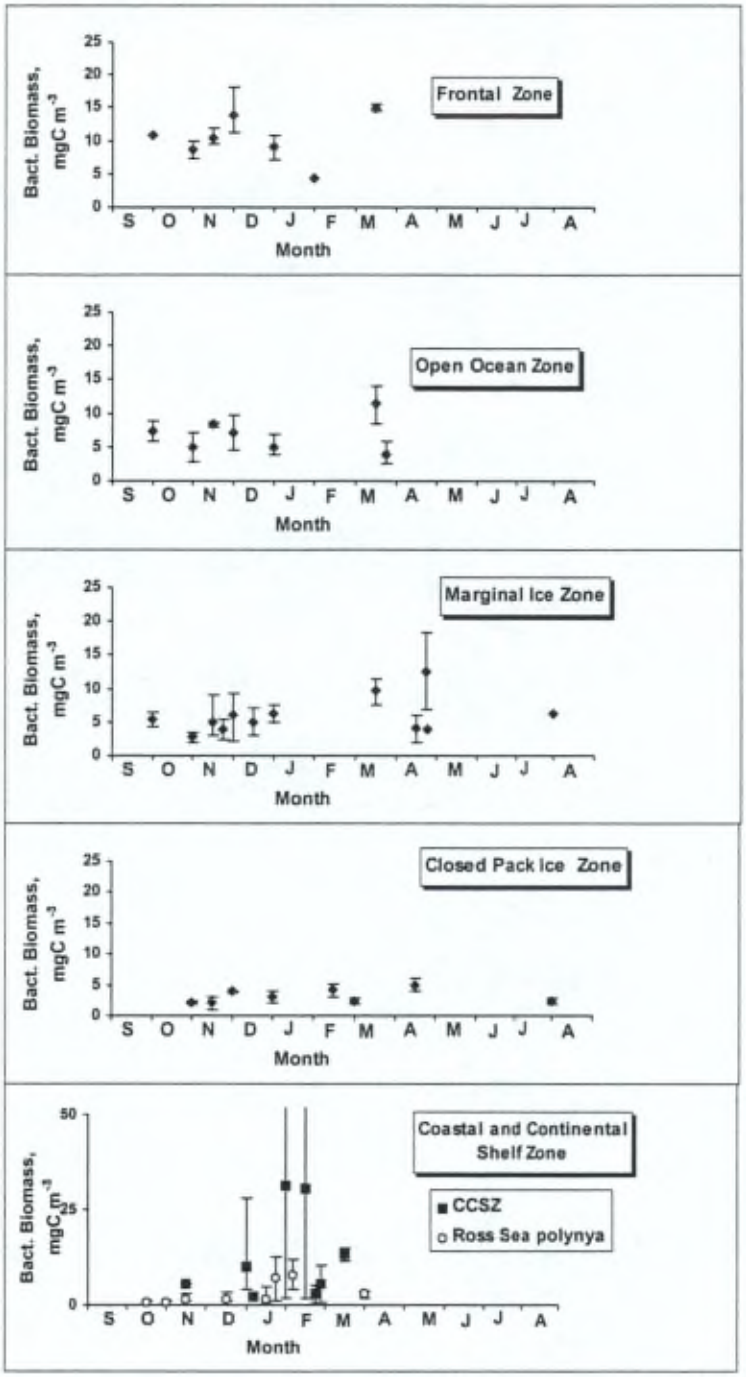

Figure 4. *Reconstructed seasonal cycle of the bacterial biomass in the FZ, the OOZ, the MIZ, the CPIZ and the CCSZ. Min., max. and mean values are indicated.*

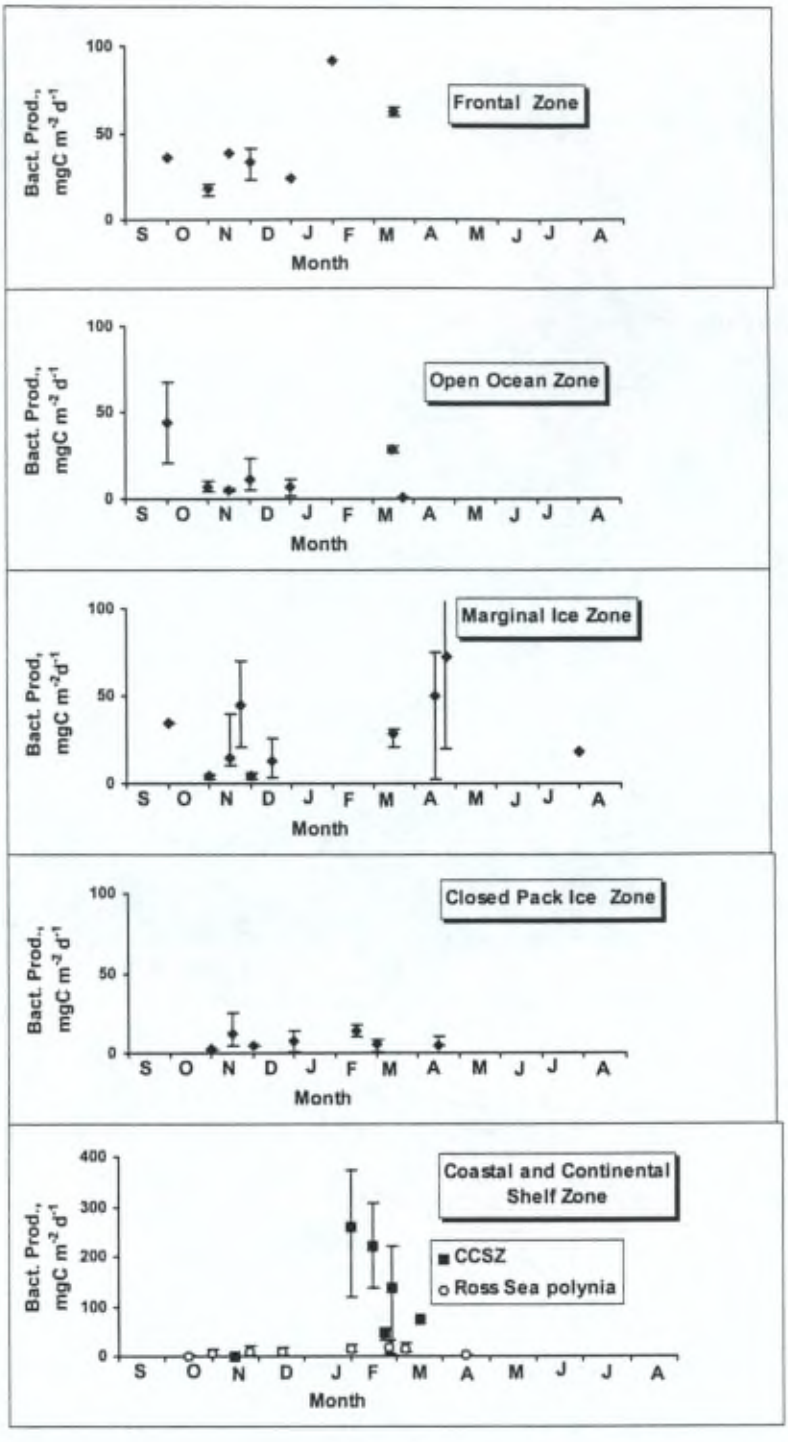

Figure 5. *Reconstructed seasonal cycle of daily rates of bacterial production in the FZ, the OOZ, the MIZ, the CPIZ and the CCSZ. Min., max. and mean values are indicated.*

Table 3. (Part 1) *Compilation of the average bacterial biomass and daily production data in the upper mixed layer of the Antarctic Ocean.*

Sub-areas Geographic localisation	Period	Biomass mgC m^{-3}	Production mgC m^{-2} d^{-1}	Reference
Frontal zones				
Polar Front (Indian sector)	Early spring	10.8	36	Yoro, 1997
Polar Front (Atlantic sector)	Early spring	7.3 - 9.9, 8.6	14 - 21, 18	Lochte *et al.*, 1997
Polar Front (Atlantic sector)	Mid spring	9.5 - 11.8, 10.3	39	Lochte *et al.*, 1997
Polar Front (Atlantic sector)	Late spring	11.2 - 18.0, 13.9	23 - 41, 34	Lochte *et al.*, 1997
Scotia-Weddell confluence	Spring-Summer	7.1 - 10.8, 9.0	24	Billen & Becquevort, 1991
Scotia-Weddell	Summer	4.3	92	Pedros-Alio *et al.* 1996
Polar Front (Indian sector)	Late summer	14.5 - 15.5, 14.8	60 - 65, 63	Talbot, 1995
Open ocean				
Indian sector	Early spring	5.8 - 8.8, 7.4	20 - 67, 44	Yoro, 1997
ACC (Atlantic sector)	Early spring	2.8 - 7.1, 5.0	4 - 10, 7	Lochte *et al.*, 1997
ACC (Atlantic sector)	Mid spring	8.0 - 8.7, 8.4	4 - 6, 5	Lochte *et al.*, 1997
ACC (Atlantic sector)	Late spring	4.6 - 9.6, 7.1	5 - 23, 11	Lochte *et al.*, 1997
Scotia-Weddell seas	Spring-Summer	3.8 - 6.8, 4.9	1.8 - 11, 7	Billen & Becquevort, 1991
Indian sector	Late summer	8.5 - 14.0, 11.4	27 - 30, 28	Talbot, 1995
Western Weddell Sea	Late summer	2.49-5.82, 3.94	0.8-1.3, 1.1	Garrison & Buck, 1989
Sea Ice associated area				
A.MIZ				
Indian sector	Early spring	4.3 - 6.4, 5.4	34.9	Yoro, 1997
ACC (Atlantic sector)	Early spring	1.9 - 3.4, 2.7	3 - 5, 4	Lochte *et al.*, 1997, Becquevort 1997
Weddell-Scotia Sea	Spring	3.0 - 9.0	10 - 40, 15	Sullivan *et al.*, 1990
Weddell Sea	Spring	2.3 - 5.3, 3.8	21 -70, 45	Garrison & Mathot, 1996
ACC (Atlantic sector)	Mid spring	2.2 - 9.3, 6.0	3 - 6, 4	Lochte *et al.*, 1997, Becquevort 1997
Weddell Sea	Spring-Summer	3.1 - 7.1, 4.9	3.1 - 26, 13	Billen & Becquevort, 1991
Eastern Weddell Sea	Summer	5.0 - 7.6		Gleitz *et al.* 1994
Indian sector	Late summer	7.5 - 11.5, 9.6	20 - 31, 28	Talbot, 1995
Weddell Sea	Autumn	2.0 - 6.0	2.5 - 75, 50	Cota *et al.*, 1990
Eastern Weddell Sea	Autumn	6.8 - 18.4	20 - 200	Gleitz *et al.* 1994
Weddell Sea	Autumn	3.8	72	Garrison & Mathot, 1996
Weddell Sea	Winter	6.3	18	Garrison &Mathot, 1996
B.CPIZ				
Weddell Sea	Winter	1.8 - 2.8		Helmke & Weyland, 1995
ACC (Atlantic sector)	Early spring	1.8 - 2.4, 2.2	2 - 3, 3	Lochte *et al.*, 1997, Becquevort 1997
Weddell-scotia Sea	Spring	1.0 - 3.0	5 - 25, 12	Sullivan *et al.*, 1990
ACC (Atlantic sector)	Mid spring	3.8 - 3.9, 3.9	5 - 5, 5	Lochte *et al.*, 1997, Becquevort 1997
Weddell Sea	Spring-Summer	2.0, 3.9, 3.0	1 - 14, 8	Billen & Becquevort, 1991
Eastern Weddell Sea	Late summer	3.0 - 5.2	10 - 18	Gleitz *et al.* 1994
Western Weddell Sea	Late summer	2.0 -2.7, 2.3	1 - 8, 6	Garrison & Buck, 1989
Weddell Sea	Autumn	4 - 6	5 - 10, 5	Cota *et al.*, 1990

Table 3. (Part 2) *Compilation of the average bacterial biomass and daily production data in the upper mixed layer of the Antarctic Ocean.*

C. CCSZ				
Prydz Bay	Summer	n.m. - 145.5, 31.4	118 - 372, 261	Leakey *et al.*, 1996
Prydz Bay	Late Summer	n.m. - 71.2, 30.6	136 - 306, 221	Leakey *et al.*, 1996
Western Bransfield Strait	Summer	4.0 - 28		Karl *et al.* 1991
Drake Passage	Summer	2.1		Hanson *et al.*, 1983
Prydz Bay	Late summer	0.8 - 5.4	33 - 58, 47	Painting *et al.*, 1985
Prydz Bay	Late summer	0.7 - 10.5	2- 220, 136	Billen *et al.*, 1987
Indian sector	Late summer	11.5 - 15.0, 13.3	76	Talbot, 1995
Ross Sea	early spring	0.1 - 1, 0.6	0.2 - 1.5, 1	Ducklow *et al.*, 1998
Ross Sea	mid-spring	0.1 - 0.4, 0.6	1 - 14, 4.5	Ducklow *et al.*, 1998
Ross Sea	late spring	1.0 - 3.0, 1.5	2 - 21, 8	Ducklow *et al.*, 1998
Ross Sea	early summer	1.0 - 3.5, 1.5	4 - 18, 8	Ducklow *et al.*, 1998
Ross Sea	summer	0.5 - 12.6, 4.0	10 - 25, 15	Ducklow *et al.*, 1998
Ross Sea	late summer	4.0 - 12, 8.0	5 - 32, 18	Ducklow *et al.*, 1998
Ross Sea	autumn	2.0 - 3.6, 3.0	1 - 4, 2	Ducklow *et al.*, 1998

Bacterial production represents between 1 and 76 % of primary production with the highest percentages recorded in the MIZ (Table 4). In the all biogeochemical provinces, the maximum percentages are observed in end-summer-autumn (FZ, 35 %; MIZ, 76 %; CCSZ, 37 %). As expected, the lowest values (< 10 %) are observed at the time of maximal phytoplankton development in spring-summer (Table 4). This suggests some uncoupling between bacterial and primary production.

Table 4. *Bacterial production in the Antarctic Ocean as percentage of primary production.*

Sub-areas Geographic localisation	Season	%	Reference
Frontal zones			
Polar Front (Indian sector)	Early spring	14	Yoro, 1997
Polar Front (Atlantic sector)	Spring	2 -11, 5	Lochte *et al.*, 1997
Scotia-Weddell confluence	Spring-Summer	5	Billen & Becquevort, 1991;
Polar Front (Indian sector)	Late summer	35	Talbot, 1995
Open ocean			
Indian sector	Early spring	18	Yoro, 1997; Lancelot pers. com.
Atlantic sector	Spring	1 - 4, 3	Lochte *et al.*, 1997
Scotia-Weddell Sea	Spring-Summer	1 - 6, 2	Billen & Becquevort, 1991; Mathot 1993
Indian sector	Late summer	13	Talbot, 1995; Lancelot pers.com.
Sea Ice associated area			
A. MIZ			
Indian sector	Early spring	11	Yoro, 1997; Lancelot pers.com.
Atlantic sector	Spring	2 - 7, 5	Lochte *et al.*, 1997
Scotia-Weddell Sea	Spring	13	Sullivan *et al.*, 1990
Weddell Sea	Spring	8 - 10	Garrison & Mathot, 1996
Weddell Sea	Spring-Summer	1 - 7, 3	Billen & Becquevort, 1991; Mathot 1993
Indian sector	Late summer	17	Talbot, 1995; Lancelot pers.com.
Weddell Sea	Autumn	76	Cota *et al.* 1990
Weddell Sea	Autumn	37	Garrison & Mathot, 1996
Eastern Weddell Sea	Autumn	4 - 48	Gleitz *et al.* 1994
Weddell Sea	Winter	56	Garrison & Mathot, 1996
B. CPIZ			
Scotia-Weddell Sea	Spring	7	Sullivan *et al.*, 1990
Weddell Sea	Spring-Summer	1 - 4, 2	Billen & Becquevort, 1991; Mathot 1993
Eastern Weddell Sea	Late summer	4 - 20	Gleitz *et al.* 1994
Weddell Sea	Autumn	14	Cota *et al.*, 1990
C. CCSZ			
Ross Sea	early spring	< 1 - 4	Ducklow *et al.* 1998
Ross Sea	spring	1 - 5, 2	Ducklow *et al.* 1998
Mc Murdo Sound	spring	1 - 4	Rivkin *et al.*, 1990
Ross Sea	summer	1 - 9, 5	Ducklow *et al.* 1998
Ross Sea	Late summer	5 - 25, 15	Ducklow *et al.* 1998
Prydz Bay	Late summer	13 - 38, 22	Painting *et al.*, 1985
Prydz Bay	Late summer	10	Billen *et al.*, 1987
Indian sector	Late summer	37	Talbot, 1995; Lancelot pers.com.

Several studies have demonstrated a lack of correlation between bacterial and phytoplanktonic production in the Southern Ocean (Davidson and Marchant 1987, Billen and Becquevort 1991, Karl *et al.* 1991, Karl and Bird 1993, Lochte *et al.* 1997, Carlson *et al.* 1998) Contrasting, Cota *et al.* (1990) and Sullivan *et al.* (1990) suggested that bacteria follow the same distribution of phytoplankton in broad terms, but more detailed analysis of data shows evidence of uncoupling between bacteria and phytoplankton developments.

Billen and Becquevort (1992) suggested that bacterioplankton development follows phytoplankton bloom in the Southern Ocean with a lag of 15-30 days. Similarly in CCSZ, bacterial maximum developments have been observed 1 month after *Phaeocystis* blooms in the Prydz Bay (Davidson and Marchant 1992) and in the Ross Sea (Ducklow *et al.* 1998). Such uncoupling between bacterioplankton production and phytoplankton production can be explained by the quantity and the nature of the dissolved organic substrates and by the metabolism of bacteria and factors controlling it such as temperature. It has been suggested that the combined effect of low substrate concentrations and the extremely low temperature prevailing in polar waters could result in a low growth efficiency (Pomeroy *et al.* 1991). However, the reported growth efficiencies range between 26-30 % (Kähler *et al.* 1997) and 40 % (Björnsen and Kuparinen 1991) i.e. in the same range of other oceanic systems (between 2 and 65 %, Ducklow and Carlson, 1992).

Organic substrates for bacteria are provided by direct exudation of dissolved organic matter by phytoplankton cells as well as autolysis and incomplete ingestion or digestion in zooplankton. The latter source is considered as the most important and is composed of organic substrates with different biodegradability. Exudation releases monomeric substrates which can be directly taken up by bacteria. On the other hand, autolysis and sloppy-feeding release polymeric substrates which have to be first hydrolyzed in monomers by ectoenzymes before being assimilated by bacteria. Therefore Billen and Becquevort (1992) suggested that the phytoplankton-bacteria delay can be explained by the macromolecular nature of DOC released from phytoplanktonic lysis or sloppy feeding by metazooplankton combined with a temperature repression of ectoenzymatic activity. Under such conditions, the DOC production and consumption processes would be decoupled and allow significant accumulation of DOC. However, no evidence of large accumulation of DOC exists in the Southern Ocean (Cadee 1992, Kähler *et al.* 1997, Carlson *et al.* 1998). Moreover, some microbiological assays indicate that a substantial part of the dissolved organic matter is biologically labile and can be efficiently transformed into bacterial carbon in 12 days (Kähler *et al.* 1997). Recently, Lochte *et al.* (1997) have suggested that the direct grazing on spring phytoplankton bloom by protozoa such as dinoflagellates might strongly reduce the carbon flow from phytoplankton to bacteria compared to the phyto-metazooplankton pathway. Due to their feeding mode, dinoflagellates completely engulf their prey or envelop it by a pallium, less DOC is released in the surrounding medium compared to the often reported sloppy feeding of metazooplankton. This would suggest that this kind of grazer greatly reduces the transfer of organic matter from phytoplankton to bacteria. However, later in the season (in late summer) the grazing by metazooplankton on phytoplankton as well as protozoa may become more prominent

and through sloppy feeding, increasing amounts of DOC and detrital particulates may be released, increasing the available substrates for bacteria and then the bacterial growth.

1.c. Protozooplankton

Protozooplankton are ubiquitous in the Antarctic pelagic ecosystem and reports on their abundance and distribution are numerous (e.g. Nöthig 1988, Garrison and Buck 1989a, Garrison *et al.* 1991, 1993, Becquevort *et al.* 1993, Scharek *et al.* 1994, Burkill *et al.* 1995, Becquevort 1996, Klaas 1996). However, their synthesis is very hazardous due to the various techniques used for their sampling, preservation and microscopic analysis, involving the use of different dyes. We thus discuss in this paper the set of existing data obtained with comparable and suitable techniques used for the sampling and the quantification of protozoa (Table 5). The reconstructed seasonal distribution of protozooplankton biomass in the five biogeochemical provinces (Fig. 6) mimics that of Chl a (Fig. 1). Protozooplankton biomass is relatively constant and low in the OOZ and in the CPIZ(< 16 mgC m^{-3}, Fig. 6). On the other hand, protozooplankton biomass of the FZ, MIZ and CCSZ is relatively elevated in spring (FZ) and summer (MIZ, CCSZ) (Fig. 6). Maxima reached are 42, 42 and 54 mgC m^{-3} in the FZ, MIZ and CCSZ, respectively (Fig. 6). Nanoprotozooplankton contributes significantly to the total protozooplankton biomass, ranging between 24 and 79% (Becquevort *et al.* 1992, submitted, Becquevort 1997, Garrison *et al.* 1989, Garrisson *et al.* 1991, Garrison & Buck 1989a, Hewes *et al.* 1991, Nöthig 1988, Nöthig *et al.* 1991). The nanoprotozooplankton biomass is mainly composed of flagellates mainly heterotrophic dinoflagellate. Ciliates are also present but at very low concentration (a few percent of the total). In contrast, ciliates and dinoflagellates contribute almost equally to the microprotozooplankton biomass of which they are the main components.

Table 5. *Compilation of protozooplankton biomass data in the Antarctic Ocean.*

Sub-areas Geographic localisation	Season	Biomass, mgC m^{-3}	Reference
PFr			
Weddell Sea	Late winter-spring	4.7-31.0, 18.0	Garrison *et al.*, 1990a, b, 1992
Polar Front (Indian sector)	Early spring	4.5	Becquevort *et al.*, submitted
Polar Front (Atlantic sector)	Early spring	4.3 - 11.7, 3.8	Becquevort, 1997
Polar Front (Atlantic sector)	Mid spring	10.3 - 11.4, 10.9	Becquevort, 1997
Polar Front (Atlantic sector)	Late Spring	11.2 - 23.3, 14.6	Becquevort, 1997
Scotia Ridge	Summer	6.0 -29.0, 18.0	Hewes et al, 1990
Scotia-Weddell Confluence	Spring-summer	18.5	Becquevort *et al.*, 1992
Polar Front (Indian sector)	Late summer	2.8-3.4, 3.1	Becquevort *et al.*, submitted
OOZ			
ACC (Indian sector)	Early spring	5.2-10.5, 7.1	Becquevort *et al.*, submitted
ACC (Atlantic sector)	Mid spring	4.2 - 16.3, 10.4	Becquevort, 1997
ACC (Atlantic sector)	Late spring	2.5 - 6.0, 4.4	Becquevort, 1997
Weddell Sea	Spring-summer	7.6	Becquevort *et al.*, 1992
Indian sector	Late summer	0.8 - 3.1, 1.8	Becquevort *et al.*, submitted
Sea Ice associated area			
A. MIZ			
Weddell Sea	Late winter	10.0 - 14.0 , 12.0	Garrison *et al.*, 1990a, b, 1992
ACC (Indian sector)	Early spring	9.9	Becquevort *et al.*, submitted
ACC(Atlantic sector)	Mid spring	1.5 - 4.8, 3.5	Becquevort, 1997
ACC(Atlantic sector)	Spring	2.9 - 4.3, 3.6	Becquevort, 1997
Weddell/Scotia Sea	Spring	2.0 - 6.0, 4.3	Garrison & Buck, 1989
Weddell Sea	Spring-summer	5.2 - 23.8, 15.9	Becquevort *et al.*, 1992
Weddell Sea	Summer	21.0 - 42.0, 28.0	Hewes et al, 1990
Weddell Sea	Summer	1.0 - 25, 13.3	Nöthig, 1988
ACC (Indian sector)	Late summer	1.6 - 4.7, 3.5	Becquevort *et al.*, submitted
B. CPIZ			
Weddell-Scotia Sea	Winter	1.7-3.5, 2.6	Garrison *et al.*, 1990a, b, 1992
Weddell Sea	Late winter-spring	2.0 - 31.0, 15.0	Garrison *et al.*, 1990a, b, 1992
ACC(Atlantic sector)	Early spring	1.3 - 3.1, 2.3	Becquevort, 1997
ACC(Atlantic sector)	Mid spring	1.2 - 5.2, 3.6	Becquevort, 1997
Weddell/Scotia Sea	Spring	0.6 -1.3, 0.9	Garrison & Buck, 1989
Weddell Sea	Spring-summer	3.9 - 6.5, 4.7	Becquevort *et al.*, 1992
Western Weddell Sea	Autumn	1.0 -2.5, 1.7	Garrison & Buck, 1989
C. CCSZ			
Bellingshausen Sea	Spring	0.3-54.0	Burkill *et al.* 1995*
Indian sector	Late summer	4.9 - 8.0 , 7.0	Becquevort *et al.*, submitted
Western Weddell Sea	Autumn	4.4 - 6.5, 5.5	Garrison & Buck, 1989

* microprotozooplankton only

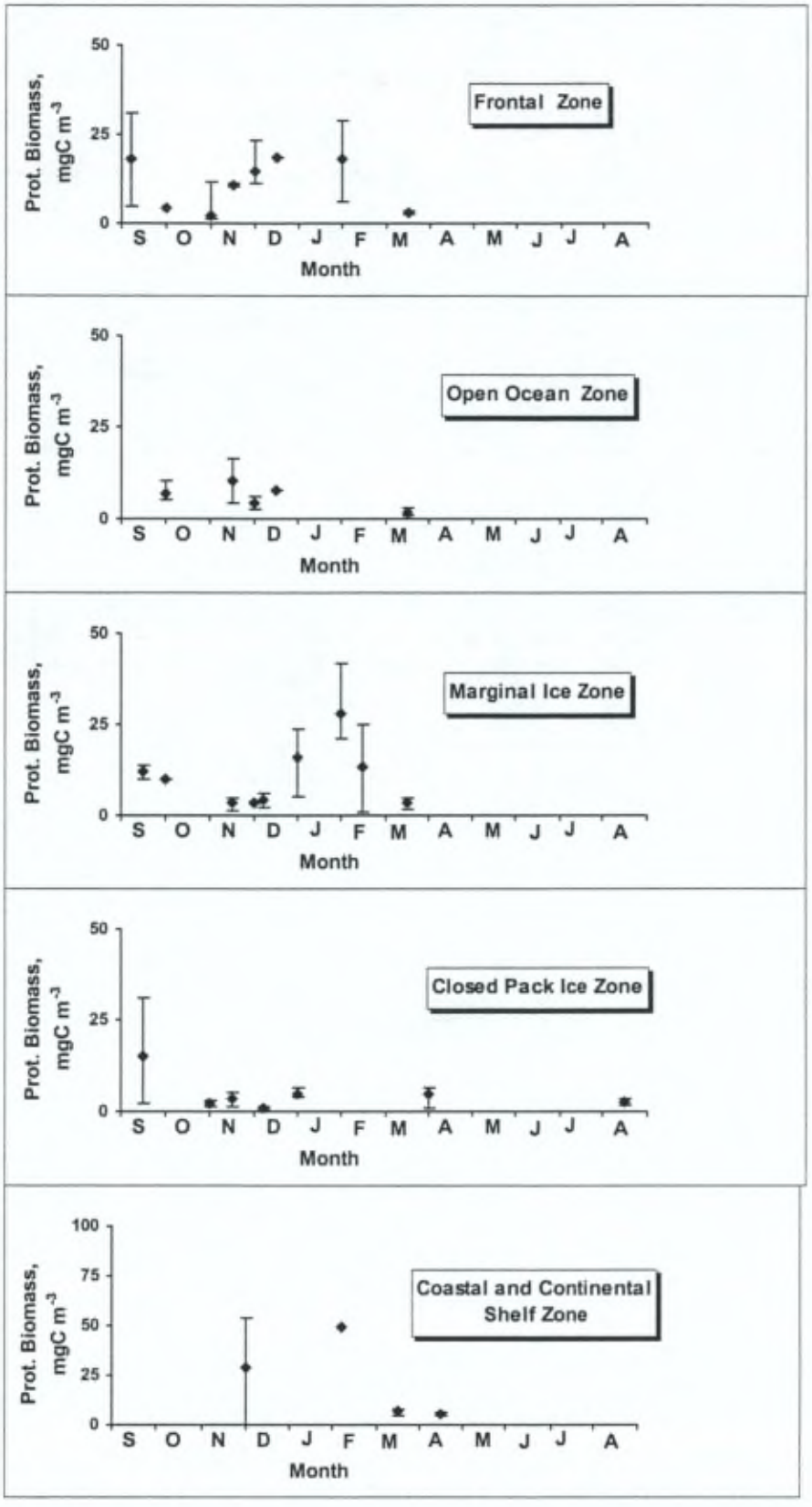

Figure 6. *Reconstructed seasonal of the protozooplankton biomass in the FZ, the OOZ, the MIZ, the CPIZ and the CCSZ. Min., max. and mean values are indicated.*

Protozoa biomass contributes to 7 and 56 % (average value 24 %) of the total microbial biomass (Table 6). No clear seasonal trend of this ratio can be pointed out (Table 6). However, a relationship between the time appearance of protozoa and their prey (bacteria, pico- and nanophytoplankton) could be masked by the observed delay between phytoplankton (Fig. 1) and bacteria (Fig. 3) and the occurrence of strictly bacterivorous and herbivorous feeding among the protozoan community.

Table 6. *Percentage of protozooplankton biomass in the total microbial biomass (bacteria, phytoplankton and protozooplankton) protozooplankton biomass data in the Antarctic Ocean.*

Sub-areas Geographic localisation	Season	% proto biomass in total microbial biomass.	References
Frontal areas			
Polar Front (Indian sector)	early spring	21	Becquevort *et al.*, submitted
Polar Front (Atlantic sector)	spring	18 - 40, 29	Becquevort, 1997
Scotia-Weddell Confluence	Spring-summer	15-25, 20	Becquevort *et al.*, 1992
Polar Front (Indian sector)	Late summer	14 - 16, 15	Becquevort *et al.*, submitted
OOZ			
Indian sector	Early spring	22 - 39, 31	Becquevort *et al.*, submitted
Atlantic sector	spring	21 - 45, 39	Becquevort, 1997
Scotia-Weddell Sea	Spring-summer	25	Becquevort *et al.*, 1992
Weddell Sea	Summer	8-11, 10	Garrison & Buck, 1989
Indian sector	Late summer	16 - 20, 23	Becquevort *et al.*, submitted
Sea Ice associated area			
A. MIZ			
Indian sector	Early spring	40	Becquevort *et al.*, submitted
Weddell/Scotia Sea	Spring	7 - 10, 9	Garrison & Buck, 1989
Atlantic sector	Spring	43 - 55, 50	Becquevort, 1997
Scotia-Weddell Sea	Spring-Summer	13 - 38, 20	Becquevort *et al.*, 1992
Scotia Ridge	Summer	9 - 24, 17*	Hewes *et al.*, 1990
Weddell Sea	Summer	16 - 36, 29*	Hewes *et al.*, 1990
B. CPIZ			
Atlantic sector	Spring	10 - 55, 47	Becquevort, 1997
Weddell/Scotia Sea	Spring	6 - 8, 8	Garrison & Buck, 1989
Weddell/Scotia Sea	Spring-Summer	16 - 28, 19	Becquevort *et al.*, 1992
Weddell Sea	Summer	9 - 16, 13	Garrison & Buck, 1989
C. CCSZ			
Bellingshausen Sea (MIZ)	Spring	25	Burkill *et al.*, 1995
Bellingshausen Sea (OOZ)	Spring	26	Burkill *et al.* 1995
Bellingshausen Sea	Late Spring	17	Burkill *et al.* 1995
Ross Sea	Summer	3 - 10, 6.4*	Garrison *et al.*, 1995

* Bacterioplankton not include

Accordingly, indirect evidence of the control of bacterioplankton and nanoplankton by the protozoan grazing pressure is given by the positive correlation between <7 µm (Fig. 7) and >7 µm (Fig. 8) grazers and their respective food. According to Becquevort *et al.* (1992), the size limit of 7 µm is chosen to distinguish nanoplanktivorous and bactivorous grazers amongst protozoa.

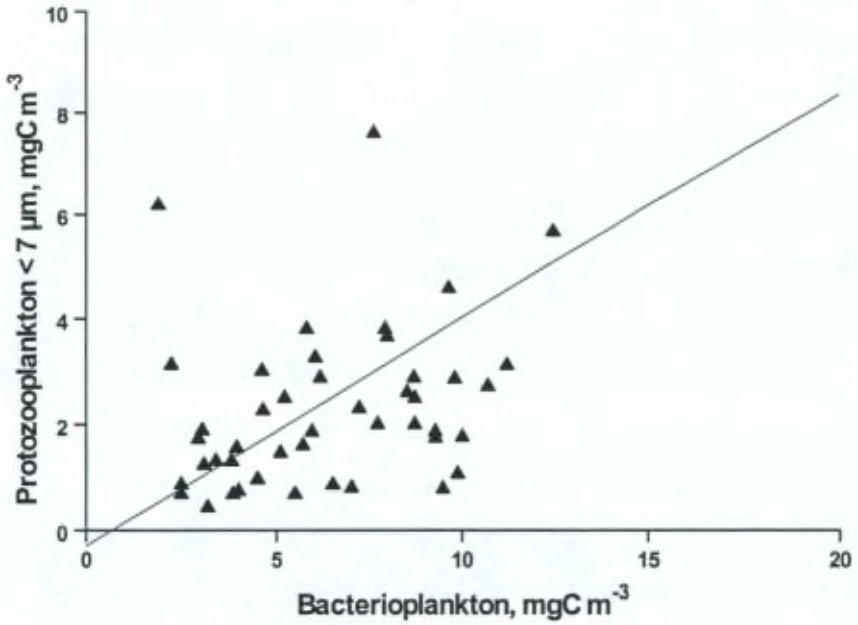

Figure 7. *Relationship between protozooplankton < 7 µm and bacterial biomass. Y= -0.3 (sd = 0.67) + 0.43 (sd = 0.09) X. R= 0.58, SD = 2.03, N = 47.*

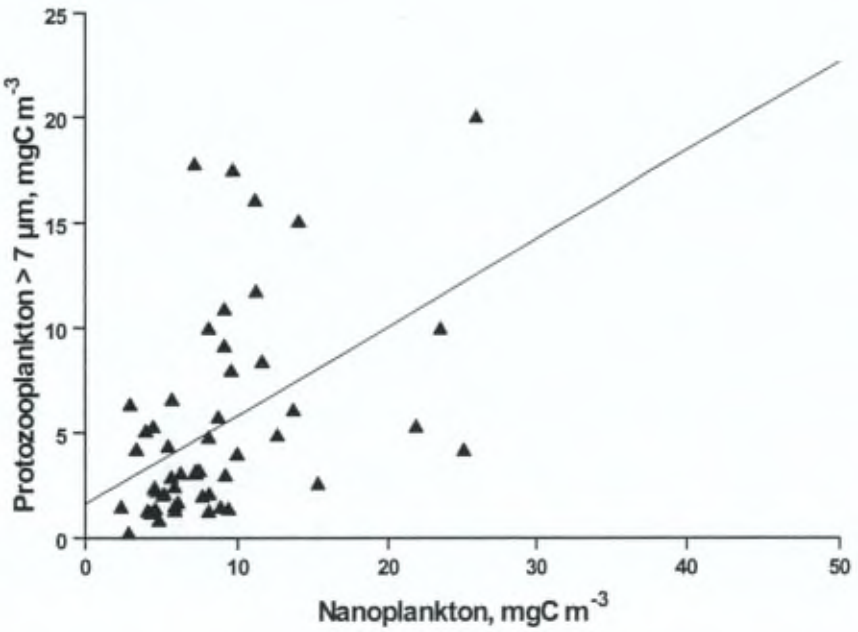

Figure 8. *Relationship between protozooplankton > 7 µm and nanoplankton biomass. Y= 1.60 (sd = 1.16) + 0.42 (sd = 0.11) X. R= 0.47, SD = 4.36, N = 51.*

The slope of the linear regression gives an indirect estimate of the growth efficiency of protozoan i.e. 0.43 and 0.42 for bacterivorous (Fig. 7) and nanoplanktivorous (Fig. 8) protozoa, respectively. These values agree perfectly well with the averaged growth yield of 40 % reported for Antarctic protozoa (Björnsen and Kuparinen 1991).

The trophic role of protozooplankton in controlling the bacterial and primary production can be best approached by direct comparison between ingestion and production rates. Unfortunately, few data are presently available on the feeding activities of Antarctic protozooplankton. Different direct and indirect methods have been well developed to estimate the protozooplankton grazing, however, none of them is satisfactory and the quantification of the protozoan grazing remains nowadays problematic. Each reported method has specific advantages as well as specific weakness and ambiguities which prevent general application under all conditions. This is mostly due to the complex feeding behavior of protozoa which are grazing on a large range of food particles. The most currently used method to estimate the daily ingestion rate of protozoa is based on published clearance rates and bacteria, phytoplankton and protozooplankton biomass data (Garrison and Buck 1989a, Garrison and Mathot 1996, Becquevort *et al.* 1992, Klaas 1997). Methods developed for measuring the specific ingestion rate of protozoa on the only phytoplankton community include both selective filtration (Hewes 1985, Björnsen and Kuparinen 1991) and the so-called dilution technique of Landry and Hasset (1982) (Taylor and Haberstroh 1988, Garrison *et al.* 1990c, d, Burckill *et al.* 1995, Froneman and Perissinotto 1996). As a first attempt to encompass the complex feeding behavior of the natural protozoan community, the method based on the double isotopic labeling of bacteria and phytoplankton (Lessard and Swift 1985) was used to measure the clearance rate of protozoa (Lessard and Rivkin 1986, Archer *et al.* 1996). Unfortunately, these experiments were restricted to specific groups of heterotrophic dinoflagellates and naked ciliates. More recently, the method based on the uptake of fluorescent prey (Sherr *et al.* 1987, Rublee and Gallegos 1989) has been used to estimate separately the bacteria and nanoplankton ingestion by protozoa (Becquevort 1997, Becquevort *et al.* submitted, Leakey *et al.* 1996). Although strongly dependent on the chosen size prey and the feeding mode of the ambient protozoan community, this method allows to identify both the ingested prey and the grazer. For this reason it is to our opinion, the best available method to distinguish the grazing pressure rate of the protozoan community on the bacteria and pico- and nanophytoplankton. Results obtained by the different techniques are gathered in Tables 7, 8 and illustrated by Fig. 9 and 10. Daily bacterial ingestion rates by protozoa range between 0.5 and 118 mgC m^{-2} d^{-1} (Table 7, Fig. 9). The lowest values are reported for the CPIZ (< 0.9 mgC m^{-2} d^{-1}). The highest average values (100 mgC m^{-2} d^{-1}, Fig.9) are observed in the CCSZ and occur during the summer-fall season. In the other biogeochemical provinces, maximum values are observed late summer - autumn but early spring too. The spatio-temporal distribution of the bacterial ingestion rates (Fig. 9) is correlated with that of bacterial production (Fig. 4). Maximum ingestion rates generally coincide with the time of maximal bacterial development occurring in end-summer As reported in Table 7, protozoa controls between 6 and > 100 % of the daily bacterial production. The

maximum occurs in the FZ (78 %) and OOZ (80 %) and lowest ones in the CPIZ (18 %). Hence, the significant control of bacteria by protozooplankton at time of maximum bacterial production, could explain the lack of significant variation on bacterial biomass observed over the whole year (Fig. 3).

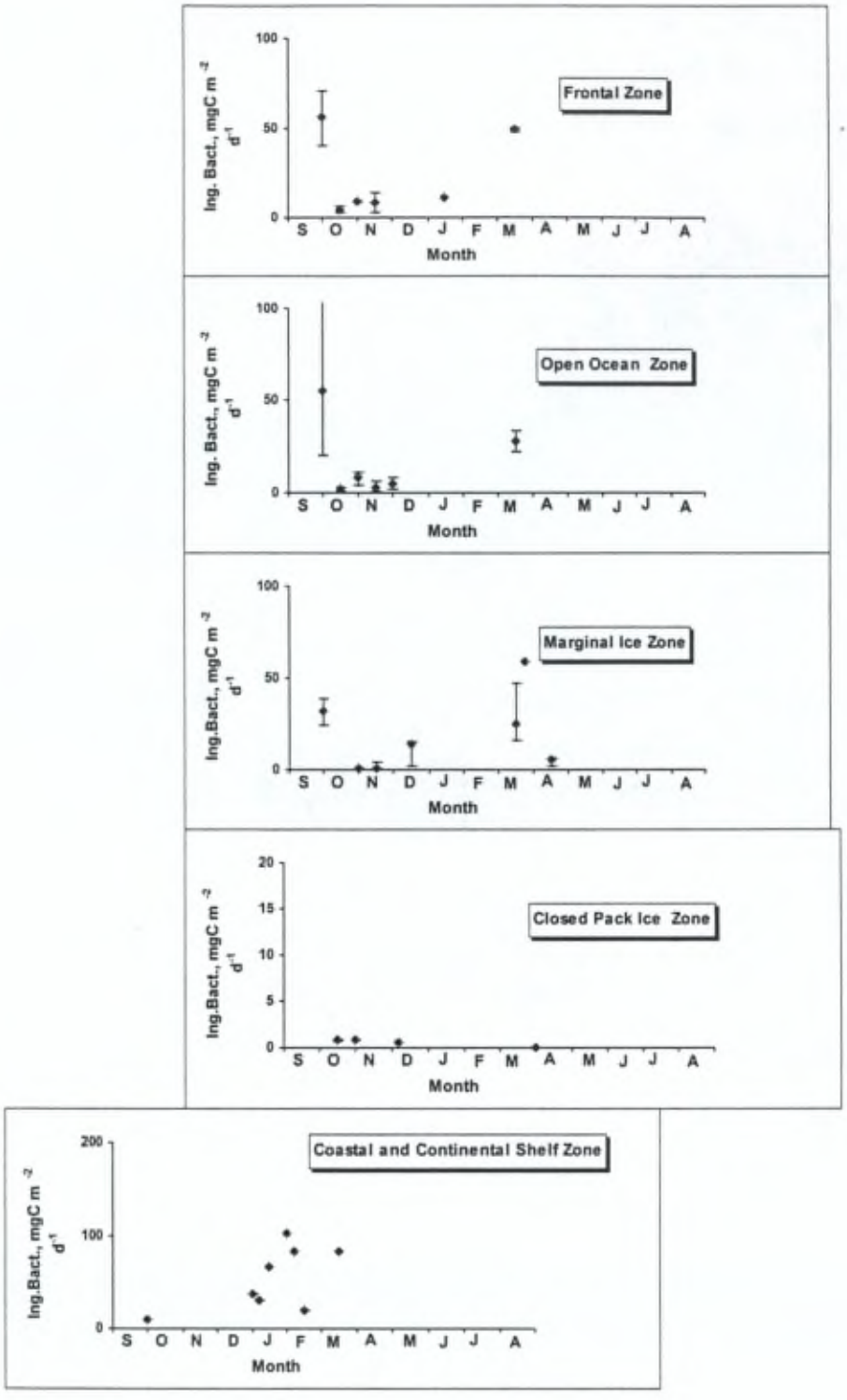

Figure 9. *Reconstructed seasonal evolution of protozooplankton ingestion rates on bacteria in the FZ, the OOZ, the MIZ, the CPIZ and the CCSZ. Min., max. and mean values are indicated.*

Table 7. *Available data on daily ingestion rates of bacteria by protozoa data in the Antarctic Ocean.*

	Season	Ing. Proto, mgC m^{-2} d^{-1}	% BP	Method	Reference
Frontal zones					
Polar Front (Indian sector)	Oct	40- 71, 56	110 - 510, 310	1	Becquevort *et al.*, submitted
Polar Front (Atlantic sector)	mid-Oct	3 - 6, 4	13 - 40, 26	1	Becquevort *et al.*, submitted
Polar Front (Atlantic sector)	end-Oct	9	23	1	Becquevort, 1997
Polar Front (Atlantic sector)	mid-Nov	3 - 14, 8	12 - 33, 21	1	Becquevort, 1997
Polar Front (Drake Passage)	Jan	11	12	2	Pedros-Alio *et al.* 1996
Polar Front (Indian sector)	March	48 - 50, 49	76 - 80, 78	1	Becquevort *et al.*, submitted
Open Ocean zone					
Indian sector	Oct	20 - 118, 55	30 - 130, 80	1	Becquevort *et al.*, submitted
ACC (Atlantic sector)	mid-Oct	1 - 3, 2	6 - 96, 37	1	Becquevort, 1997
ACC (Atlantic sector)	end-Oct	4 - 11, 8	64 - 256, 160	1	Becquevort, 1997
ACC (Atlantic sector)	mid-Nov	1 - 6, 3	19 - 28, 22	1	Becquevort, 1997
ACC (Indian sector)	March	22 - 33, 28	76 - 115, 101	1	Becquevort *et al.*, submitted
Sea Ice					
1. MIZ					
Weddell Sea Indian sector	Oct	23.6 - 39.3, 31.5	113	1	Becquevort *et al.*, submitted
ACC (Atlantic sector)	end-Oct	0.5 - 1, 1	8 - 34, 21	1	Becquevort, 1997
ACC (Atlantic sector)	mid-Nov	0.5 - 4, 1	8 - 100, 33	1	Becquevort, 1997
Weddell-Scotia Seas	start-Dec	2 - 15, 14		2	Becquevort *et al.*, 1992
ACC (Indian sector)	March	16 - 47, 25	51 - 138, 85	1	Becquevort *et al.*, submitted
Weddell Sea	March	59	53	2	Garrison & Buck, 1989
Weddell Sea	Winter	12	68	2	Garrison *et al.* 1990c,d; 1992, 1993.
2. CPIZ					
ACC (Atlantic sector)	mid-Oct	0.7 - 0.9	28 - 39, 34	1	Becquevort, 1997
ACC (Atlantic sector)	End-Oct	0.9- 0.9, 0.9	16 - 17, 16	1	Becquevort, 1997
Weddell Sea	start-Dec	0.05 - 0.1, 0.5	12 - 13, 14	2	Becquevort *et al.*,1992
Weddell Sea	March	0.01	11	2	Garrison & Buck, 1989
3. CCSZ					
McMurdo	spring		1- 15	1	Putt *et al.*, 1991
McMurdo	summer		2 - 30	1	Putt *et al.*, 1991
Prydz Bay	End-Dec	37	22	1	Leakey *et al.*, 1996
Prydz Bay	Start-Jan	31	11	1	Leakey *et al.*, 1996
Prydz Bay	Mid-Jan	67	21	1	Leakey *et al.*, 1996
Prydz Bay	End-Jan	103	36	1	Leakey *et al.*, 1996
Prydz Bay	Start-Feb	84	34	1	Leakey *et al.*, 1996
Prydz Bay	Mid-Feb	20	10	1	Leakey *et al.*, 1996
Indian sector	March	84	111	1	Becquevort *et al.*, submitted

1: Fluorescent labeled bacteria (Sherr *et al.* 1987) 2: Estimated from published clearance rates (Fenchel 1987, Lessard and Rivkin 1986, Vaqué *et al.* 1994).

Existing data on phytoplankton ingestion rate of protozoa are gathered in Table 8 and illustrated by Fig. 10. In order to better understand the trophic position of these micrograzers, these data are compared with total primary production and pico- and nanophytoplankton abundance and production when available (Table 8). As a general trend, the highest daily rates of phytoplankton ingestion rates by protozoa are to be observed in the most productive areas (FZ, MIZ, CCSZ, Fig. 2, Fig. 10).

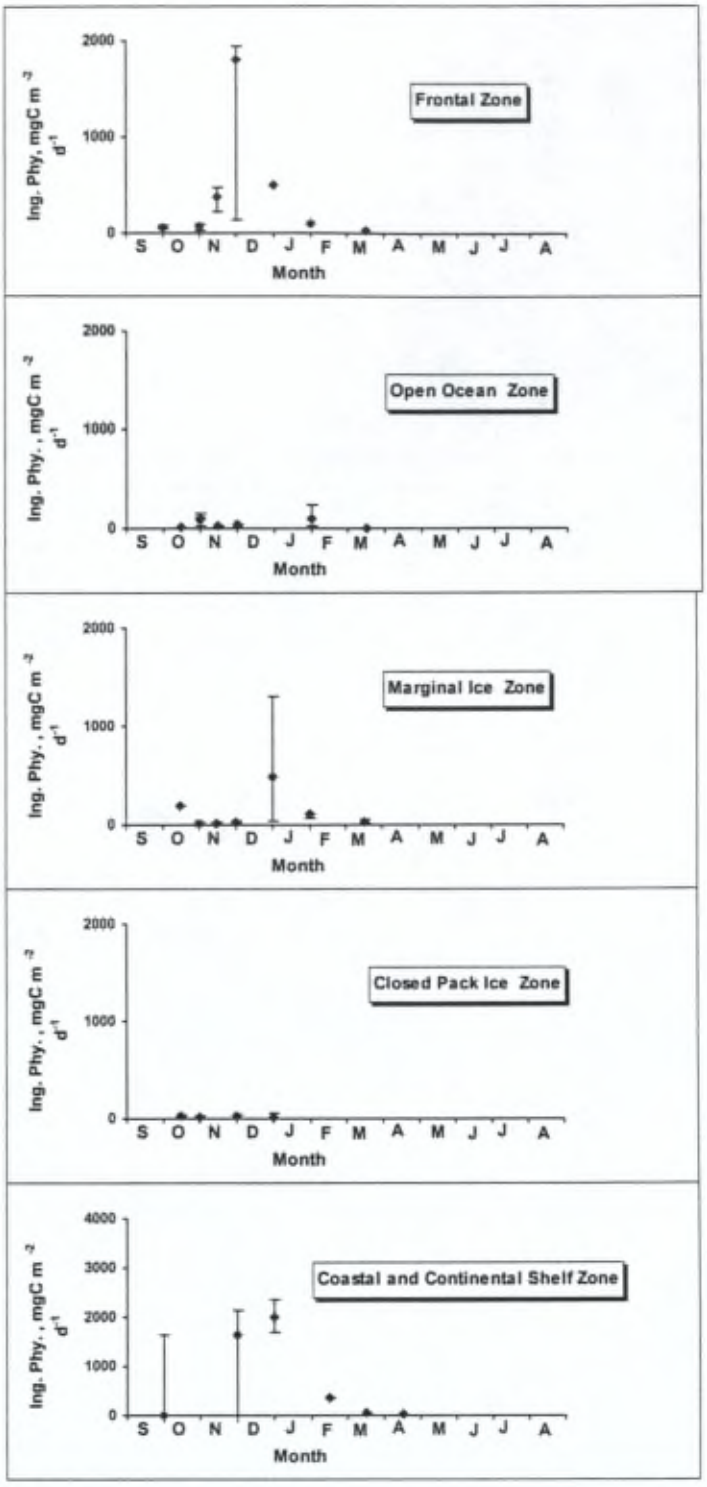

Figure 10. *Reconstructed seasonal cycle of protozooplankton ingestion on nanoplankton in the FZ, the OOZ, the MIZ, the CPIZ and the CCSZ. Min., max. and mean values are indicated.*

On a global average, the protozooplankton community controls between 1 and > 100 % of the total primary production (Table 8). Highest values are however reported in MIZ (226 % and 284 % of total primary production and nanophytoplanktonic production, respectively; Table 8) and in the CPIZ (607 % and 714 % of total primary production and nanophytoplanktonic production, respectively; Table 8) when the phytoplankton community is dominated by pico- and nano sized

cells. In the area dominated by micro sized phytoplankton (> 50 % of the total *chlorophyll a*, only 28 % (6 to 95 %) of the total primary production is controlled by protozoan grazing (Table 8). At the stations where blooms of large species (> 82 -85 % of the total *chlorophyll a*) are recorded (i.e. in the PFr and in the Weddell-Scotia Confluence in spring) only 10 to 41 % of the total primary production is therefore controlled by protozoan grazing.

Table 8. *Available data on daily phytoplankton ingestion rates by protozoa in the Antarctic Ocean.*

	Season	% pico- and nano in Chl a	Ing. Proto, mgC m^{-2} d^{-1}	% total PP	% nano PP	Method	Reference
Frontal zones							
Polar Front (Indian sector)	Oct	90-91, 91	35 - 88, 62	25 - 68, 47	45 - 124, 85	1	Becquevort *et al.*, submitted
Polar Front (Atlantic sector)	mid-Oct	31 - 59, 45	33- 100, 66	14 - 95, 55	46 - 161, 104	1	Becquevort *et al.*, submitted
Polar Front (Atlantic sector)	end-Oct	43 - 80, 56	222 - 473, 372	13	28	1	Becquevort, 1997
Polar Front (Atlantic sector)	mid-Nov	15 - 19, 17	134 - 150, 142	10 - 13, 11	61	1	Becquevort, 1997
Weddell-Scotia Confluence	end-Nov	18	499	41	192	2	Becquevort *et al.* 1992
Polar Front (Atlantic sector)	Jan.- Feb.	77	100	20	26	3	Froneman & Perissinotto, 1996b
Polar Front (Indian sector)	March	81	21.8	12	15	1	Becquevort *et al.*, submitted
Open Ocean zone							
ACC (Indian sector)	Oct	81 - 93, 85	33 - 118, 79	24 - 84, 51	43 - 152, 92	1	Becquevort *et al.*, submitted
ACC (Atlantic sector)	mid-Oct	52	19	16	31	1	Becquevort, 1997
ACC (Atlantic sector)	end-Oct	70 - 72, 71	33 - 150, 92	16 - 48, 32	22 - 68, 45	1	Becquevort, 1997
ACC (Atlantic sector)	mid-Nov	72 - 83, 79	13 - 33, 27	16 - 20, 18	19 - 27, 23	1	Becquevort, 1997
Weddell-Scotia Seas	start-Dec	19 - 43, 31	28-42, 35	6 - 12, 9	27 - 30, 28	2	Becquevort *et al.*, 1992
Weddell-Scotia Seas	end-Dec	80	30	94	99	2	Becquevort *et al.*, 1992
ACC (Atlantic sector)	Jan. -Feb.		24 - 242, 99	8 - 44, 22		3	Froneman & Perissinotto, 1996a
ACC (Indian sector)	March	22-90, 63	1 - 12, 6	4	5	1	Becquevort *et al.*, submitted
Sea Ice							
1. MIZ							
ACC (Indian sector)	Oct	55 - 76, 66	189 - 190, 189	58 - 72, 65	105 - 129, 117	1	Becquevort *et al.*, submitted
ACC (Atlantic sector)	end-Oct	70 - 80, 74	6 -33, 17	4 - 26, 13	6 - 32, 17	1	Becquevort, 1997
ACC (Atlantic sector)	mid-Nov	45 - 100, 63	4 - 24, 15	4 - 24, 11	4 - 52, 21	1	Becquevort, 1997
Weddell-Scotia Seas	start-Dec	13 -94, 70	11- 39, 21	1 - 4, 2	1 - 9, 5	2	Becquevort *et al.* 1992
Weddell-Scotia Seas	end-Dec	75 - 100, 90	41 - 1301, 492	45 - 226, 71	55 - 284, 75	2	Becquevort *et al.* 1992
ACC (Atlantic sector)	Jan. - Feb.	37 - 100, 69	63 - 116, 108	18 -24		3	Froneman & Perissinotto, 1996a
ACC (Indian sector)	March	22 - 55, 43	17 - 51, 21	11 - 41, 26	14 - 52, 33	1	Becquevort *et al.*, submitted
2. CPIZ							
ACC (Atlantic sector)	mid-Oct	48 - 95, 68	13 - 39, 24	60 - 295, 151	63 - 547, 246	1	Becquevort, 1997
ACC (Atlantic sector)	End-Oct	82 - 85, 84	6 - 33, 20	4 - 607, 305	5 - 714, 359	1	Becquevort, 1997
Weddell-Scotia Seas	start-Dec	40 - 90, 61	2 - 45, 29	3 - 29, 17	4 - 31, 25	2	Becquevort *et al.* 1992
Weddell-Scotia Seas	end-Dec	49 - 84, 76	4 - 53, 20	3 - 29, 17	2 - 16, 8	2	Becquevort *et al.* 1992
3. CCSZ							
Ross Sea	October		7	21 - 35, 22		2	Garrison *et al.* 1991
Lazarev Sea	End-Dec.	34 - 76, 41	76 - 288, 142	33 - 94		3	Froneman *et al.* 1997
Bellingshausen Sea	Nov.-Dec.		21 - 3260, 1640	21 - 271		3	Burkill *et al.* 1995
Prydz Bay	Jan. -Feb.		68 - 725, 375	1.5 - 28, 15		4	Archer *et al.*, 1996
Indian sector	March	80	63	30	38	1	Becquevort *et al.*, submitted
Ross sea	May		10	42 - 53, 50		2	Garrison *et al.* 1991

1: Fluorescent labeled algae (Rublee and Gallegos 1987). 2: Estimated from published clearance rates (Lessard and Rivkin 1986). 3: Dilution technique (Landry and Hasset 1982). 4: ^{14}C-labeled algae (Lessard and Swift 1985).

2. Annual carbon budget

The annual budget of carbon cycling through first trophic levels of the food web has been estimated in the different biogeochemical provinces (Table 7) based on the integration of the seasonal cycle of the daily rates of primary production (Fig. 2), bacterial production (Fig. 4) and bacterial (Fig. 7) and nanoplankton (Fig. 8) ingestion by protozoa.

Table 7 . *Annual net primary production, bacterial production, bacterivorous and nanoplanktivorous protozoa ingestion. Mean and extremes values. In the Coastal and Continental Shelf Zone are distinguished Ross Sea polynya and other areas.*

Biogeochemical provinces	Net primary production gC m^{-2} mean (min. - max.)	Bacterial production gC m^{-2} mean (min. - max.)	Bacterivorous ingestion gC m^{-2} mean (min. - max.)	Nanoplanktivorous ingestion gC m^{-2} mean (min. - max.)
Frontal Zone	**139** (96 - 202)	**11.1** (0.8 - 16.2)	**5.1** (4.9 - 6.6)	**45** (25 - 55)
Open Ocean Zone	**61** (48 - 68)	**4.7** (3.7 - 5.3)	**4.6** (3.1 - 6.3)	**28** (15 - 45)
Marginal Ice Zone	**111** (79 - 142)	**5.0** (4.1 - 10.0)	**4.0** (3.1 - 6.3)	**55** (13 - 76)
Closed Pack Ice Zone	**43** (31 - 70)	**2.0** (1.0 - 3.2)	**1.2** (1.1 - 1.4)	**23** (15- 25)
Coastal and Continental Shelf Zone (Ross Sea Polynya)	**277** (95 - 595)	**9.9** (6.9 - 11.5)		
Coastal and Continental Shelf Zone (other areas)	**312** (206 - 435)	**23.1** (7.9 - 31.6)	**11.9**	**116**

Net annual primary production in the Southern Ocean varies between 43 and 312 gC m^{-2} (Table 7). Maximum value is estimated in the CCSZ and minimum values in the CPIZ and in the OOZ (Table 7). Intermediate values of 139 and 111 gC m^{-2} are estimated in the FZ and in the MIZ, respectively (Table 7). Based on annual primary production reported on Table 7 and considering the surface of each biogeochemical provinces, the global annual primary production of the Southern Ocean can be estimated to 4.1 GT in perfect agreement with recent evaluations based on remote sensing (Arrigo *et al.* 1998). From 52 to 65 % of the annual net primary production is assimilated directly and indirectly in the microbial food web, composed of bacterioplankton, bacterivorous and nanoplanktivorous protozoa. The percentage of net primary production incorporated in the microbial food web is the highest (60 - 65 %) in the OOZ, MIZ and CPIZ. Lowest percentages (52 - 57 %) are estimated in the FZ and CCSZ where microphytoplankton blooms are recorded.

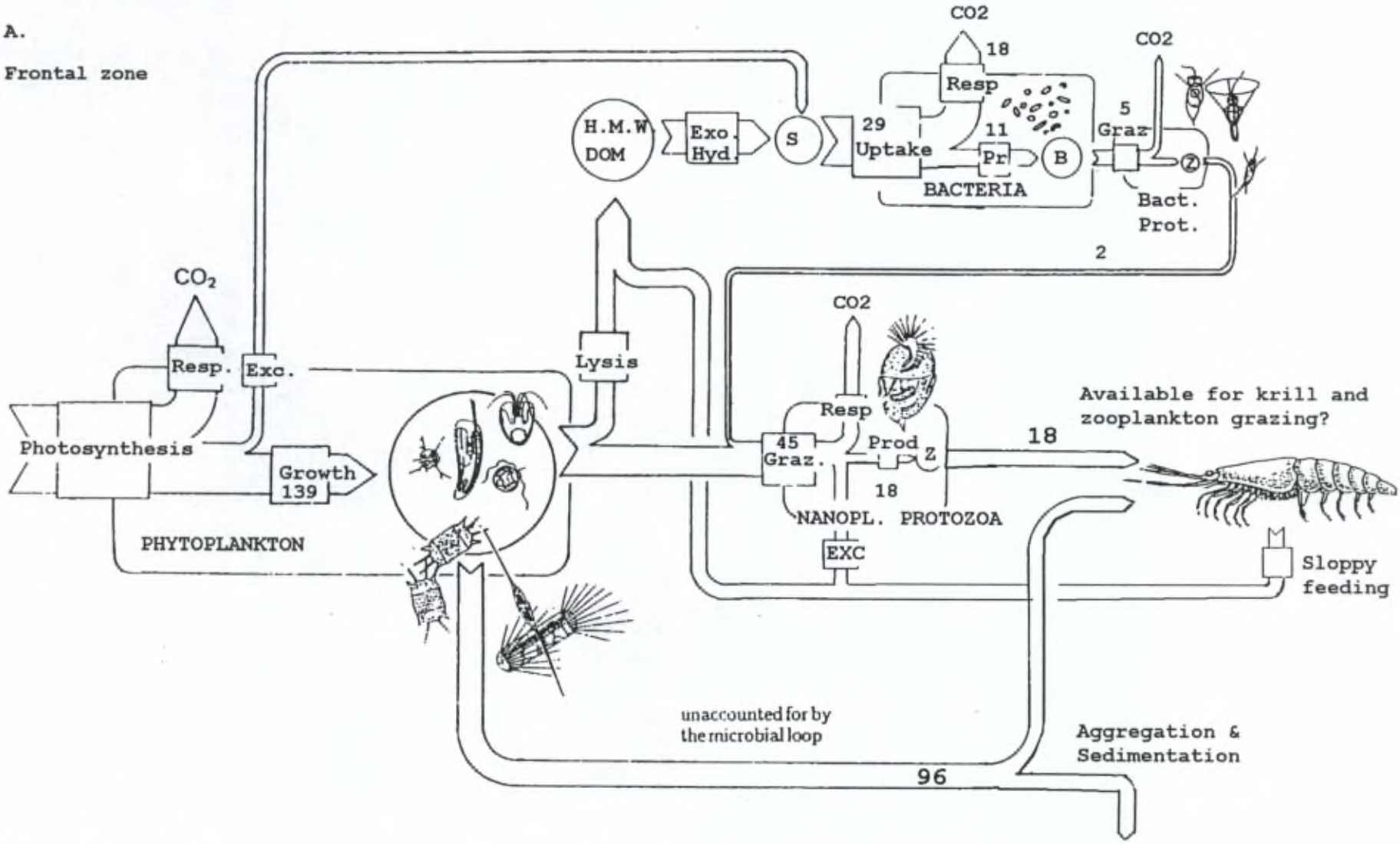

Figure 14A. *Annual budgets of carbon cycling at the first trophic levels of the food web in the wind mixed layer in the Frontal Zone. Fluxes in gC m^{-2}.*

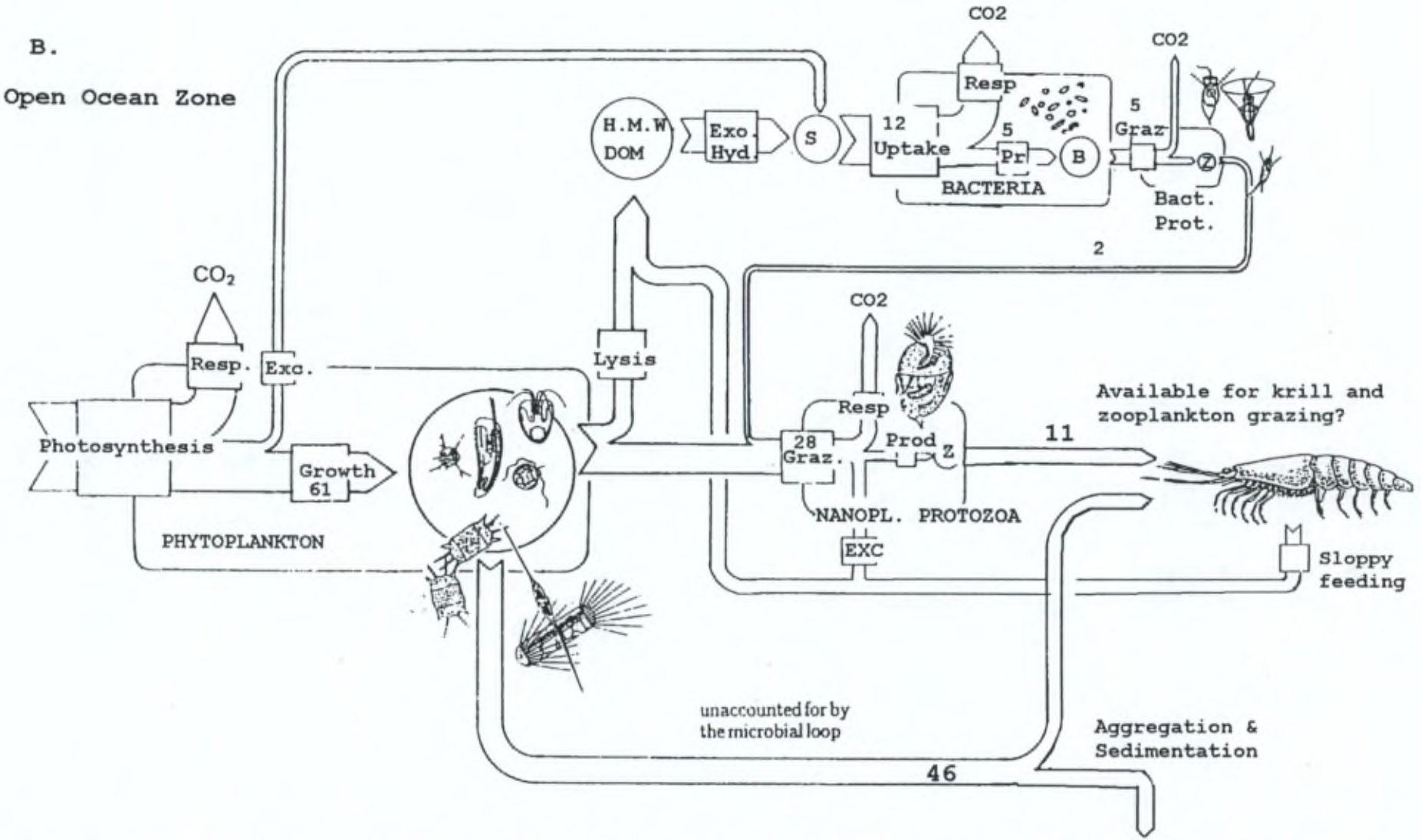

Figure 14B. *Annual budgets of carbon cycling at the first trophic levels of the food web in the wind mixed layer in the Open Ocean Zone. Fluxes in* $gC\ m^{-2}$.

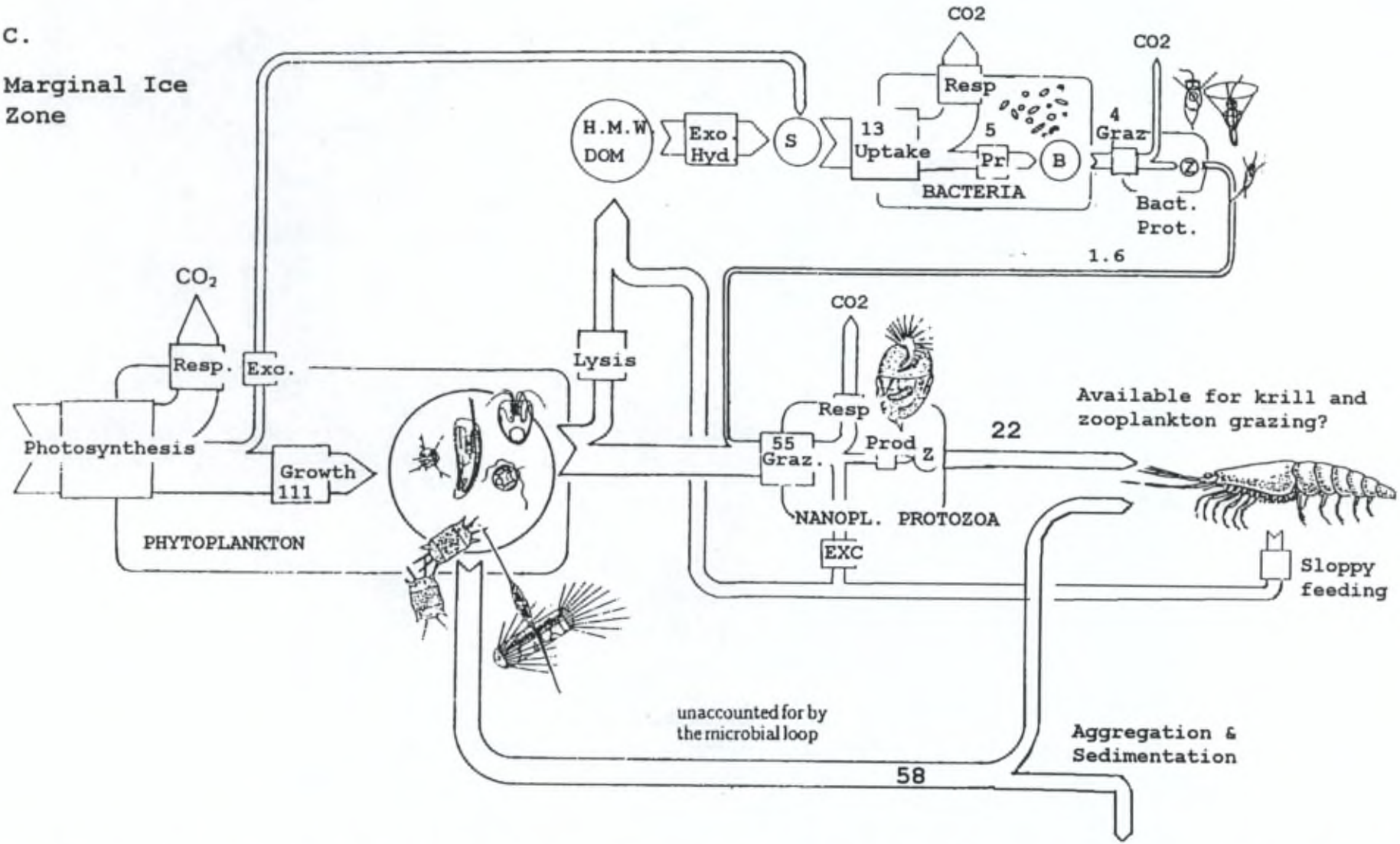

Figure 14C. *Annual budgets of carbon cycling at the first trophic levels of the food web in the wind mixed layer in the Marginal Ice Zone. Fluxes in gC m^{-2}.*

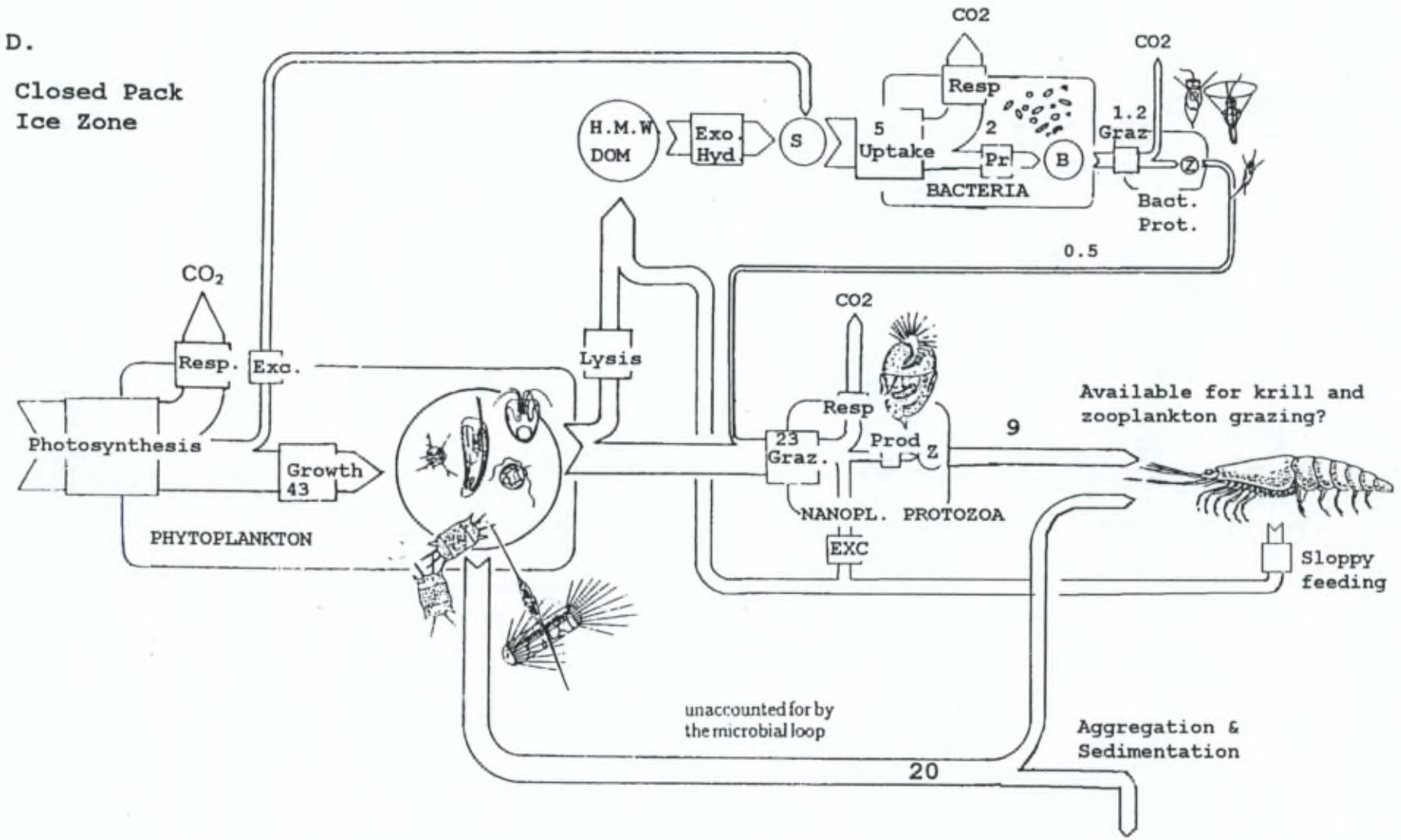

Figure 14D. *Annual budgets of carbon cycling at the first trophic levels of the food web in the wind mixed layer in the Closed Pack Ice Zone.Fluxes in gC* m^{-2}.

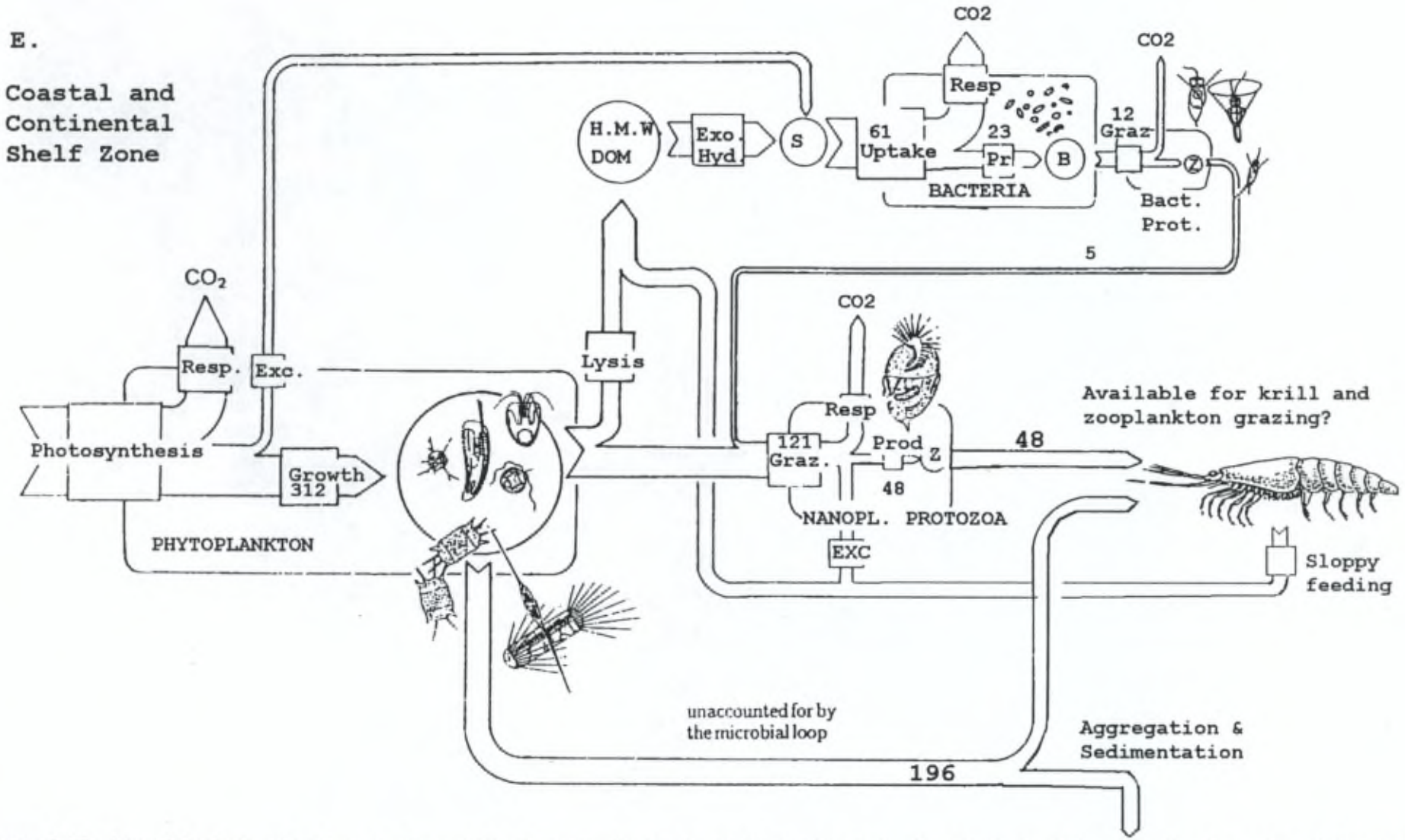

Figure 14E. *Annual budgets of carbon cycling at the first trophic levels of the food web in the wind mixed layer in the Coastal and Continental Shelf Zone. Fluxes in gC m^{-2}.*

Assuming a growth yield of 38 % for bacterioplankton (Bjornsen & Kuparinen, 1991), the bacterial carbon demand amounts for 12 - 21 % of the net primary production. Bacterivorous protozoa are perfectly controlling bacterial production in the lowest productive provinces OOZ (Fig. 14b) and CPIZ (Fig. 14d) as well as in the MIZ (Fig. 14c). On the contrary, nanograzers are controlling only 50 % (46 - 52 %) of the bacterial production in the most productive regions FZ (Fig. 14a) and CCSZ (Fig. 14e). This values agrees however with the average of 68 % given by Garrison (1991) for the control of bacteria by natural assemblages of bacterivorous protozoa in Antarctic waters. Nanoplanktivorous protozoa are directly controlling 50 % of primary production in the Sea Ice Zone, MIZ (Fig. 14c) and CPIZ (Fig. 14d). This control is lower in the other biogeochemical provinces, particularly in the FZ (Fig. 14a) and the CCSZ (Fig. 14e) where it reaches 31 and 37 % on the annual base. Altogether this is comparable very well with the averaged 41 % given by Garrison (1991) for the natural micrograzer communities of the Antarctic Ocean.

Assuming a growth yield of 40 % (Bjornsen and Kuparinen, 1991) for each protozoan group, the total net microbial food web secondary production ranges between 9 and 48 g C m^{-2}, which represents a mean microbial food web efficiency of 30 % (25 - 33 %). This indicates that the microbial food web trophic efficiency is very constant along the different biogeochemical provinces of the Antarctic Ocean. Consequently, 70 % of the net primary production assimilated by the microbial food web is on an average respired.

The "non-assimilated by nanoplanktivorous protozoa" phytoplanktonic production constitutes a maximal estimate of the carbon amount available for metazoan including krill and for carbon export production to the deep ocean. This excess phytoplankton production ranges between 20 and 196 gC m^{-2} d^{-1}, with highest values in the CCSZ (Fig. 14e) and in the FZ (Fig. 14a), and lowest value in the CPIZ (Fig. 14d). This production added to the total net microbial food web secondary production, gives a total amount of 114, 46, 80, 30 and 244 gC m^{-2} in the FZ, the OOZ, the MIZ, the CPIZ and the CCSZ, respectively. This amount represents the maximum predicted food resources available for krill and other metazooplankton. Considering the respective surface of the biogeochemical provinces, the global amount carbon available for metazoan food demand and export production is estimated at 2.6 GT $year^{-1}$ i.e. twice as high as the annual food demand of krill calculated from their annual biomass production (Voronima 1998). However, the microbial food web secondary production represents as much as 50 % of the annual krill food demand.

The contribution of the microbial food web to this flux varies however geographically and is negatively correlated with the total primary production (Fig. 15).

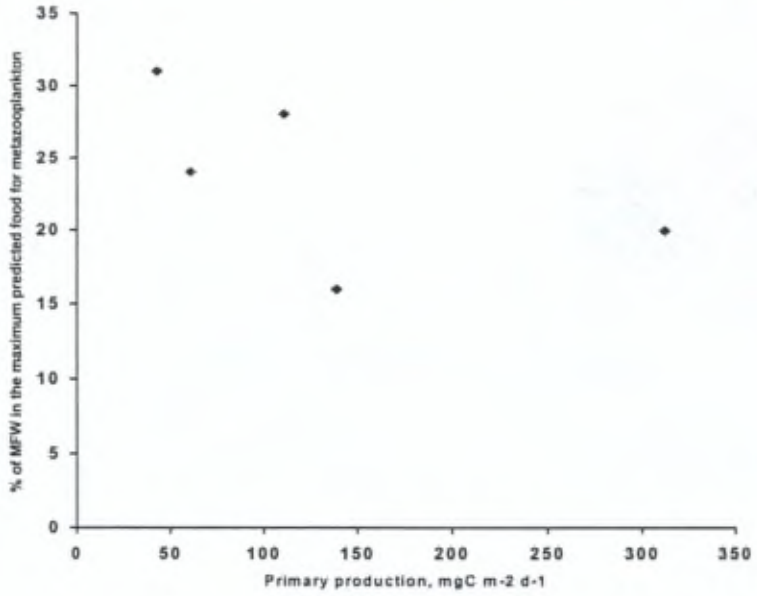

Figure 15. *Relationship between the contribution of the MFW via protozooplankton to the maximum predicted food resources available for krill and other metazooplankton, and the primary production.*

This suggests that protozoa can play a key role in the transfer of energy and materials to larger zooplankton. Supporting that, protozooplankton prey were indeed observed in zooplankton guts in Antarctic waters (Hopkins 1985, 1987, Hopkins and Torres 1989). A laboratory-controlled grazing study estimated to 45 % "the microbial food web component" including heterotrophic dinoflagellates, ciliates and *cryptomonas* of the ingested food by the dominant copepods in the shelf region of South Georgia. Furthermore, this study showed that larger copepods grazed on microzooplankton at the same rates than on diatoms of similar size (Atkinson 1994, Atkinson and Shreeve 1995). Froneman *et al.* (1996) as well reported that microplankton (ciliates and dinoflagellates) represented an important source of carbon for all meso- and macrozooplankton including copepods, krill and salps in the MIZ of Lazarev Sea during summer. The ability of metazoans to consume both autotrophic and heterotrophic prey could be a necessary adaptation to the seasonality and patchiness of food distribution in the Antarctic (Atkinson 1994). Recent studies conducted in winter in the Weddell Sea and in early summer in the vicinity of Elephant Island demonstrated indeed that the energy derived from the consumption of phytoplankton alone could not meet the daily metabolic requirements of copepods (Bathmann *et al.* 1993, Drists *et al.*

1994). Here also protozoa and detritus as well were suggested as alternative food sources of copepods (Bathmann *et al.* 1993).

On the other hand, the complexity of the microbial networks leads to the release of high catabolic products as CO_2 and regenerated nutrients including ammonium, phosphate but also iron. The dominance of a microbial food web is indeed always associated with regenerated-based production. Even if bacteria are generally considered as the principal nutrients regenerators, their importance in nutrient recycling could be considerably biased due to their efficiently competition with autotrophs to assimilate the mineral compounds to fulfil their own requirements (Currie and Kalf 1984). Nowadays, there are increasing evidences of a significant role of protozoa in nutrient regeneration in the marine ecosystems (Caron *et al.* 1985, Goldman *et al.* 1985, Andersen *et al.* 1986). Nevertheless, little information on nutrient regeneration by protozoa is available in the Antarctic Ocean. For instances, the significant role of protozoa in ammonium remineralization has been reported in the marginal ice zone of the north-western Weddell Sea in spring (Goeyens *et al.* 1991). In the Fe-limited ecosystems, the careful assessment of trace metal regeneration processes is of prime importance. Some information is available although this is a very new topic. Hutchins *et al.* (1993) for instance demonstrated that iron can be rapidly recycled from labelled living phytoplankton. However, bacterial release of trace metals from phytoplankton cells and debris has been observed to be a relatively slow process, occurring on a time frame of days to weeks (Lee & Fisher 1992), even when the microbial community is artificially enriched (Lee & Fisher 1994). Contrasting, some evidences demonstrating the significant role of protozoa in Fe remineralization are reported in Hutchins & Bruland (1994). The acidic conditions which initiate the digestive process in most grazers seems to be exceptionally well suited to render most trace metals soluble. The pH within the feeding vacuoles of some protozoa may drop to 3 (Fok *et al.* 1982). The combination of enzymatic degradation and low pH thus appears to be ideal for returning organically bound cellular metals to inorganic dissolved forms.

Although very important to progress in our understanding of the structure and functioning of the Antarctic Ocean ecosystems, these carbon budgets have to be considered with caution due to the complex trophic interactions that can additionally take place in the food web i.e. mixotrophy, trophic triangles (Turner & Roff, 1993). Indeed, apparently unimportant pathways in terms of the magnitude of flux can have major effects in complex networks. Such pathways can be limiting or may have indirect effects on other pathways. Such problems raise the questions of tradeoff between complexity and simplicity in analyses of the Antarctic Ocean.

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Conclusions et perspectives

L'effort international de recherche sur l'océan Antarctique fut en premier lieu motivé par le souci d'exploiter ses ressources biologiques marines sans perturber l'écosystème et la biodiversité qui le caractérise. Actuellement, des efforts considérables sont également investis afin d'évaluer le rôle relatif de l'océan Antarctique dans le cycle global du carbone et son influence dans la régulation du climat mondial. Dans ces deux problématiques, la connaissance des processus déterminant les flux de carbone vers les niveaux trophiques supérieurs et vers l'océan profond via la pompe biologique est primordiale. L'importance de ces processus dépend non seulement du niveau de la production primaire (assimilation de CO_2 par la photosynthèse) mais aussi du groupe phytoplanctonique dominant (nanophytoplancton versus microphytoplancton) lequel détermine la structure des réseaux trophiques pélagiques (réseau trophique microbien versus chaîne trophique linéaire). La chaîne trophique linéaire est en effet source d'exportation de carbone vers le fond de l'océan mais aussi vers les organismes supérieurs marins. Le réseau microbien en revanche recycle rapidement par sa respiration le carbone assimilé par la photosynthèse et le carbone est ainsi maintenu dans la couche de surface de la colonne d'eau.

Comme il a été montré dans ce travail, la biomasse de ces deux grands groupes de phytoplancton varie suivant la latitude, la saison et les conditions météorologiques locales par des facteurs tel que (1) la disponibilité en lumière déterminée par le rayonnement solaire incident, la couverture de glace, la transparence de l'eau et la profondeur de la couche de mélange; la disponibilité en fer; et la pression exercée par le broutage du zooplancton. La synthèse des connaissances actuelles sur le fonctionnement de l'écosystème antarctique combinée aux simulations mathématiques générées par le modèle biogéochimique mécanistique SWAMCO montrent que l'ensemble des facteurs physico-chimiques et biologiques interagissent entre eux de manière complexe. Ainsi la nature HNLC - concentrations en nutriments majeurs élevées contrastant avec une biomasse ~~biomasse~~ phytoplanctonique faible- typique de l'océan Antarctique résulterait du développement sélectif du pico- et nanophytoplancton, compétitif à des concentrations faibles en fer dissous mais dont la croissance est rapidement contrôlé et efficacement par le protozooplancton herbivore. A ce système microbien se surimpose dans des régions riches en fer des efflorescences de diatomées de grande taille et de colonies de *Phaeocystis* observées épisodiquement lors de conditions météorologiques favorables. Ces régions sont les eaux côtières et continentales (mer de Ross, baie de Prydz) enrichies en fer originaire des sédiments côtiers et du continent Antarctique, les eaux du "Polar Frontal Jet " qui mémorisent un signal significatif en fer provenant des sources côtières et de manière moins importante les régions influencées par la retraite de la banquise ayant accumulé des apports éoliens en fer.

Une part significative de la biomasse produite annuellement par le phytoplancton dans l'océan Antarctique alimente dés lors directement ou indirectement le réseau trophique microbien via le pico- et nanophytoplancton et/ou les bactéries assimilant le carbone organique dissout provenant de la lyse des mocroorganismes et du broutage du zooplancton. Les développements du bactérioplancton et du pico- et nanophytoplancton sont contrôlés rapidement et efficacement par le protozooplancton. Le protozooplancton, ubiquiste dans l'océan Antarctique, représente une part significative (24 %) de la biomasse microbienne planctonique totale.

Les bilans annuels du carbone établis dans la couche de surface dans les différentes provinces biogéochimiques caractérisant l'océan Antarctique suggère que le réseau trophique microbien via les protozoaires constitue un apport potentiel non négligeable de nourriture pour le métazooplancton. Il a été estimé que 50 % de la demande en carbone du krill peut être produite par le réseau trophique microbien via le protozooplancton. Cependant, la multitude et la complexité des étapes trophiques, typique du réseau trophique microbien, conduit à la production importante de catabolites comme du CO_2 et des nutriments régénérés tel que l'ammonium, le phosphate mais aussi le fer.

Si ce manuscrit de cette thèse a mis en avant l'importance du réseau trophique microbien et particulièrement du protozooplancton et a contribué à comprendre la nature "HNLC" de l'océan Antarctique et il débouche sur deux problématiques corrélées à la dynamique du réseau trophique microbien sur lesquelles les recherches futures devaient se focaliser.

- Premièrement, la dominance du réseau trophique microbien est toujours associée à de la production dite régénérée. Actuellement, si le rôle des protozoaires comme régénérateurs de nutriments a été mis en évidence dans de nombreux écosystèmes marins, il a été très peu étudié dans les eaux antarctiques. Dans un écosystème limité par la disponibilité en fer, l'étude des facteurs contrôlant la régénération des métaux en trace est de première importance.
- Deuxièmement, il a été démontré dans de nombreux écosystèmes que le réseau microbien est souvent associé aux particules de la neige marine (Silver *et al.* 1984). L'association de microrganismes aux particules qui forment la neige marine modifie grandement la nature chimique et la densité de ces particules et par voie de conséquence le devenir de celles-ci. Il se crée en effet au niveau des particules un véritable réseau microbien qui transforme et minéralise la matière organique des particules durant leur transfert de la couche océanique de surface vers l'océan profond et par conséquent modifie la vitesse de sédimentation de ces microenvironnements. La présence du réseau microbien sur ces particules augmente d'autre part leurs qualités nutritives et par voie de conséquence leurs susceptibilités d'être consommées par le métazooplancton. L'ensemble de ces processus liés à l'agrégation phytoplanctonique pourraient

être particulièrement importants dans certaines régions de l'océan Antarctique, notamment dans les régions où sont observées des efflorescences importantes de colonies de *Phaeocystis*, comme en mer de Ross (El-Sayed 1983, Putt *et al.* 1994) et en baie de Prydz (Davidson et Marchant 1987). En raison de leur grande taille, les colonies de *Phaeocystis* ne sont pas consommées par le métazooplancton en revanche elles sont largement colonisées par des bactéries (Becquevort *et al.* 1997, Putt *et al.* 1994) mais aussi par des protozaires (Lancelot & Rousseau 1994).

Annexe

Méthodes d'estimation du broutage des bactéries et du phytoplancton par les protozoaires en milieu aquatique

Différentes méthodes ont été développées depuis une vingtaine d'année et sont actuellement utilisées pour estimer le broutage des protozoaires en milieux aquatiques. Des revues très complètes sur les méthodes existantes et sur la signification de leurs mesures ont été réalisées par Mac Manus & Furhman (1988) et par Landry (1994). Chacune des méthodes a ses avantages spécifiques aussi bien que ses faiblesses propres et ses ambiguïtés qui empêchent leur utilisation lors de toutes problématiques et dans toutes les conditions environnementales rencontrées.

Ces méthodes peuvent être classées en trois groupes:

(1) Les méthodes basées sur le suivi de la biomasse des particules alimentaires en présence ou non de consommateurs capables de les ingérer.

Différentes techniques sont ainsi proposées pour supprimer l'ingestion:

La filtration sélective a été introduite par des chercheurs russes (Gak *et al.* 1972). Elle a été appliquée à l'étude de l'ingestion des bactéries et du phytoplancton par les protozoaires dans différents milieux (Capriulo & Carpenter 1980, Verity 1986, Wright & Goffin 1984, Kuuppo-Leinikki & Kuosa 1990, Caron *et al.* 1991). Cette technique consiste à suivre pendant 6 à 24 heures l'abondance des bactéries ou du phytoplancton dans un échantillon d'eau où les protozoaires ont été éliminés par filtration et parallèlement dans un échantillon brut. La différence d'augmentation bactérienne ou phytoplanctonique entre les deux échantillons représente la mortalité due aux organismes retenus par la filtration.

Le choix d'une porosité de filtre adéquate est une étape limitante de cette technique. D'une part, il est clair à présent que les particules alimentaires et les consommateurs peuvent être proches en taille et d'autre part que certains organismes peuvent passer à travers des membranes filtrantes de porosité inférieur à leur taille grâce à une certaine flexibilité (Fuhrman & Mc Manus 1984). La filtration peut d'autre part augmenter significativement le substrat des bactéries en induisant la lyse des cellules. Cette apport supplémentaire en substrats augmente la croissance bactérienne dans l'échantillon filtré et par conséquence on surestime la mortalité bactérienne (Furhman & Bell 1985).

Des inhibiteurs spécifiques des eucaryotes ou des procaryotes peuvent être utilisés pour inhiber soit l'ingestion (par exemple le thyram, le rouge neutre, la colchicine et/ ou la cycloheximide) ou soit la croissance bactérienne (par exemple la pénicilline, la vancomycine). Dans les deux cas, la mortalité bactérienne est estimée par comparaison des évolutions bactériennes entre l'échantillon d'eau non traité et l'échantillon d'eau traité (Newell *et al.* 1983, Furhman & Mc Manus 1984, Sherr *et al.* 1986, Sanders & Porter 1986).

Ces méthodes ont l'avantage de nécessiter le minimum de traitement préalable de l'échantillon d'eau par contre cela implique que les inhibiteurs soient (1) suffisamment spécifiques, qu'ils ne soient (2) pas un substrat de croissance pour les bactéries et (3) qu'ils ne provoquent pas la lyse phytoplanctoniques et donc la production de substrats organiques pour les bactéries (Taylor & Pace 1987).

La méthode de dilution a été développée par Landry & Hassett (1982) pour mesurer l'ingestion du phytoplancton par le microzooplancton et ensuite appliqué par Landry *et al.* (1984) et par Ducklow & Hill (1985) pour mesurer l'ingestion de bactéries. Le principe de la méthode est de suivre les changements en phytoplancton ou en bactéries dans des échantillons de plus en plus dilué par de l'eau filtré (exempte de phytoplancton ou de bactéries) du même échantillon. Cette méthode fait les hypothèses suivantes:

(1) La croissance phytoplanctonique ou bactérienne est indépendante de la densité cellulaire, c'est à dire les taux de croissance spécifiques sont constants sous toutes les conditions de dilution.

(2) La mortalité est fonction du taux de rencontre des particules alimentaires et des prédateurs.

(3) La croissance phytoplanctonique ou bactérienne suit une équation exponentielle du type:

$$N_f = N_i \cdot e^{(\mu - n.k).t} \quad (1)$$

μ et k sont respectivement les taux de croissance et de mortalité (h^{-1}). La densité du phytoplancton ou des bactéries au temps initial est N_i et au terme du temps t N_f.

n représente le taux de dilution de l'échantillon.

A partir de (1), on obtient $1/t \cdot \text{Ln } N_f/N_i = \mu - n.k$.

donc la représentation de 1/t . Ln N_f/N_i en fonction du taux de dilution n est une droite de pente k et d'ordonnée à l'origine μ. Ainsi la pente de la droite k correspond au taux de mortalité.
La limitation de cette méthode est dans le respect des trois hypothèses cités ci-dessus.
Ainsi la filtration de l'eau nécessaire à la dilution augmente les composés organiques dissous dans le filtrat résultant de la rupture de cellules et peut donc violer la première hypothèse (Fuhrman & Bell 1985). D'autre part le choix d'une exponentielle pour décrire la croissance peut affecter l'estimation de l'ingestion (Ducklow & Hills 1985).

(2) Les méthodes basées sur le suivi de l'assimilation des proies marquées au sein des consommateurs.

Différents types de proies ont été utilisées:
En 1980, Hollibaugh *et al.* propose d'utiliser **bactéries ou phytoplankton marqués à ^{3}H-thymidine** et au **^{14}Carbone** afin d'estimer leur ingestion par le microzooplancton. Après un temps d'incubation du microzooplancton avec les bactéries marquées, les consommateurs sont isolés des particules alimentaires soit par filtration sélective soit à l'aide de micropipettes. La radioactivité associée aux consommateurs est mesurée. Elle représente la radioactivité des particules alimentaires ingérées.
Caron *et al.* (1993) montre que des temps d'incubation trop long peuvent amener (1) à une sous-estimation de l'ingestion due à la digestion des particules alimentaires marquées et la perte du marqueur par la respiration et (2) à mesurer des transfers trophiques multiples du marqueur. D'autre part, l'isolement des consommateurs reste problématique (voir ci-dessus).

Des **particules de plastique fluorescent** (McManus & Fuhrman 1986) et des **billes en latex fluorescent** (Borsheim 1984, Bird & Kallf 1986) ont été utilisées pour estimer l'ingestion par des populations naturelles de protozoaires. Le principe est basée sur l'addition d'un inoculum de particules fluorescentes et le suivi pendant un temps très court du nombre de particules contenu dans les vacuoles digestives des consommateurs grâce à la microscopie à épifluorescence. L'avantage de ces méthodes sont les temps d'incubation très courts et les manipulations minimales de l'échantillon. Elles permettent d'autre part de déterminer les taux d'ingestion au niveau de l'espèce. Leur principal désavantage est que les consommateurs puissent différencier les particules artificielles des bactéries naturelles et du phytoplancton (Sherr *et al.* 1987).

Sherr *et al.* (1987) proposaient de remplacer les particules fluorescentes par **des bactéries fluorescentes (FLB, Fluorescently Labelled Bacteria)**. Les bactéries sont colorées par un fluorochrome, ce qui rend possible leur visualisation au sein des protozoaires comme les particules fluorescentes, par la microscopie à épifluorescence. Les travaux de Sherr *et al.* (1989) montraient qu'ils n'existent pas de sélectivité entre bactéries FLB qui sont mortes et les bactéries vivantes. Cependant Gonzàlez *et al.* (1993) observaient des taux d'ingestion plus élevé avec des bactéries vivantes fluorescentes dans des échantillons contenant une grande proportion de bactéries mobiles.

Rublee & Gallegos (1989) appliquaient cette méthode à la mesure de broutage par les protozoaires du phytoplankton et utilisaient donc des cellules phytoplanctoniques fluorescentes (FLA, **Fluorescently Labelled Algae).**

Une des étapes limitantes des dernières méthodes -particules et bactéries/phytoplancton fluorescents- est la fixation des organismes avant observation microscopique. Certains fixateurs provoquent l'éjection des bactéries ou particules contenues dans les vacuoles digestives des consommateurs (Sieracky *et al.* 1987, Sherr *et al.* 1989). D'autre part la discrimination entre les proies analogues fluorescentes et les proies naturelles reste problématique.

(3) **Les méthodes basées sur le suivi de la digestion.**

L'utilisation de minicellules marquées radioactivement par ^{35}S-méthionine a été proposé par Wikner *et al.* (1986) pour mesurer la mortalité des bactéries. Les minicellules sont produites par des cellules mutantes d'*Escherichia coli* qui se divisent assymétriquement. Ces divisions produisent des cellules de 0.2 à 0.9 µm de diamètre qui ne possèdent pas d'ADN donc ces cellules ne se multiplient pas. Le taux de mortalité est mesuré par la décroissance de la radioactivité associée aux minicellules. Cependant, même si le biovolume de ces minicellules est proche de celui des bactéries du milieu naturel , il ne varie pas suivant la saison, la richesse du milieu etc. Or, la taille des bactéries est un des principaux paramètres déterminant leur ingestion.

Une seule méthode existe jusqu'à présent permettant de mesurer l'ensemble des processus de mortalité bactérienne. Cette méthode est basée sur **le marquage de l'ADN bactérien à la thymidine tritié et le suivi de la décroissance de cette radioactivité** (Servais *et al.* 1985, 1989, Menon 1993).

Le principe de la méthode est le suivant: la mortalité bactérienne est estimée par le suivi de la décroissance de la radioactivité associée à l'ADN bactérien. Bien que la thymidine tritié s'incorpore dans d'autres macromolécules que l'ADN, Servais *et al.* (1989) ont montré que la décroissance de la radioactivité contenue spécifiquement dans l'ADN est parallèle à la décroissance de la radioactivité contenue dans la fraction insoluble à l'acide trichloroacétique. Ce résultat montre que le taux de turn-over de la thymidine tritiée incorporé dans les autres macromolécules est plus faible que la vitesse de mortalité bactérienne et donc le suivi du marquage de la thymidine tritié contenue dans la fraction insoluble au TCA froid mesure bien la mortalité bactérienne.

Dans la mesure où le marquage présent dans l'ADN ne subit pas de turn-over métabolique (à l'exception des processus de réparation), cette décroissance représente bien la mortalité bactérienne.

La mortalité bactérienne pourrait cependant être sous estimée si une partie de tritium provenant des bactéries se retrouve incorporé dans les consommateurs.

Le devenir de l'ADN durant l'ingestion par les protozoaires a été examiné récemment par Turk *et al.* (1992). Ils concluaient que la majorité de l'ADN bactérien ingéré par le flagellé *Ochromonas* était relâché dans le milieu. En accord avec ces auteurs, Caron *et al.* (1993) montraient que le tritium était incorporé dans la biomasse des protozoaires avec une efficience considérablement faible par rapport à l'efficience brute de croissance des protozoaires.

Le principal désavantage de cette technique est le temps d'incubation très long et donc la la possibilité de modification du milieu. Différentes solutions ont été envisagées pour réduire le temps d'incubation (Garcia-Lara *et al.* 1991, Becquevort 1987)

La méthode de Servais *et al.* (1985) décrite ci-dessus peut également estimé la mortalité due à l'ingestion par des organismes. En effet , nous pouvons comparer la mortalité bactérienne dans un échantillon non-traité avec celle d'un échantillon où l'activité d'ingestion des organisme est exclue (par filtration ou/et par inhibition spécifique). La différence entre les deux taux de mortalité mesurés dans chacun des deux échantillons donne le taux de mortalité des bactéries par les organismes retenus par filtration ou/et inhibés. Les désavantages de cette méthodes sont ceux précités ci-dessus pour la filtration et l'inhibition sélective.

Le dosage de **l'acide lysozyme**, enzyme nécessaire à la digestion des bactéries, a été proposé récemment afin d'estimer l'ingestion des bactéries par les protozoaires (Gonzàles *et al.* 1993). Cette méthode est originale, elle est la première méthode basée sur la mesure de l'activité des

enzymes digestifs dans les vacuoles digestives des protozoaires. Cependant elle nécessite encore des mises au point.

Jusqu'à présent aucune méthode n'a été considérée comme "la meilleur". Toutes ces méthodes ont des avantages et des désavantages. Leur efficacité à estimer l'ingestion des bactéries et du phytoplancton par le protozooplancton dans chaque situation particulière est dépendant de différentes choses tel que l'environnement (c'est à dire eutrophe versus oligotrophe), l'objectif du travail (c'est à dire détermination du taux d'ingestion au niveau d'une communauté versus au niveau de l'espèce) et bien sûr des organismes composants la communauté étudiée. La table 1 reprend les mérites relatifs et les déficiences des différentes méthodes.

Parmi ces méthodes, notre choix à porter sur deux méthodes. La méthode de Servais *et al.* (1985) car jusqu'à présent elle est la seule méthode permettant d'estimer une mortalité bactérienne totale en milieu naturelle. Deuxièmement, la méthode FLB/FLA (Sherr *et al.* 1987, Gallegos & Rublee 1989) nous a paru intéressante par la possibilité de visualisation directe par microscopie à épifluorescente de l'ingestion et donc l'estimation possible du taux d'ingestion de chaque organisme et la possibilité d'étudier ainsi la sélectivité alimentaire des protozoaires.

Table 1. *Résumé des méthodes pour estimer le broutage des protozoaires dans les milieux aquatiques.*

Méthodes	Usage de proies naturelles	Temps d'incubation	Interruption du "Feed-Back"	Perturbation de la communauté	Processus de mortalité estimé	taux d'ingestion au niveau de l'espèce	taux d'ingestion au niveau de la communauté	Références principales
Taux de perte de l'ADN	oui	long	non	minimal	mortalité bactérienne totale	non	oui	Servais *et al.*, 1985, 1989.
Inhibiteurs spécifiques	oui	long	oui	physiologique	mortalité due à l'ingestion par les organismes inhibés	non	oui	McCambridge & McMeekin, 1980 Sherr *et al.*, 1986 Caron *et al.*, 1991
filtration sélective	oui	long	oui	physique	mortalité due à l'ingestion par les organismes exclus par la filtration	non	oui	Wright & Coffin,1984
dilution en série	oui	long	oui	comportement	mortalité due à l'ingestion	non	oui	Landry *et al.*, 1984
particules, billes, et bactéries/phytoplancton fluorescents	oui/non	très court	non	minimal	mortalité due à l'ingestion	oui	oui	Sherr *et al.* 1987, McManus & Fuhrman 1986, Vaqué & Pace 1992, Rubblee & Gallegos 1989
particules alimentaires radioactives	oui	court	non	minimal	mortalité due à l'ingestion	non	oui	Hollibaugh *et al.*, 1980 Wikner *et al.*, 1986
Dosage d'enzymes digestifs	oui	court	non	minimal	mortalité due à l'ingestion	non	oui	Gonzales *et al.*, 1993

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Comparaison de deux méthodes d'estimation du broutage des bactéries par les protozoaires en milieu aquatique

Comparison of two methods assessing the grazing of bacteria by protozoa in aquatic ecosystems

Titre court : Broutage des bactéries par les protozoaires

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SUMMARY

The goal of the present work was to compare two methods allowing to estimate, in aquatic ecosystems, the carbon flux due to grazing of bacteria by protozoa. The first method follows the decrease of labeling in the DNA of natural assemblages of bacteria previously labeled with tritiated thymidine (SERVAIS *et al.*, 1985) and the second procedure is based on the estimation of bacterial ingestion rate by protozoa using fluorescently labeled bacteria (FLB). Both methods were applied in parallel on river Meuse (Belgium) samples. Using the first method, grazing rates in the range 0.002 h^{-1} to 0.016 h^{-1} were observed; they represented in average 72 % of the total bacterial mortality rates. A very good correlation between both estimates of the grazing fluxes was found but the data obtained by the FLB method were systematically lower (around 30% in average) than those estimated with the other method. A part of this difference is probably due to he fact that the FLB method does not take into account grazing by organism higher than 100 µm.
Key-words : bacteria, protozoa, grazing, mortality, thymidine.

RÉSUMÉ

L'objectif du présent travail est de comparer deux méthodes indépendantes permettant d'estimer, dans les milieux aquatiques, le flux de carbone transitant du compartiment bactérien vers les protozoaires. Les deux méthodes utilisées sont, d'une part, celle basée sur le suivi de la décroissance de radioactivité du matériel génétique bactérien après marquage à la thymidine tritiée (SERVAIS *et al.*, 1985) et, d'autre part, celle de mesure du taux d'ingestion de bactéries fluorescentes (FLB) par les protozoaires. Elles ont été appliquées en parallèle sur des échantillons de la rivière Meuse (Belgique). L'emploi de la première méthode a montré des taux de broutage compris entre 0.002 h^{-1} et 0.016 h^{-1} qui représentent en moyenne 72 % des taux de mortalité totale. Une excellente corrélation entre les estimations de flux de broutage obtenues par les deux techniques a été trouvée, mais les valeurs estimées à partir de la méthode FLB sont systématiquement inférieures (d'environ 30% en moyenne) à celles obtenues par l'autre méthode. Une part de cette différence peut vraisemblablement s'expliquer par la non prise en compte par la méthode FLB du broutage par des organismes de taille supérieure à 100 µm.
Mots clés : bactéries, protozoaires, broutage, mortalité, thymidine,

Grâce aux efforts méthodologiques accomplis au cours des vingt dernières années dans le domaine de l'écologie microbienne, il est aujourd'hui possible de quantifier correctement la biomasse et l'activité des bactéries dans les milieux aquatiques. De nombreuses études ont montré que, dans ces milieux, la biomasse bactérienne représente un compartiment très actif de l'écosystème qui utilise une part importante du carbone fixé par les organismes phototrophes (COLE *et al.*, 1988; WHITE *et al.*, 1991). Ces observations vont à l'encontre de l'idée classique d'une chaîne trophique linéaire (phytoplancton - zooplancton - poissons). Au contraire, il apparaît que les bactéries jouent un rôle important tant dans le recyclage des éléments nutritifs que dans le transfert d'une partie de la production primaire vers les niveaux trophiques supérieurs via un réseau trophique complexe appelé boucle microbienne (AZAM *et al.* 1983; GARNIER et BARILLIER, 1991; MASSANA *et al.*, 1996). Dans ce contexte, de nombreux travaux ont été consacrés au développement de méthodes permettant d'étudier le devenir de la biomasse bactérienne et plus particulièrement de quantifier l'importance du broutage de celle-ci par les protozoaires qui semble constituer un processus quantitativement dominant dans la mortalité bactérienne (SANDERS *et al.*, 1992).

Diverses méthodes ont été proposées pour l'estimation du taux de broutage des bactéries par les protozoaires dans les milieux aquatiques (Mc MANUS et FUHRMAN, 1988). Un premier groupe de méthodes est basé sur la comparaison de la croissance bactérienne en présence et en l'absence de brouteurs. Les procédures utilisées pour éliminer les brouteurs incluent la filtration sélective (WRIGHT et COFFIN, 1984), la dilution de l'échantillon avec de l'eau exempte de bactéries (DUCLOW et HILL, 1985; LANDRY *et al.*, 1984) ou l'addition de diverses substances inhibitrices de l'activité de broutage (NEWELL *et al.*, 1983; FUHRMAN et McMANUS, 1984; SANDERS et PORTER, 1986). Un second groupe de méthodes est basé sur l'estimation du taux d'ingestion de bactéries marquées par les protozoaires. Ces bactéries marquées peuvent être constituées d'un assemblage de cellules marquées par un traceur radioactif (NYGAARD et HESSEN, 1990), de minicellules de *Escherichia coli* marquées génétiquement (WIKNER *et al.*, 1986), de particules inertes fluorescentes (BORSHEIM, 1984; LANDRY *et al.*, 1984) ou de bactéries marquées par un fluorochrome (ALBRIGHT *et al.*, 1987; SHERR *et al.*, 1987). Par ailleurs, SERVAIS *et al.* (1985, 1989) ont proposé, une méthode qui permet d'estimer à la fois le taux de mortalité totale des bactéries ainsi que la part de la mortalité due au broutage. Cette méthode consiste à suivre la décroissance du marquage radioactif du matériel génétique de bactéries préalablement marquées avec de la thymidine tritiée.

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L'objectif du présent travail était de comparer deux méthodes totalement indépendantes permettant d'estimer le flux de carbone transitant du compartiment bactérien vers les protozoaires. Les deux méthodes utilisées sont, d'une part, celle basée sur le suivi de la décroissance de radioactivité du matériel génétique bactérien et, d'autre part, celle de mesure du taux d'ingestion de bactéries fluorescentes par les protozoaires (appelée méthode FLB - Fluorescently Labeled Bacteria) qui semble être actuellement la plus utilisée dans les études de broutage (LANDRY, 1994). Cette comparaison a été réalisée dans le cadre d'une étude sur les relations trophiques entre micro-organismes en milieu fluvial (SERVAIS *et al.*, 1997). La Haute Meuse belge (partie du cours de la Meuse située entre la frontière franco-belge et la ville de Namur) a été choisie comme modèle d'écosystème fluvial. Les échantillons utilisés pour les mesures présentées ici ont été collectés à la station de La Plante, située à trois kilomètres en amont de Namur, entre janvier et octobre 1996.

La mortalité bactérienne totale inclut la mortalité due à l'ingestion des bactéries par les brouteurs ainsi que la lyse bactérienne spontanée ou induite. La méthode proposée par SERVAIS *et al.* (1985) permet d'évaluer la mortalité totale d'une population bactérienne autochtone par suivi au cours du temps de la décroissance de la radioactivité associée à l'ADN bactérien, préalablement marqué par de la ^{3}H-thymidine. SERVAIS *et al.* (1989) ont montré la validité de cette approche. La décroissance du marquage radioactif suit une cinétique du premier ordre (droite en représentation semi-logarithmique) et peut donc être caractérisée par une constante du premier ordre kd. La mesure effectuée en parallèle dans un échantillon naturel non modifié et un échantillon filtré sur une membrane de porosité 2 µm retenant les brouteurs de bactéries permet de déterminer par différence la part de la mortalité due au broutage. Pratiquement, on ajoute à un échantillon de 200 ml d'eau de Meuse placé à température *in situ* et à l'obscurité de la ^{3}H-thymidine (activité spécifique 40-50 Curies/mmole) pour obtenir une concentration finale de 4 nM. L'échantillon est incubé pendant une vingtaine d'heures afin de permettre à la thymidine tritiée d'être incorporée dans l'ADN bactérien et ainsi éliminée du milieu. A ce moment l'échantillon est divisé en deux sous-échantillons de 100 ml. Le premier n'est pas modifié, le second est filtré sur une membrane de porosité 2 µm (filtre Nuclépore) et des inhibiteurs de l'activité des protozoaires sont ajoutés : colchicine (concentration finale 100 mg/l) et cycloheximide (concentration finale 200 mg/l). La filtration et l'addition des inhibiteurs permettent d'éliminer dans ce sous-échantillon le broutage des protozoaires. L'incubation des deux sous-échantillons se poursuit à température *in situ* et des aliquotes de 5 ml sont prélevées

toutes les l0 à 20 heures pendant environ 150 heures et additionnées de 5 ml de TCA 15 % froid. La fraction macromoléculaire est recueillie par filtration (membrane de porosité 0.2 µm) et la radioactivité associée au filtre est mesurée par scintillation liquide. Les taux de mortalité en présence et en l'absence de broutage sont déterminés par les vitesses de décroissance de la radioactivité dans les deux sous-échantillons et le taux de mortalité due au broutage est estimé par différence. La précision des taux ainsi estimés est 0.001 h^{-1} (MENON, 1993)

La figure 1 présente l'évolution saisonnière du taux de mortalité totale (kd) et du taux de mortalité due au broutage (kg) en Meuse.

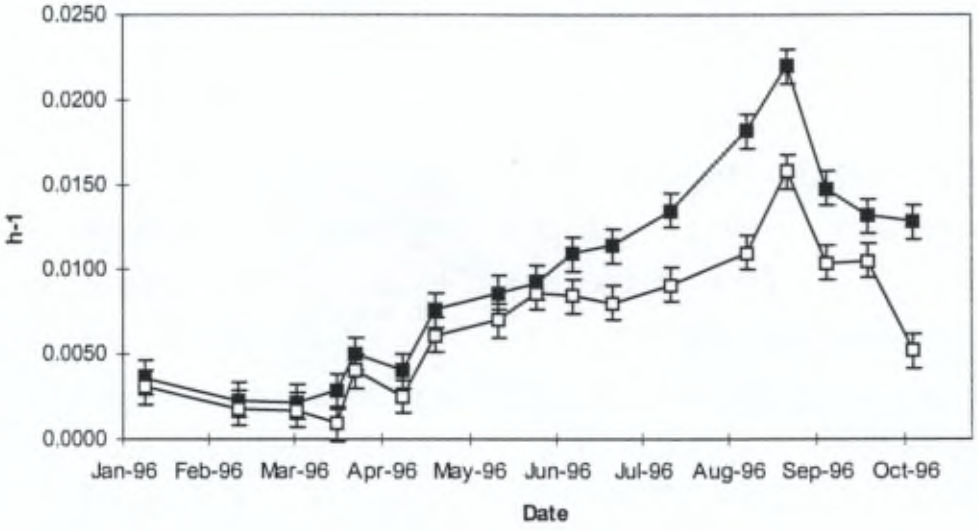

Figure 1. Evolution saisonnière des constantes du premier ordre de mortalité bactérienne totale (kd) (■) et de mortalité due au broutage (kg)( ) obtenues par la méthode basée sur le marquage à la thymidine.

Figure 1. Seasonal variations of the first order rate constants of total mortality (kd) (■) *and mortality attributable to grazing (kg)*( ) *measured by the method based on labeling by thymidine.*

Les valeurs de taux de mortalité totale sont comprises entre 0.002 h^{-1} et 0.022 h^{-1}. Ces valeurs sont dans la gamme des valeurs observées en général en milieux aquatiques (SERVAIS *et al.*, 1992). Le taux de mortalité augmente au cours de l'année pour atteindre un maximum en août, il décroît par la suite. Ce type d'évolution saisonnière de la mortalité bactérienne avec un maximum estival

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a été observé dans divers milieux aquatiques (SERVAIS *et al.*, 1989, 1992). Le broutage apparaît comme étant le processus prépondérant dans la disparition des bactéries; il représente en moyenne 72 % de la mortalité totale. Les valeurs plus élevées de broutage durant la période estivale sont à mettre en relation avec des températures élevées et avec des abondances de protozoaires également élevées qui contribuent à accroître la pression de broutage des protozoaires sur les bactéries. Bien que souvent faible (entre 0.001 et 0.008 h^{-1}), une mortalité par lyse est observée dans chacune des situations étudiées. En multipliant le taux de mortalité due au broutage par la biomasse bactérienne, on obtient pour chaque prélèvement le flux de carbone transitant du compartiment bactérien vers celui des protozoaires. A cet effet, la biomasse bactérienne a été estimée sur base de dénombrements en microscopie à épifluorescence après coloration au DAPI (PORTER et FEIG, 1980) et d'une estimation du biovolume moyen converti en contenu en carbone bactérien par la relation carbone-biovolume proposée par SIMON et AZAM (1989). Les valeurs de flux ainsi obtenues varient entre 0.8 et 4.0 µgC/l.h; elles vont être comparées ci-dessous aux estimations basées sur la méthode FLB.

La méthode FLB développée par SHERR et al. (1987, 1988) a été appliquée aux estimations de taux d'ingestion des bactéries par les protozoaires en parallèle avec les mesures décrites ci-dessus. Le principe de cette méthode est d'ajouter une aliquote de bactéries fluorescentes à l'échantillon et à suivre au cours du temps le nombre de bactéries ingérées par protozoaire en visualisant directement celles-ci, par microscopie à épifluorescence, au sein des protozoaires, après ingestion par ces derniers. Lors de la manipulation, les bactéries FLB sont ajoutées en concentration trace (moins de 10 % de la concentration totale en bactéries de l'échantillon). Afin d'éviter l'interférence du processus de digestion des bactéries avec le processus d'ingestion, le taux d'ingestion des bactéries FLB par les protozoaires est estimé sur des temps courts (10 à 60 minutes selon les organismes).

Les bactéries FLB sont préparées en filtrant de l'eau du milieu naturel sur un filtre de porosité 2 µm, le filtrat est ensuite ensemencé avec de l'extrait de levure et incubé à température ambiante durant 12 heures. Une concentration faible en extrait de levure (0.5 mg/l) permet d'engendrer pendant l'incubation une augmentation de l'abondance des bactéries autochtones sans modifier significativement leur taille. Les bactéries sont alors concentrées par centrifugation et le culot bactérien est remis en suspension dans 10 ml de solution saline d'hydrogénophosphate de sodium 0.05 M. Les bactéries sont colorées selon le protocole établi par SHERR *et al.* (1987) avec 0.2 mg/ml de DTAF pendant 2 heures à 60°C. La coloration est suivie de trois lavages par

centrifugation. Les bactéries colorées sont alors conservées dans une solution saline de tetrasodium diphosphate 0.02 M. L'échantillon du milieu naturel (250 ml), auquel est additionnée une aliquote de bactéries FLB, est incubé à température *in situ* (10 min. à 1h). Durant l'incubation, des aliquotes de 20 ml sont prélevées à 6 reprises et fixées au lugol alcalin (0.5 % en concentration finale). Un volume de 5 ml de chaque échantillon fixé est immédiatement filtré sur une membrane noire de porosité 0.8 µm, puis coloré par une solution de DAPI (1 µg/ml). A chaque prélèvement, le nombre de bactéries FLB au sein des protozoaires est mesuré. Cette estimation se fait en distinguant parmi les protozoaires les flagellés, les dinoflagellés et les ciliés. De plus, dans chacun de ces types de protozoaires, les organismes strictement hétérotrophes sont distingués des organismes mixotrophes qui peuvent avoir à la fois un comportement phototrophe et hétérotrophe. Cette distinction s'effectue en microscopie à épifluorescence grâce à l'utilisation de combinaisons de filtres d'excitation et d'émission permettant de visualiser les organismes ayant ingéré des bactéries FLB et contenant de la chlorophylle (organismes mixotrophes)(BOUVIER *et al.*, 1998). Pour chacune des six classes de protozoaires le nombre de bactéries FLB ingérées est porté en fonction du temps. Le taux d'ingestion par protozoaire et par heure I_{FLB} est calculé comme la pente à l'origine de cette relation. Le taux d'ingestion des bactéries I est calculé par la relation suivante qui prend en compte le rapport entre l'abondance des bactéries autochtones (N_{aut}) et l'abondance des bactéries FLB ajoutées (N_{FLB}) : $I = I_{FLB} (N_{FLB} + N_{aut})/ N_{FLB}$. Les mesures effectuées permettent ainsi de calculer pour chaque prélèvement le taux d'ingestion pour les six classes de protozoaires. Le tableau 1 reprend les gammes des valeurs de taux d'ingestion obtenus lors de sept campagnes réalisées en Meuse (de une à deux fois par mois entre mars et juin 1996). On observe des variations temporelles importantes des taux d'ingestion des bactéries par chacune des classes en raison de variations de la composition des populations de protozoaires et de la température. Clairement, des valeurs plus élevées sont observées pour les ciliés et dinoflagellés que pour les flagellés, ce qui est en accord avec les résultats de la littérature. Les taux mesurés en Meuse sont, par ailleurs, du même ordre de grandeur que ceux mesurés en lac par BLOEM *et al.* (1989) et CHRZANOWSKI et SIMEK (1990). Les résultats obtenus en Meuse montrent clairement que les taux de broutage des organismes mixotrophes ne sont pas significativement inférieurs à ceux du même type d'organismes strictement hétérotrophes. Vu leur abondance, les organismes mixotrophes contribuent pour une part significative (de 10 à 40 %) au broutage des bactéries. Une contribution importante des organismes mixotrophes au broutage des bactéries a déjà été mise en évidence dans d'autres milieux aquatiques (SCHNEPF et ELBRACHTER, 1992; LI *et al.*, 1996).

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Tableau 1 Taux d'ingestion minimum (I min) et maximum (Imax) des bactéries par les ciliés, dinoflagellés et flagellés, strictement hétérotrophes et mixotrophes.

Table 1 *Minimum ingestion rates (I min) and maximum ingestion rates (I max) of strictly heterotrophic and mixotrophic ciliates, dinoflagellates and flagellates.*

	I min (bact/protozoa.h)	**I max (bact/protozoa.h)**
Ciliés hétérotrophes	**5.1**	**82.5**
Ciliés mixotrophes	**5.3**	**79.5**
Dinoflagellés hétérotrophes	**5.1**	**112**
Dinoflagellés mixotrophes	**2.3**	**84.1**
Flagellés hétérotrophes	**0**	**27.5**
Flagellés mixotrophes	**0**	**27.0**

A partir des taux d'ingestion, de l'abondance des diverses classes de protozoaires et du contenu en carbone des bactéries, il est possible de calculer les flux de carbone transitant du compartiment bactérien vers les protozoaires. Ceux-ci peuvent être comparés aux flux de broutage calculés ci-dessus sur base de la méthode faisant appel au marquage radioactif à la thymidine. A la figure 2 sont portées, l'une en fonction de l'autre, les deux estimations de flux de broutage pour les campagnes où les deux types de mesures ont effectuées en parallèle. La figure 2 montre une excellente corrélation entre les deux estimations ($r^2 = 0.9$, $n = 7$), mais met en évidence que les valeurs obtenues à partir de la méthode FLB sont systématiquement un peu inférieures à celles obtenues par l'autre méthode. Comme l'ordonnée à l'origine de la corrélation est très faible, sa pente est caractéristique du rapport moyen entre les flux obtenus par la méthode FLB et ceux obtenus par la méthode thymidine; ce rapport vaut 0.68.

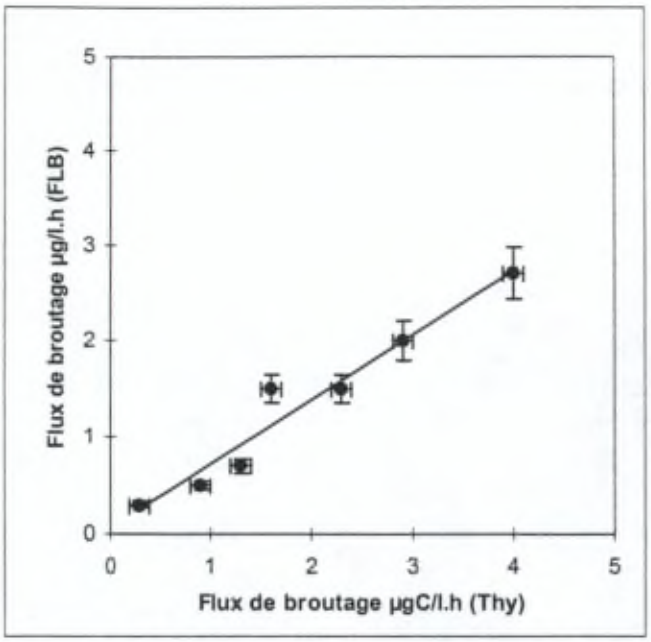

Figure 2. Flux de broutage des bactéries estimés à partir de la méthode FLB portés en fonction des flux de broutage estimés à partir de la méthode basée sur le marquage à la thymidine (Thy) sur les mêmes échantillons.
Droite de corrélation : $y = 0.68\ x - 0.03$ ($r^2 = 0.97$, $n = 7$).

Figure 2. Flux of bacterial grazing estimated by the FLB method plotted against flux of bacterial grazing estimated on the same samples by the method based on thymidine (Thy) labeling.
Correlation straight line : $y = 0.68\ x - 0.03$ ($r^2 = 0.97$, $n = 7$).

Il indique qu'en moyenne, les valeurs mesurées par la méthode FLB sont de 32 % inférieures à celles estimées par l'autre technique. Diverses raisons peuvent être responsables de cette différence. Dans le cas de la méthode FLB, les techniques microscopiques utilisées et les volumes filtrés n'ont pas permis de prendre en compte l'éventuel broutage des bactéries par des organismes de taille supérieure à 100 µm. Ce type de broutage est par contre pris en compte par la méthode de marquage radioactif. La présence de rotifères (par exemple, *Brachionus calyciflorus*) et de cladocères (par exemple, *Daphnia magna* et *Bosmina longirostris*) a été récemment mise en évidence en Meuse (JOAQUIM-JUSTO *et al.*, 1995; GOSSELAIN *et al.*, 1996). Pendant la période où notre comparaison a été effectuée en 1996 (entre mars et juin), les rotifères dominaient le zooplancton en Meuse; ils se sont développés à partir d'avril pour atteindre une abondance de 3500 individus par litre en juin (GOSSELAIN et al., 1998). Même si ces organismes sont surtout connus pour avoir un effet de prédation sur le phytoplancton, on ne peut exclure une contribution de leur part au broutage de bactéries non prises en compte par la méthode FLB. D'autre part, certains auteurs ont évoqué une possible sous-estimation du broutage par la méthode FLB pour des raisons méthodologiques. Même si l'utilisation de FLB, bactéries colorées et

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mortes, semble donner des estimations de taux d'ingestion acceptables dans certaines conditions (SHERR *et al.*, 1989), un broutage plus faible des bactéries colorées et mortes, par rapport à celui exercé sur des bactéries colorées mais vivantes, a été montré (LANDRY *et al.*, 1991; MONGER and LANDRY, 1992). Par ailleurs, certains auteurs (SIERACKI *et al.*, 1987) ont mis en évidence, au moment de la fixation de l'échantillon, un possible relargage de bactéries qui avaient été ingérées. Les trois raisons évoquées ci-dessus paraissent des explications plausibles à la différence des flux de broutage estimés en Meuse.

Les deux méthodes testées, dans cette étude, pour évaluer le broutage, bien que totalement indépendantes à la fois dans leur principe et dans les techniques expérimentales mises en oeuvre, sont très bien corrélées et donnent des estimations du même ordre de grandeur des flux de carbone transitant du compartiment bactérien vers les protozoaires. Ceci semble attester de la pertinence de ces deux méthodes. Néanmoins des différences sont observées entre les deux estimations de flux de carbone transitant des bactéries vers les protozoaires pour lesquelles un certain nombre d'hypothèses explicatives peuvent être émises. Si l'objectif est simplement d'évaluer le flux de bactéries consommées par broutage, la méthode basée sur le marquage à la thymidine apparaît nettement plus simple à mettre en oeuvre et ne pose pas certains problèmes méthodologiques pouvant entraîner une sous-estimation de ce flux lors de l'utilisation de la méthode FLB. Par contre, la méthode FLB permet une étude beaucoup plus complète du broutage, puisqu'elle donne des informations sur le type d'organismes principalement responsables de la consommation des bactéries. Elle a ainsi permis de mettre en évidence dans cette étude le rôle important des organismes mixotrophes. Elle présente, par contre, le désavantage de nécessiter de nombreuses énumérations microscopiques longues et fastidieuses.

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Lili rêva des baleines: elles étaient aussi hautes que les collines et plus bleues que le ciel. Elle chantaient d'une voix semblable au souffle du vent et bondissaient hors de l'eau en murmurant son nom: "Lili, Lili!"
Le chant des baleines . D. Sheldon & G. Blythe.