

## RAPID RESPONSE PAPER

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### Primary production, sinking fluxes and the microbial food web

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**Abstract**—The size distribution of pelagic producers and the size and trophic position of consumers determine the composition and magnitude of sinking fluxes from the surface communities in a simple model of oceanic food webs. Picoplankton, the dominant producers in the model, contribute little to the sinking material, due primarily to the large number of trophic steps between picoplankton and the consumers that produce the sinking particles. Net phytoplankton are important contributors to the sinking material, despite accounting for a small fraction of the total primary production. These net phytoplankton, especially those capable of nitrogen fixation, also dominate the fraction of the new production that is exported on its first pass through the food chain. The sinking flux is strongly determined by the community structure of the consumers and varies by an order of magnitude for different food webs. The model indicates that generalist grazers, zooplankton that consume a broad size spectrum of prey (including pico- and nanoplankton), play a critical role in exporting particles. The role of generalists that occasionally form swarms, such as thaliaceans (salps and doliolids), can be particularly difficult to assess. Short-term studies probably miss the relatively infrequent population blooms of these grazers, events that could control the average, long-term exports from surface oceanic communities.

#### INTRODUCTION

FLUX of non-living organic particles from the euphotic zone to the deep sea is known to be controlled by biological processes. The biological regulation results from the much greater rate of production of large, rapidly sinking particles by biological activities than by strictly physical or chemical processes (MCCAVE, 1984). A major goal of recent oceanographic research has been to predict the rate of mass flux from the euphotic zone, based on readily measured biological parameters such as primary productivity or phytoplankton biomass. Correlations between particle flux and primary productivity have been suggested in some studies (EPPLEY and PETERSON, 1979; SUESS, 1980; BETZER *et al.*, 1984), though they are less obvious in others (MARTIN *et al.*, 1987).

The purpose of this paper is to explore the consequences of one biological feature of pelagic communities that has received little attention, the influence of the structure of the pelagic food web on the resulting particle flux from the surface community. FROST (1984) has suggested that structural differences between food webs may lead to very different fluxes of organic matter out of the euphotic zone. We explore these food web relationships through a simple flow analysis (FASHAM, 1985; HANNON, 1985) in order to identify those organisms or interactions in the food web that are critical in determining flux. Such

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insights are valuable to identify key processes presently not receiving attention commensurate with their importance in regulating particle flux.

### *Biology of the model*

Our model explores the consequences of the size distribution of pelagic producers and the size and trophic position of consumers for the resultant particle fluxes from surface communities. Because the production in most oceanic food webs is increasingly recognized to be dominated by very small organisms (LI *et al.*, 1983; PLATT *et al.*, 1983), we selected the microbial food web described by AZAM *et al.* (1983) to represent trophic relationships among these microbial producers and their predators. We then modified that food web to include other interactions which may influence sinking fluxes. First, we ask what fraction of the material leaving the euphotic zone is derived from small vs large primary producers and whether this is in proportion to a producer group's contribution to primary production. Second, we use the model to clarify the importance of outputs from zooplankton that have different food sources: ones that use one, two, or several trophic levels as prey. As a special case, we consider the role of generalist consumers that simultaneously consume both producers and their protozoan consumers, using thaliaceans (salps and doliolids) as examples.

The flows in the model are expressed in terms of nitrogen, generally perceived to be the limiting nutrient in most oceanic regions. Although we use daily rates throughout the paper, we consider these webs to represent conditions averaged over annual to multi-annual periods. For one analysis, we also make the distinction between new (nitrate and newly fixed dinitrogen) and regenerated (ammonium, urea, dissolved organics, etc.) forms of nitrogen (DUGDALE and GOERING, 1967), and we examine the relationship between the particular size groups of autotrophs that contribute to new production and the resulting export of new production during its "first pass" through the food web.

In this paper, we base the flux models on generally accepted views of pelagic food webs and particle sinking scenarios. We make the following assumptions:

1. Only large particles, with consequently high potential sinking rates, can exit the euphotic zone. This means that the wastes or bodies of protozoa and algae, with the exception of some large algae or large colonies of smaller algae, as we explain below, decompose within the euphotic zone. We also ignore the vertical flux of suspended forms of nitrogen (e.g. dissolved organic nitrogen, picoplankton) by physical mixing along concentration gradients. The wastes, bodies or products of metazoan consumers are the dominant source of sinking particles because these are large enough to exit the system rapidly before decomposing.

2. The output by flux producers is dependent on their trophic level: the further removed from the producers, the smaller the consumer's contribution of sinking materials because of the losses of materials through preceding trophic levels (trophic efficiency arguments such as those advanced by RYTHER, 1969).

3. To simplify calculations and to use a common convention, we assume that the food web is in steady state, i.e. that over long periods, populations neither increase nor decrease.

Microbially dominated, oligotrophic systems are often assumed to be at steady state (GOLDMAN *et al.*, 1979; HAYWARD *et al.*, 1983). However, recent analyses of time-series data from the Sargasso Sea (JENKINS and GOLDMAN, 1985) and models of nutrient inputs into the mixed layer (KLEIN and COSTE, 1984) indicate that production in these

environments may be dominated by spatial and temporal pulses on a variety of scales. Although steady-state food webs such as ours will not accurately reflect trophic relationships over short time intervals (hours to weeks or even months), these steady-state webs still may reflect the mean flows of materials between groups of organisms, when averaged over long time intervals (annual to multi-annual), where steady-state assumptions may be more realistic. Thus, we view our model as a simplified approach to fluxes over large spatial and long time scales, and we discuss the need to modify such a stance for more realistic short-term and regional predictions.

#### METHODS

The basic modeling strategy is to create food webs as representations of predator-prey relationships and analyse the movement of materials through those webs with standard network analysis techniques. The purpose of the analysis is to determine the relative importance of different size categories of primary producers in contributing to the outputs of particles from the euphotic zone. Thus the analysis is particularly concerned with relationships that redistribute material in the critical, first few trophic steps, and with processes that lead to particles sufficiently large to settle from the zone.

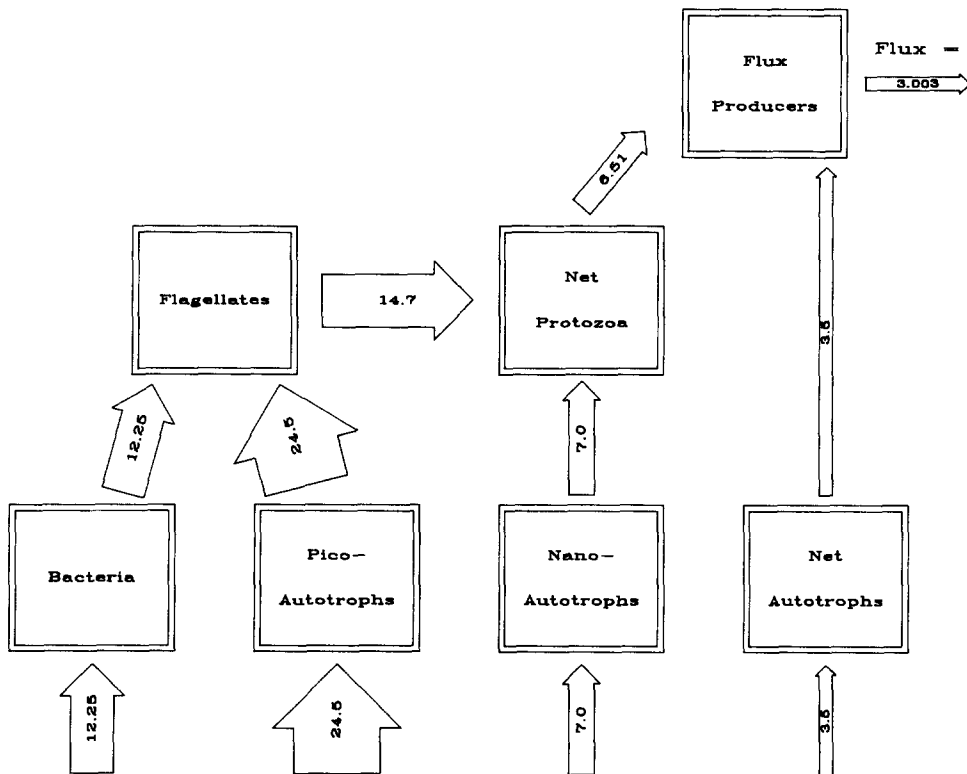


Fig. 1. The basic food web. Modified from AZAM *et al.* (1983). the numbers inside the arrows are nitrogen flows in  $\text{mg N m}^{-2} \text{day}^{-1}$ . The widths of the arrows are in proportion to the magnitude of the flow.

The “basic microbial food web”, incorporating aspects of AZAM *et al.*'s (1983) model and our changes to the model, is illustrated in Fig. 1. The food web contains three groups of primary producers, distinguished by size: picoautotrophs (cells  $\leq 2 \mu\text{m}$ ), nanoautotrophs (cells  $2\text{--}20 \mu\text{m}$ ), and net-autotrophs (cells  $>20 \mu\text{m}$ ) and one group of secondary producers, the bacteria. Consumers, as in the model of AZAM *et al.* (1983), are predicted by simple, size-related grazing rules (predators are 5–10 times larger than prey). Thus, bacteria and picoautotrophs are eaten by flagellates. Flagellates and nanoautotrophs are eaten by ciliates, and the ciliates and net-autotrophs are eaten by metazoan zooplankton. We rename the ciliate category “net-protozoa” to indicate that the entire range of large protozoa, including sarcodines, are also represented. AZAM *et al.* (1983) carry the food web farther, through a series of higher grazers. For our analyses, we redefine the first level of metazoan zooplankton as those capable of producing sinking material, which could include feces, bodies, or wastes (including those considered “marine snow”) and truncate the food web at that point. Higher trophic levels can be neglected in our simple analysis because the basic redistribution of producer materials has already been established by the first zooplankton step in the model, and knowledge about this redistribution is the goal of our study. Furthermore, a more sophisticated analysis of the products of zooplankton is not required, nor is the loss of sinking zooplankton products by decomposition or detritivory, because major redistribution of producer nitrogen likely does not occur in such processes.

All of the flows in the food webs are considered in terms of average daily nitrogen fluxes ( $\text{mg N m}^{-2} \text{ day}^{-1}$ ) and are given for particulate matter only. Only flows between living organisms are expressed as direct connections in the food webs. Primary incorporation of nitrogen into phytoplankton and bacteria, as either nitrate, ammonium, dissolved organic nitrogen (DON) or dinitrogen gas ( $\text{N}_2$ ) is a constant and is considered an exogenous import into those compartments. Excretion of ammonium, urea or DON by grazers is treated as dissipation. The recycling of dissipations from grazers back to the producers is implicit in this formulation of the food web. The production of sinking material by the larger grazers and producers, either through the direct loss of biomass via mortality or through the production of waste products (e.g. feces, mucus wastes, moults) is the only export from the food webs.

Inputs of nitrogen to the various producers were selected to reflect the current view of the dominance of the smallest size classes of producers. Because we are attempting to model a fairly typical mesotrophic or oligotrophic oceanic environment, we set primary production by phytoplankton at  $35 \text{ mg N m}^{-2} \text{ day}^{-1}$  (approximately  $200 \text{ mg C m}^{-2} \text{ day}^{-1}$ ). The exact primary production value is not important because we are mostly interested in differences between webs at the same production rate. Of that production, 70% is by the picoautotrophs, 20% by nanoautotrophs, and 10% by the net-autotrophs (Fig. 1). This size division of the autotrophic production is within the range of published values for oceanic systems (LI *et al.*, 1983; PLATT *et al.*, 1983). The bacterial secondary production rate is set at 50% of the picoautotroph production rate. This bacterial production rate of  $12.25 \text{ mg N m}^{-2} \text{ day}^{-1}$  also falls within the range of published values, especially considering the recent data on the use of inorganic nitrogen by bacteria (WHEELER and KIRCHMAN, 1986). All of the daily production is assumed to be lost via consumption or sinking (see below).

Rules for grazers in the model are set as follows for the “basic food web”. First, all of the daily production is consumed by two types of protozoan and one type of metazoan

grazer. The large protozoan grazers (net-protozoa) eat the small microflagellate grazers as well as their nanoplanktonic algal prey. The metazoan grazers (flux producers) eat the netplankton sized organisms, net-autotrophs and net-protozoa. Second, the smallest grazers, the microflagellates, have the highest growth efficiencies (40%, FENCHEL, 1982) to emphasize the dominance of the smallest size categories in the food web; however even the net-protozoa have a growth efficiency of 30% to indicate the close coupling of the lower trophic levels. These protozoan growth efficiencies are deliberately set at the high end of the published range (NEWELL and LINLEY, 1984; VALIELA, 1984) to accentuate the flow of production from small primary producers up the trophic web. Third, we assume that flux-producing zooplankton convert 30% of their ingested food into wastes that can sink (VALIELA, 1984). Obviously our choice of the zooplankton conversion factor will determine directly the magnitude of sinking losses from the food webs. However, information about the exact proportion of production that sinks from the euphotic zone is not as important as information about the relative sources of exports from the different webs, as we stressed above.

In addition to the basic food web, we also consider some alternative food webs that have been discussed in the literature (Table 1). In the first variation, called the "lean" food web, the conversion efficiencies of the protozoans are reduced to 20 and 10%, reflecting possibly higher metabolic rates or low assimilation efficiencies, and we use variable conversions of ingested material into sinking nitrogen (VALIELA, 1984), depending on whether the prey are autotrophic or heterotrophic (Table 1). The second variation of the basic web, called the "algal flux" web, sustains losses of nitrogen through the direct sinking of living algal cells from the euphotic zone (Fig. 2). Such losses of large cells or colonies of smaller cells are now well documented, especially in particular seasons or geographic regions (SMETACEK, 1985). The third set of variations involves the addition of new grazing connections into the food web. In the "2-level food webs", the flux-producing grazers feed at different intensities on net- (net-protozoa and net-autotrophs) and nano- (flagellates and nanoautotrophs) sized prey (Fig. 3). Net-protozoa are also able to feed on picoplankton-sized prey. We chose two different intensities of "two-level" grazing, 20 and 50%. These intensities indicate the fraction of the grazer's diet that comes from the alternative food sources (see Table 1). In the "salp" food webs, we

Table 1. Summary of the conversion factors used in the "basic web" and the modifications to the "basic web". Each modification is unique and only applies to that web

Web	Modification
Basic web	Flagellates trophic efficiency = 40%, net-protozoa trophic efficiency = 30%. For flux-producers, 30% of ingested prey is converted into sinking material.
Lean web	Flagellates trophic efficiency = 20%, net-protozoa trophic efficiency = 10%. For flux-producers, 30% of algal prey is converted into sinking material, 10% of animal prey into sinking material.
Algal flux	50% of the net-autotroph production sinks out of the system.
20% 2-Level	20% of the food of each grazer derived from prey one size smaller than traditional prey (except flagellates who have no smaller prey).
50% 2-Level	Same as 20% 2-level, except 50% of diet derived from smaller prey.
10% Salp	10% of the production from all compartments except flux-producers is grazed by salps.
50% Salp	Same as 10% salp, except that 50% of production is grazed by salps.

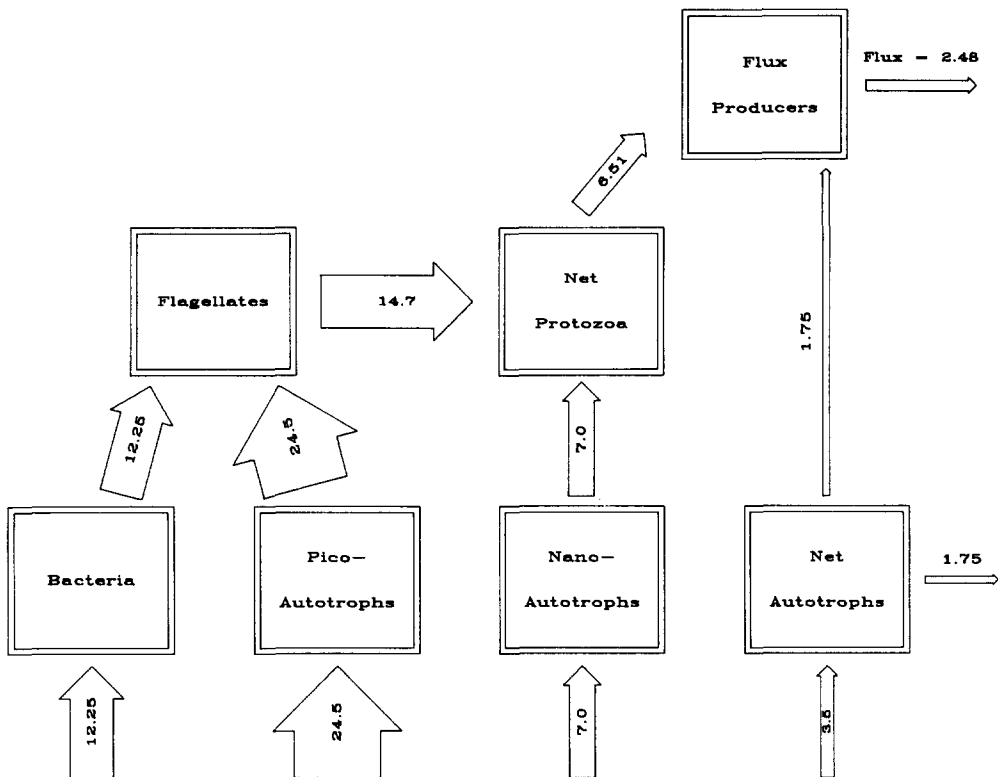


Fig. 2. The algal flux food web. Similar to the basic web, this web adds a direct loss of net phytoplankton cells through sinking. The widths of the arrows are in proportion to the magnitude of the flow.

add a new grazer, typified by thaliaceans and larvaceans, that can feed on a wide range of prey sizes, including the picoplankton (Fig. 4). For the “salp” grazer, we assume that they can remove all bacteria, primary producers and protozoan grazers. Such completely indiscriminant feeding is unlikely, as discussed below, but is used to examine the role of a generalist consumer. We set two different levels of “salp” feeding, 10 and 50%, which reflect the fraction of the primary or secondary production of each group that is grazed by “salps” (see Table 1).

The flows of nitrogen through the food web are analysed using the flow analysis techniques described by ULANOWICZ (1984) and HANNON (1985). These techniques are basically flow accounting procedures that describe and summarize the movement of material through a food web. For this analysis we use portions of the NETWRK3 package developed by ULANOWICZ (1984) and translated into PASCAL by J. J. KAY (personal communication). We use only the flow analysis and input–output routines. The flow analysis routine results in matrices of flows between all compartments in the food web, by both direct and indirect routes. The input–output routine examines the fate of a single unit of input into a compartment. These routines allow us to calculate the following parameters from the food webs:

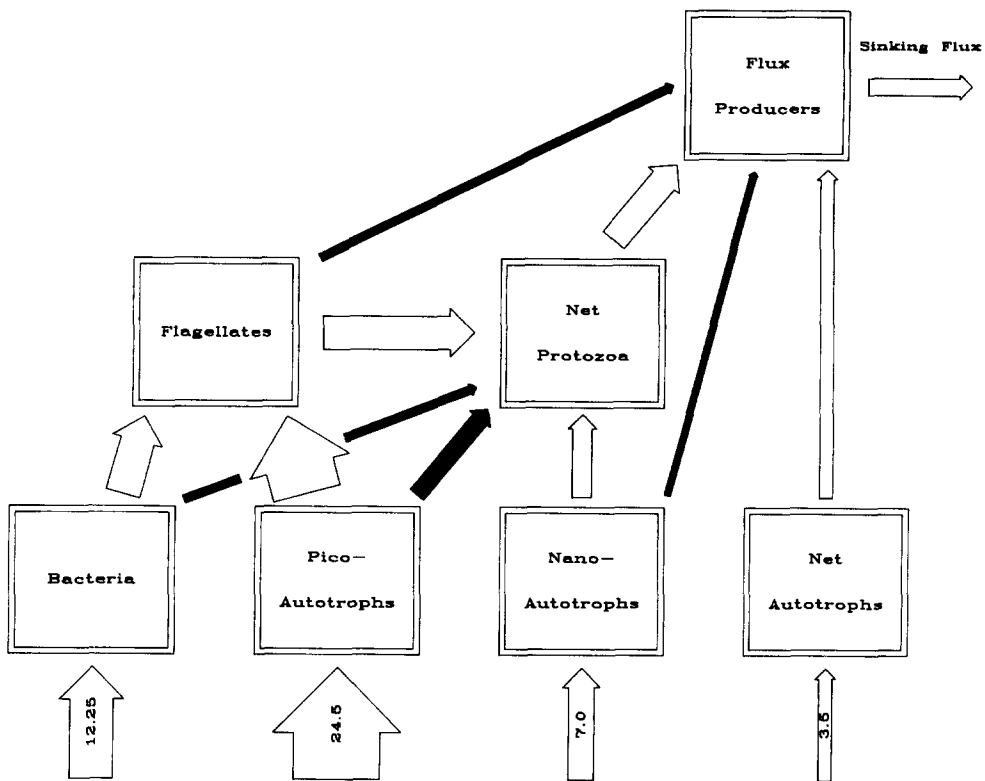


Fig. 3. The two-level food web. A modification of the basic web, expanding the size range of prey ingested by the grazers. The widths of the arrows are in proportion to the flows for the 20% two-level food web.

#### *Extended diets for all of the grazers*

Extended diets show the fraction of the nitrogen ingested by a grazer that is derived from another group of organisms, by all routes, direct and indirect. For our purposes, we concentrated on the primary producers as the sources of the materials. By comparing grazer utilization of nitrogen originally incorporated by each of the algal groups, we could determine the relative contribution of each size class of producer to the sinking material.

#### *Fates of the nitrogen entering different size classes of producers*

The input-output analysis details the subsequent fate of the exogenous inputs. The probability that an inorganic nitrogen atom, incorporated into an algal group, would export the system in the same day was calculated from the fraction of the input into an algal group that was exported as sinking material.

#### *Fates of new production by the different primary producers*

We assume that the new production rate (i.e. production based on nitrate or newly fixed dinitrogen) is the same as the rate of loss of material through sinking exports. We apportion that new production to the different primary producers in two different ways

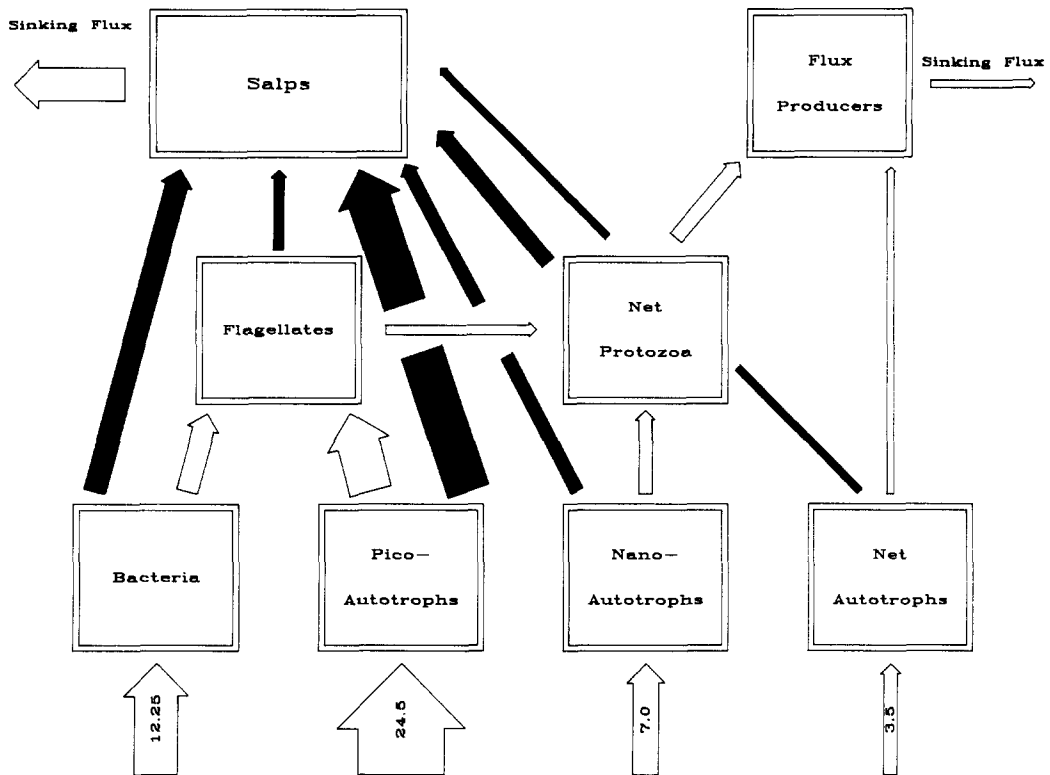


Fig. 4. The salp food web. A modification of the basic web, which adds a new grazer, typified by salps, that can ingest food from the entire size range of organisms. The widths of the arrows are in proportion to the flows for the 50% salp food web.

and subsequently determine what we term "direct exports of new production". A direct export is the fraction of the new production by an algal group that is exported in the first pass through the food web; the remainder of the export is based on regenerated nitrogen sources. The first case involves a proportional allocation of new production to each group, i.e. the percent production based on new nitrogen sources is the same for each algal group. In the second case, we assume that new production by net-autotrophs is 50% of their total production (i.e. 10%/2 or 5% of total phytoplankton production) and divide the remainder of the new production proportionally between the pico- and nano-autotrophs. Such an assumption appears justified because CARPENTER (1983) suggested a global average nitrogen fixation rate of  $1.5 \text{ mg m}^{-2} \text{ day}^{-1}$ , and *Trichodesmium* and other netplankton producers account for nearly all of this. This fixation rate is about 50% of the total nitrogen assimilation by the netplankton in our food webs.

#### *Special case: Thaliaceans as generalist grazers*

To clarify the role of a generalist grazer, and one that is only moderately abundant under most circumstances, we calculate the average contribution of thaliacean (salp and doliolid) wastes to the exports from the euphotic zone. For this exercise we use the only available data set from the literature with the appropriate temporal and spatial resolu-



tion. We analyse the frequency distribution of thaliacean abundance in the California Current from extensive zooplankton net collections, the CalCOFI series made between 1949 and 1958 (BERNER, 1967). We analyse abundances of two of the most common thaliaceans, the doliolid *Doliolletta gegenbauri* and the salp *Salpa fusiformis* from quantitative plankton samples collected between Southern Baja California and the California–Oregon border, a total of over 1400 samples (BERNER, 1967). A sinking export of nitrogen due to salp grazing and the resultant fecal pellet production are calculated using published clearance rates for these species (summary from ALLDREDGE and MADIN, 1982; DEIBEL, 1982; ANDERSEN, 1985) and published PON concentrations for coastal environments (SHARP, 1983).

## RESULTS

### *Role of different producers in contributing to flux*

Nitrogen incorporated into phytoplankton and bacteria has two potential fates: (1) Regeneration into dissolved reduced forms such as ammonium, urea and dissolved organic nitrogen (DON). These dissolved forms remain in the euphotic zone and are not explicitly tracked in our model. (2) Export from the euphotic zone as sinking particulate organic nitrogen (PON).

For the basic food web, the probability that a nitrogen atom will be exported is highest for nitrogen incorporated into net phytoplankton, and relatively small for nitrogen assimilated into bacteria and picoautotrophs (Table 2). The difference in export probability clearly results from the short food chains, i.e. those starting with large producers have fewer steps to the zooplankton that cause the flux. The probability that netplankton nitrogen will be exported remains constant for all of the different food webs, except for the “algal flux web” where half of the large algal cell production sinks out of the euphotic zone and the probability of net phytoplankton nitrogen exports rises to 65% (Table 2). The probability that nitrogen inputs into nanoplankton, picoplankton and bacteria will be exported varies with the different food webs. In webs with generalist zooplankton grazers such as salps, these grazers can ingest smaller food items and package them into sinking particles, consequently increasing the probability of export of the small producers. The “lean” food web has the lowest probabilities of the export of small phytoplankton, because each of the several steps leading to the zooplankton conserves even less of the nitrogen than the basic web.

For the basic web, net phytoplankton are the source of 35% of the nitrogen export (Table 3), despite accounting for only 10% of the primary production and 7.4% of the

Table 2. The probability that nitrogen incorporated into each group will ultimately be exported as sinking material in that time period

Web	Bacteria	Picoautotrophs	Nanoautotrophs	Net-autotrophs
Basic	0.036	0.036	0.090	0.30
Lean basic	0.005	0.005	0.024	0.30
Algal flux	0.036	0.036	0.090	0.65
20% 2-Level	0.052	0.052	0.115	0.30
50% 2-Level	0.081	0.081	0.195	0.30
10% Salp	0.070	0.070	0.111	0.30
50% Salp	0.189	0.189	0.195	0.30

Table 3. *Origins of the sinking material, the percent contribution of each algal group and bacteria to the sinking nitrogen*

Web	Bacteria	Picoautotrophs	Nanoautotrophs	Net-autotrophs
Basic	15.0	29.0	21.0	35.0
Lean basic	5.0	9.9	14.2	70.9
Algal flux	10.4	20.9	14.9	53.8
20% 2-Level	16.8	33.7	21.5	28.0
50% 2-Level	18.4	36.7	25.4	19.5
10% Salp	19.5	39.0	17.7	23.9
50% Salp	24.7	49.5	14.6	11.2

total nitrogen incorporation (phytoplankton + bacteria). In the lean food web, net phytoplankton constitute an even larger fraction of the exports (70%). Netplankton are also a large fraction in the web with direct exports of algal cells. As the grazers become more generalized, the relative importance of net phytoplankton decreases. In the "50% salp" food web, the flux contribution by each algal group is approximately in the same proportions as their primary contribution to nitrogen assimilation.

The nitrogen exports, as a percentage of the total primary production of  $35 \text{ mg m}^{-2} \text{ day}^{-1}$ , are presented for different types of food webs in Table 4. The absolute magnitude of the flux and its fraction of the total production should be interpreted cautiously because they are sensitive to the assumptions of the model. Under natural conditions, long-term average rates of new production would be dictated largely by the rate of nitrate input into the euphotic zone (DUGDALE and GOERING, 1967; EPPLEY and PETERSON, 1979). Consequently, there is only one steady-state rate of nitrogen export for any given system. However, the differences in exports between food webs, at essentially the same parameter values can indicate patterns caused by the structure of the food web. The "basic" web exports 8.6% of the primary production. The percentages for the other webs vary from 3.4 to 26.7%. As expected, the percent flux is lower for the "lean" web. The sinking of large algal cells results in a larger flux. The webs with more generalized grazers also export a higher fraction of the production.

#### *Partitioning of new nitrogen among producers*

If we assume that some fraction of the nitrogen taken up by each algal group is new, we can follow the fate of this new production in the food web. For the first of these partitioning calculations, we neglect nitrogen fixation and assume that all algal groups take up the same proportions of new and regenerated nitrogen and arbitrarily make that

Table 4. *Sinking fluxes as a percent of the total nitrogen input of  $35 \text{ mg N m}^{-2} \text{ day}^{-1}$ . See text for qualifications*

Web	% Exported
Basic	8.6
Lean basic	3.4
Algal flux	12.1
20% 2-Level	10.7
50% 2-Level	15.4
10% Salp	12.5
50% Salp	26.7

fraction equal the percent exports for each web. The magnitude of the new fraction does not affect the results. Under these assumptions, the percent direct exports for each web is similar to the pattern of total nitrogen exports (Table 5). In all webs, the net phytoplankton dominate these direct exports, because netplankton nitrogen is exported at the highest rates.

Nitrogen fixation is also a source of new production, although the rates of nitrogen fixation generally have been considered to be low. However, most of the nitrogen fixation may occur in the large, netplankton fraction and thus the export rates of this newly fixed nutrient will be strongly affected by the fates of the large cells. The results, under the assumption that nitrogen fixation accounts for 50% of the production by the netplankton, show the central role of these large cells in removing new production (Table 5). The direct exports of new production are up to 30 times higher when half of the netplankton production is via nitrogen fixation than when it occurs under the equal allocation scheme, discussed above. These exports reach a maximum in the "lean-basic" web, in which 92% of the new production is directly exported.

### *Thaliacean exports*

Our analysis of thaliacean abundance patterns from the published CalCOFI data (BERNER, 1967) demonstrate the very patchy distribution of these generalist grazers (Fig. 5). Most samples contain fewer than 0.05 specimens  $m^{-3}$ , and 96–97% of these individuals are found in the 5–7% of the samples with the highest abundances. The mean abundances of these two species, averaged over all stations, are 6.3  $m^{-3}$  for *D. gegenbauri* and 0.4  $m^{-3}$  for *S. fusiformis*. A sinking export of nitrogen due to thaliacean grazing and the resultant fecal pellet production can be calculated for a typical coastal PON concentration of 10–50  $\mu g N l^{-1}$  (published values range from 1 to 420  $\mu g N l^{-1}$ , SHARP, 1983) from published thaliacean filtration rates (summary from ALLDREDGE and MADIN, 1982; DEIBEL, 1982; ANDERSEN, 1985) and using a 70% assimilation efficiency. This fecal flux estimate ranges from 0.3 to 1.4  $mg N m^{-2} day^{-1}$  for *D. gegenbauri* and from 0.5 to 2.4  $mg N m^{-2} day^{-1}$  for *S. fusiformis*.

Table 5. Direct exports of new production. The first two columns consider nitrate as the only source of new production. The second two columns consider both nitrate uptake and dinitrogen fixation into netplankton. For each web, we present the fraction of the new production in that time period that is exported and the percentage of these direct exports that involved the net phytoplankton. The new production for the nitrate-only case was allocated to each algal group as the same percent of the total production by that group. For the dinitrogen case, 50% of the production by net phytoplankton is assumed to be new production by nitrogen fixation. See text for details

Web	Nitrate only		Nitrate and dinitrogen	
	Fraction direct exports	% Netplankton	Fraction direct exports	% Netplankton
Basic	0.073	41	0.195	90
Lean basic	0.032	75	0.919	>99
Algal	0.108	60	0.301	89
20% 2-Level	0.089	34	0.180	78
50% 2-Level	0.126	24	0.175	56
10% Salp	0.101	30	0.169	70
50% Salp	0.201	15	0.211	27

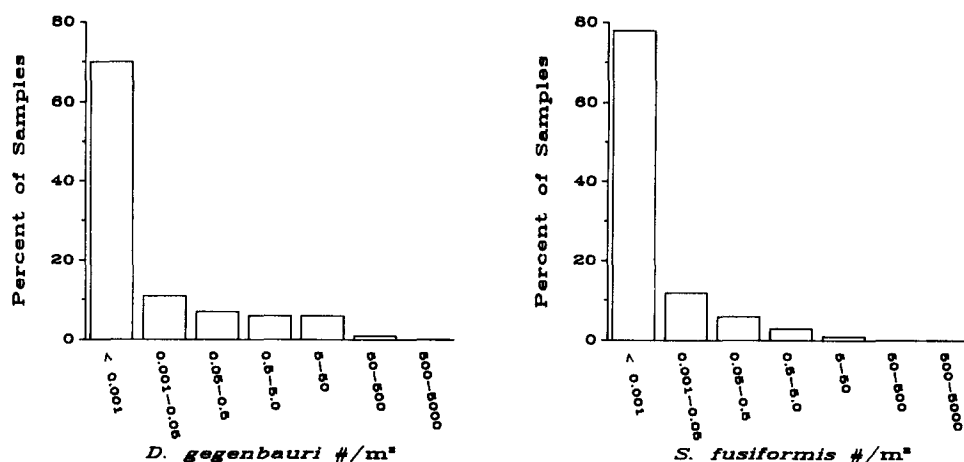


Fig. 5. The frequency distribution of *Doliolletta gegenbauri* and *Salpa fusiformis* in the California Current (data from BERNER, 1967). Shows the percent of the CalCOFI samples with salp abundances of each density.

#### DISCUSSION

The results of the network analysis of the AZAM *et al.* (1983) microbial food web, as modified here, are surprising and perhaps counter-intuitive. Although picoautotrophs and bacteria dominate the primary production in oceanic ecosystems, our model suggests they are relatively unimportant as a source of sinking material. Net plankton are more important than their production implies, primarily because of the few trophic steps (0-1) between large algal producers and zooplankton that generate sinking material. This result indicates that vertical movements of large algal cells, and the community interactions between large algal cells and their grazers, are important in determining the spatial and temporal variation of sinking losses from surface communities. The sinking fluxes in highly productive areas with sizeable netplankton populations are often dominated by either the direct sinking of algae or the wastes of large herbivores (STARESINIC *et al.*, 1978, 1983; SMETACEK, 1980, 1985; SKJOLDAL and WASSMAN, 1986). However, the present analysis suggests that, even in more oligotrophic, pico- and nanoplankton dominated environments, the interactions of large algae with their consumers are very important in determining the exports from the euphotic zone. Furthermore, the sinking of portions of the netplankton populations, even in oceanic environments, can make substantial contributions to particle flux.

The critical role of large algal cells in assimilating exportable nitrogen is a key result of our model, and one readily predicted from size considerations between plants and their consumers. Very recently, GOLDMAN (in press) has suggested that new production in oligotrophic oceans may be dominated by sporadic patches of large algal cells which grow on nutrients mixed into the euphotic zone during short-lived, local events. These results come at a time when researchers are emphasizing the importance of the smallest primary producers, particularly the picoplankton, in pelagic communities. Thus, little attention is being directed towards the large, relatively rare, but individually biomass-rich cells disproportionately important in generating the particle flux. For example, estimates of

phytoplankton biomass often are not size-fractionated, and thus the proportion of these large cells to the total phytoplankton stock is not usually known. Furthermore, samples of phytoplankton stocks are usually made from aliquots of a few tens to hundreds of milliliters, volumes much too small to determine accurately the abundance of very large algal cells, or aggregates of cells which may occur in abundances from a few individuals per liter to a few per cubic meter in oceanic settings (SEMINA and TARKHOVA, 1972; ALLDREDGE and SILVER, 1982). This model indicates that an increase in the study of the relatively rare, large algal cells is warranted to understand the biological processes that generate flux.

The large algae also play prominent roles in the direct export of new production. When nitrate or dinitrogen is assimilated by a large cell, it is much more likely to be removed by the grazer chains utilizing that cell than when incorporated into very small cells. Large organisms such as *Trichodesmium* (CARPENTER, 1983) and the prokaryote-diatom associations (MARTINEZ *et al.*, 1983) are responsible for much of the oceanic nitrogen fixation. Since these large cells are comparatively rare, changes in their populations may be difficult to detect and the major roles of these cells in new production cycles therefore difficult to document. Furthermore, these organisms often are clumped into tufts of floating aggregates, making average cell densities especially difficult to determine.

The fraction of the sinking material derived from bacteria and from each of the algal groups varies with each web (Table 3). These differences in the ultimate sources of the sinking nitrogen lead to dramatic differences in the composition of the detrital material. In the basic web, the bacteria, pico- and nanoautotroph nitrogen is exported indirectly, via grazing by the flux producers on net-protzoa (Fig. 1). Net-autotrophs are the source of all of the detrital algal material in that web. In the 2-level and salp webs, where the flux producers directly graze the smaller autotrophs, the detrital algal material becomes more diverse. The sinking material in the salp web contains nitrogen derived directly from each algal group as well as indirectly, through grazing on the two protozoan groups (Fig. 4). These compositional differences will affect the distribution of chemical signatures in the sinking material, such as pigment degradation products and organic molecules particular to phytoplankton or zooplankton (e.g. WAKEHAM and CANUEL, in press). The diets of the flux-producing grazers also may determine the nutritional value of sinking material and consequently affect the detrital communities below the euphotic zone.

In the calculation of algal exports via consumer grazing, our model does not specify the type of particle produced by the consumer. Although the most studied exports by grazers from the euphotic zone are fecal pellets, other particles are also known. In an increasing number of studies, amorphous wastes, sometimes called "fecal matter" or "marine snow", are found to dominate the sinking material (BISHOP *et al.*, 1978, 1980; FOWLER and KNAUER, 1986). Although the origins of the amorphous material are usually not known, many biological sources have been suggested: exudates and decay products of phytoplankton, bacterially cemented particles, zooplankton exudates (e.g. mucus, molts) decomposed feces of zooplankton and fish, etc. (ALLDREDGE, 1986).

Although we presently cannot predict the rate at which such amorphous materials would be formed and exit the euphotic zone, our calculations may still accurately represent sources of this material if our food webs correctly portray the biological connections and flows of materials. For example, the exported materials from zooplankton are not specified and could well be mucus, along with some fecal wastes. So long as

the consumers utilize the plants in the proportion represented by our food webs, and so long as only the zooplankton export materials, then our predictions regarding the phytoplankton sources of nitrogen should be accurate. Adjustments to our model would be required, on the other hand, if exportable materials were produced lower on the food chain (other than by large algae, which we did consider), if the trophic level represented by "flux producers" consisted of several categories with differential feeding habits and export rates, and so on. We already know, for example, that foraminifera, a common netplankton protozoan, can produce substantial amounts of mucus in the water column and the mucus can be a moderate contributor to sinking fluxes (GOWING and SILVER, unpublished data). However, in this initial model we have sought to examine the simplest and most general cases, and we leave further adjustments for the future.

Our network analysis indicates that large annual exports from microbially dominated systems are only possible when generalist grazers are present (Table 4). FROST (1984) has suggested that the persistence of generalist grazers, such as salps, would cause an oligotrophic system to run down due to the low rates of diffusion of new nitrogen into the euphotic zone. However, many communities generally considered to be oligotrophic or mesotrophic (thus dominated by very small producers) are characterized by having new production rates being 15–30% of the total production (EPPLEY and PETERSON, 1979). This implies that, on average, exports from these systems are likewise 15–30% of the production (EPPLEY and PETERSON, 1979). PLATT and HARRISON (1985) have suggested that the oligotrophic Sargasso Sea may have a seasonal new production rate and, by implication, particle export that is 30% of the total. How could these oceanic systems, likely dominated by microbial food webs, export so much material?

Oceanic communities could produce relatively large amounts of sinking material and maintain long-term steady state by at least two routes. First, generally oligotrophic systems could actually represent a patchwork of both nutrient-poor and nutrient-rich habitats. JENKINS and GOLDMAN (1985) have suggested that nutrient inputs into the Sargasso Sea may be episodic, on a variety of scales, and lead to local microcosms of eutrophic activity. These patches could produce netplankton-enriched communities which directly export large algae [especially if, as GOLDMAN'S (in press) model suggests, they are located at the base of the euphotic zone] or support large herbivores which, as we discussed above, could produce large amounts of sinking material. Second, occasional swarms of generalist grazers may bring about large, pulse-like fluxes.

#### *Generalist consumers—salps and other thaliaceans*

The importance of different groups of zooplankton and nekton as contributors to sinking fluxes will depend on their access to food and on the sinking rate of their wastes. Among the major groups of zooplankton, the thaliaceans—salps and doliolids—are examples of consumers that can play a critical role as mediators of detrital flux. First, the thaliaceans can ingest particles in the pico- and nanoplankton size range although they are less efficient at trapping the smallest picoplankton than the larger nanoplankton (HARBISON and McALISTER, 1979; SILVER and BRULAND, 1981; ALLDREDGE and MADIN, 1982; MULLIN, 1983; ANDERSEN, 1985). Further, some salp species inhabit and appear adapted to the areas of low productivity where small producers dominate (HARBISON *et al.*, 1986). [Other species occur in richer shelf or upwelling systems (BERNER, 1957; DIEBEL, 1985).] In our model, we assume removal of all size fractions, but it is likely that the picoplankton (especially the bacterial fraction) is not removed efficiently. Second,

many salp species produce very large pellets, with sinking rates up to 2 km day<sup>-1</sup> (BRULAND and SILVER, 1981; ISEKI, 1981; MADIN, 1982); doliolids and some small salps produce pellets that sink at lower rates, tens to hundreds of meters per day, but still sufficiently high to exit the euphotic zone usually within a day of formation (POMEROY and DEIBEL, 1980; BRULAND and SILVER, 1981). (In our model, the effects of such rapid sinking are not important because we assume that all exportable wastes are lost from the euphotic zone within a day of their production.) Third, salps and doliolids occasionally occur in dense and unpredictable swarms, dominating the zooplankton communities at these times, although their usual abundance is much lower (BERNER, 1967; ALLDREDGE and MADIN, 1982).

For two of the more common thaliacean species in the California Current region, we calculate the average contribution of the wastes of each species to the exports from the euphotic zone. These estimates of mean fecal nitrogen flux range between 0.3 and 2.4 mg N m<sup>-2</sup> day<sup>-1</sup>. Assuming an average sinking organic carbon flux for the California Current of 115 mg C m<sup>-2</sup> day<sup>-1</sup> (MARTIN *et al.*, 1987) and a C:N ratio of 7 for phytoplankton, the average nitrogen flux would be 16.4 mg N m<sup>-2</sup> day<sup>-1</sup>. Thus, on average over the year and for a large area like the central California Current, these two thaliacean species could account for up to 22% of the nitrogen exports from the euphotic zone. However, at any one time and location the normal salp contribution to flux is quite small and the total effect of such organisms would be difficult to assess from local studies. Although we have chosen these two thaliaceans as extreme examples of patchy, generalist grazers, the abundances of most other grazers are also variable on a range of temporal and spatial scales. These fluctuations in the grazer's community structure will necessarily cause significant variations in both the quantity and composition of sinking material.

#### CONCLUSIONS

Picoplankton are rarely a source of sinking particles; rather they are involved primarily in regeneration cycles, even in systems where they are the dominant producers. In contrast net phytoplankton are considerably more important contributors to the sinking material than their relatively minor fraction of the total production implies.

Both the quantity and composition of sinking material are strongly determined by the community structure of the consumers. The sinking flux varies by an order of magnitude for different conceptualizations of the microbial food web.

The fraction of the new production directly exported on its first pass through the food chain is also variable and dependent on food web structure. Netplankton are often the dominant source of these direct exports. Nitrogen fixation into netplankton appears to have a significant impact on the direct removal of new production, because of the high contribution of the large cells to exported materials.

To predict the time-varying response of ocean systems to nutrient inputs, an understanding of the population dynamics of both large algae and generalist grazers is most important.

Pelagic ecosystems with extremely patchy populations of generalist grazers, like thaliaceans, may be in steady state over annual or longer time periods and large spatial scales, but locally almost always out of equilibrium. Measurements in these systems as most frequently seen (i.e. without the grazer), give misleading data in terms of annual averages because they miss important, but infrequent, events.

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## REFERENCES

- ALLDREDGE A. L. (1986) Aggregate dynamics: Biological processes which form, alter and destroy aggregates in the ocean. In: *Aggregate dynamics in the sea: Workshop report*, A. L. ALLDREDGE and E. O. HARTWIG, editors, American Institute of Biological Sciences, Washington D.C., pp. 109–130.
- ALLDREDGE A. L. and L. P. MADIN (1982) Pelagic tunicates: unique herbivores in the marine plankton. *Bioscience*, **32**, 655–663.
- ALLDREDGE A. L. and M. W. SILVER (1982) Abundance and production rates of floating diatom mats (*Rhizosolenia castracanei* and *R. imbricata* var. *shrubsolei*) in the eastern Pacific Ocean. *Marine Biology*, **66**, 83–88.
- ANDERSEN V. (1985) Filtration and ingestion rates of *Salpa fusiformis* Cuvier (Tunicata: Thaliacea): effects of size, individual weight and algal concentration. *Journal of Experimental Marine Biology and Ecology*, **87**, 13–29.
- AZAM F., T. FENCHEL, J. G. FIELD, J. S. GRAY, L. A. MAYER-REIL and T. THINGSTAD (1983) The ecological role of water-column microbes in the sea. *Marine Ecology Progress Series*, **10**, 257–263.
- BERNER L. D. (1957) Studies on the Thaliacea of the temperate northeast Pacific Ocean. Ph.D. Thesis, University of California, Los Angeles, 144 pp.
- BERNER L. D. (1967) Distributional atlas of Thaliacea in the California Current region. CalCOFI Atlas No. 8, California Cooperative Oceanic Fisheries Investigations, Scripps Institute of Oceanography, La Jolla, 322 pp.
- BETZER P. R., W. J. SHOWERS, E. A. LAWS, C. D. WINN, G. R. DiTULLIO and P. M. KROOPNICK (1984) Primary productivity and particle fluxes on a transect of the equator at 153°W in the Pacific Ocean. *Deep-Sea Research*, **31**, 1–11.
- BISHOP J. K. B., D. R. KETTEN and J. M. EDMOND (1978) The chemistry, biology and vertical flux of particulate matter from the upper 400 m of the Cape Basin in the southeast Atlantic Ocean. *Deep-Sea Research*, **25**, 1121–1161.
- BISHOP J. K. B., R. W. COLLIER, D. R. KETTEN and J. M. EDMOND (1980) The chemistry, biology and vertical flux of particulate matter from the upper 1500 m of the Panama basin. *Deep-Sea Research*, **27**, 615–640.
- BRUTLAND K. W. and M. W. SILVER (1981) Sinking rates of fecal pellets from gelatinous zooplankton (salps, pteropods, doliolids). *Marine Biology*, **63**, 295–300.
- CARPENTER E. J. (1983) Nitrogen fixation by marine *Oscillatoria* (*Trichodesmium*) in the world's oceans. In: *Nitrogen in the marine environment*, E. J. CARPENTER and D. G. CAPONE, editors, Academic Press, New York, pp. 65–104.
- DEIBEL D. (1982) Laboratory-measured grazing and ingestion rates of the salp *Thalia democratica* Forskal, and the doliolid *Doliolletta gegenbauri* Uljanin (Tunicata: Thaliacea). *Journal of Plankton Research*, **4**, 189–201.
- DEIBEL D. (1985) Blooms of the pelagic tunicata *Doliolletta gegenbauri*: are they associated with Gulf Stream frontal eddies? *Journal of Marine Research*, **43**, 211–236.
- DUGDALE R. C. and J. J. GOERING (1967) Uptake of new and regenerated forms of nitrogen in primary productivity. *Limnology and Oceanography*, **12**, 196–206.
- EPPLEY R. W. and B. J. PETERSON (1979) Particulate organic matter flux and planktonic new production in the deep ocean. *Nature*, **282**, 677–680.
- FASHAM M. J. R. (1985) Flow analysis of materials in the marine euphotic zone. In: *Ecosystem theory of biological oceanography*, R. E. ULANOWICZ and T. PLATT, editors, *Canadian Bulletin of Fisheries and Aquatic Science*, **213**, 139–162.
- FENCHEL T. (1982) Ecology of heterotrophic microflagellates II. Bioenergetics and growth. *Marine Ecology Progress Series*, **8**, 225–231.
- FOWLER S. W. and G. A. KNAUER (1986) Role of large particles in the transport of elements and organic compounds through the oceanic water column. *Progress in Oceanography*, **16**, 147–194.
- FROST B. W. (1984) Utilization of phytoplankton production in the surface layer. In: *Global Ocean Flux Study: Proceedings of a workshop, September 10–14, 1984*. National Academy press, Washington D.C., pp. 125–135.
- GOLDMAN J. C. (in press) Spatial and temporal discontinuities of biological processes in pelagic surface waters. In: *Toward a theory on biological and physical interactions in the world ocean*, B. J. ROTHSCHILD, editor, D. Reidel, Dordrecht, Netherlands.



- GOLDMAN J. C., J. J. MCCARTHY and D. G. PEAVEY (1979) Growth rate influence on the chemical composition of phytoplankton in oceanic waters. *Nature*, **279**, 210–215.
- HANNON B. (1985) Ecosystem flow analysis. In: *Ecosystem theory of biological oceanography*, R. E. ULANOWICZ and T. PLATT, editors, *Canadian Bulletin of Fisheries and Aquatic Science*, **213**, 97–118.
- HARBISON G. R. and V. L. MCALISTER (1979) The filter feeding rates and particle retention efficiencies of three species of *Cyclosalpa* (Tunicata: Thaliacea). *Limnology and Oceanography*, **24**, 875–892.
- HARBISON G. R., V. L. MCALISTER and R. W. GILMER (1986) The response of the salp *Pegea confoederata* to high levels of particulate material: starvation in the midst of plenty. *Limnology and Oceanography*, **31**, 371–382.
- HAYWARD T. L., E. L. VENRICK and J. A. MCGOWAN (1983) Environmental heterogeneity and planktonic community structure in the central North Pacific. *Journal of Marine Research*, **41**, 711–729.
- ISEKI K. (1981) Particulate organic matter transport to the deep sea by salp fecal pellets. *Marine Ecology Progress Series*, **5**, 55–60.
- JENKINS W. J. and J. C. GOLDMAN (1985) Seasonal oxygen cycling and primary production in the Sargasso Sea. *Journal of Marine Research*, **43**, 465–491.
- KLEIN P. and B. COSTE (1984) Effects of wind-stress variability on nutrient transport into the mixed layer. *Deep-Sea Research*, **31**, 21–37.
- LI W. K. W., D. V. SUBBA-RAO, W. G. HARRISON, J. C. SMITH, J. J. CULLEN, B. IRWIN and T. PLATT (1983) Autotrophic picoplankton in the tropical ocean. *Science*, **219**, 292–295.
- MADIN L. (1982) Production, composition and sedimentation of salp fecal pellets in oceanic waters. *Marine Biology*, **67**, 39–45.
- MARTIN J. H., G. A. KNAUER, D. M. KARL and W. W. BROENKOW (1987) VERTEX: Carbon cycling in the northeast Pacific. *Deep-Sea Research*, **32**, 267–286.
- MARTINEZ L., M. W. SILVER, J. M. KING and A. L. ALLDREDGE (1983) Nitrogen fixation by floating diatom mats: A source of new nitrogen to oligotrophic ocean waters. *Science*, **221**, 152–154.
- MCCAVE I. N. (1984) Size spectra and aggregation of suspended particles in the ocean. *Deep-Sea Research*, **22**, 491–502.
- MULLIN M. M. (1983) *In situ* measurement of filtering rates of the salp *Thalia democratica* on phytoplankton and bacteria. *Journal of Plankton Research*, **5**, 279–289.
- NEWELL R. C. and E. A. S. LINLEY (1984) The significance of microheterotrophs in carbon and nitrogen flow through plankton communities in the western English Channel. *Marine Ecology Progress Series*, **6**, 123–136.
- PLATT T. and W. G. HARRISON (1985) Biogenic fluxes of carbon and oxygen in the ocean. *Nature*, **318**, 55–58.
- PLATT T., D. V. SUBBA-RAO and B. IRWIN (1983) Photosynthesis of picoplankton in the oligotrophic ocean. *Nature*, **301**, 702–704.
- POMEROY L. R. and D. DEIBEL (1980) Aggregation of organic matter by pelagic tunicates. *Limnology and Oceanography*, **25**, 643–652.
- RYTHER J. H. (1969) Photosynthesis and fish production in the sea. *Science*, **166**, 72–76.
- SEMINA H. J. and I. A. TARKHOVA (1972) Ecology of phytoplankton in the North Pacific Ocean. In: *Biological oceanography of the north Pacific Ocean*, A. Y. TAKENOUTI, editor, Idemitsu Shoken, Tokyo, pp. 118–124.
- SHARP J. H. (1983) The distribution of inorganic nitrogen and dissolved and particulate organic nitrogen in the sea. In: *Nitrogen in the marine environment*, E. J. CARPENTER and D. G. CAPONE, editors, Academic Press, New York, pp. 1–36.
- SILVER M. W. and K. W. BRULAND (1981) Differential feeding and fecal pellet composition of salps and pteropods, and possible origin of the deep-water flora and olive-green “cells”. *Marine Biology*, **62**, 263–273.
- SKJOLDAL H. R. and P. WASSMAN (1986) Sedimentation of particulate organic matter and silicon during spring and summer in Lindaspollene, Western Norway. *Marine Ecology Progress Series*, **30**, 499–563.
- SMETACEK V. S. (1980) Annual cycle of sedimentation in relation to plankton ecology in Western Kiel Bight. *Ophelia* (Suppl.), **1**, 65–76.
- SMETACEK V. S. (1985) Role of sinking in diatom life-history cycles: ecological, evolutionary and geological significance. *Marine Biology*, **84**, 239–251.
- STARESINIC N., G. T. ROWE, D. SHAUGHNESSEY and A. J. WILLIAMS III (1978) Measurement of the vertical flux of particulate organic matter with a free-drifting sediment trap. *Limnology and Oceanography*, **23**, 559–563.
- STARESINIC N., J. FARRINGTON, R. B. GAGOSIAN, C. H. CLIFFORD and E. M. HURLBURT (1983) Downward transport of particulate matter in the Peru coastal upwelling: role of the anchoveta, *Engraulis ringens*. In: *Coastal upwelling, its sediment record. Part A. Responses of the sedimentary regime to present coastal upwelling*, E. SEUSS and J. THIEDE, editors, Plenum Press, New York, pp. 225–240.
- SUESS E. (1980) Particulate organic carbon flux in the oceans—surface productivity and oxygen utilization. *Nature*, **288**, 260–263.

- ULANOWICZ R. E. (1984) Community measures of marine food webs and their possible applications. In: *Flows of energy and materials in marine ecosystems: theory and practice*, M. J. R. FASHAM, editor, Plenum Press, New York, pp. 23–48.
- VALIELA I. (1984) *Marine ecological processes*. Springer-Verlag, New York, 546 pp.
- WAKEHAM S. G. and E. A. CANUEL (in press) Organic geochemistry of particulate matter in the eastern tropical North Pacific Ocean: Implications for particle dynamics. *Journal of Marine Research*.
- WHEELER P. A. and D. L. KIRCHMAN (1986) Utilization of inorganic and organic nitrogen by bacteria in marine systems. *Limnology and Oceanography*, **31**, 998–1009.