Size-dependent carbon flow in the epipelagic food web of the Western Equatorial Pacific

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ABSTRACT: The present study examines the complexity of plankton food-web structure related to size diversity in lower trophic levels of the Equatorial Pacific and its possible effects on community stability and food availability of mesozooplankton. Food-web interactions and carbon flows in the plankton community were estimated from size-dependent predation, carbon transfer between trophic levels and size–biomass measurements determined in 5 independent field investigations. The community was separated into 10 different functional groups, which consisted mainly of pico-, nano- and micro-phytoplankton, bacteria, heterotrophic nanoflagellates, heterotrophic dinoflagellates, ciliates, nauplii, copepods and chaetognaths. The major carbon flow on all 5 occasions was consistent with a general conceptual food-web model, even though the study region was subjected to different oceanographic conditions — warm pool in 1990 to 1993, equatorial divergence in 1994. The 5 food webs showed distinct differences in structure, dependent on the size composition within each functional group, suggesting potential inherent non-steady-state dynamics at the intra-functional group level. The apparent stability of food-web dynamics in the equatorial plankton community may be a consequence of complex food-web interaction and resulting fluctuations, the effects of which neutralize each other over time.

KEY WORDS: Pelagic food web · Equatorial Pacific · Size-dependent predation · Food-web complexity · Community stability · Functional group

INTRODUCTION

Every heterotrophic organism in a given natural community is part of an ecosystem, and is supported by primary producers that are sometimes composed of species of a great biodiversity. Studies over the last decade have tried to identify possible relationships between biodiversity and ecosystem functioning, using a variety of field and laboratory experiments and theoretical approaches (Loreau 2000, Kinzig et al. 2001, Loreau et al. 2001). These studies suggested that ecosystem functioning can be influenced by the biodiversity of the community. For example, species richness of primary producers affects primary productivity (cf. Tilman 1999). Consumer species diversity controls ecosystem stability (Naeem & Li, 1997), the biomass of their prey (Naeem & Li 1998) and their own grazing rates (Cardinale 2002). Theories on community stability and the complexity of food-web structures have also been advanced (cf. Polis & Strong 1996) to explain why most natural food webs seem to have a complex stable structure, in contrast to the theoretical model, which predicts a decrease in community stability concurrent with an increase in food-web complexity (May 1973). However, observations on the complexity of the food-web structure in a given field community are limited because most natural communities consist of too many species and feeding relationships that are too complex to be practically described (Polis 1991).

Food-web structures in pelagic open-ocean ecosystems are still conceptual, despite efforts to estimate accurately the primary productivity and metabolic activity of major taxonomic groups by field and laboratory experiments. One reason for this poor understand-

ing of the open ocean is due to the dominance of small primary producers that are difficult to assess. In addition, high species diversity, especially in tropical regions (Woodd-Walker et al. 2002, Irigoien et al. 2004), indicates a great complexity of food-web structure. Petipa (1979) described food-web structure at the genus level of mesozooplankton in the tropical open ocean, but diversity of organisms at lower trophic levels such as phytoplankton and protozoans was not considered. Access to remote pelagic areas has also precluded extensive food-web studies of the open ocean. Food-web structure in the pelagic open-ocean thus remains an essential subject requiring further research (Raffaelli 2000, Landry 2002), since it is of particular importance in determining ecosystem functions, such as fishery productivity (Ryther 1969, Pauly & Christensen 1995), vertical material transport by mesozooplankton (Small et al. 1983, Al-Mutairi & Landry 2001) and community stability (McCann et al. 1998b, Hart 2002).

The present study focused on the diversity of individual size within each taxonomic group and size-dependent predation of planktonic predators. Sheldon et al. (1977) first defined the size-dependent predation of zooplankton by a predator:prey size ratio (P:P ratio) of around 14, based upon literature values of field grazing experiments in pelagic plankton communities. Since then, conceptual plankton food web models have been simplified, under the assumption that prey are eaten by predators of around 1 order of magnitude greater size (e.g. Sieburth et al. 1978, Azam et al. 1983). The concept of size-dependent food webs is the basis of many theoretical studies involving carbon flow to higher trophic levels (e.g. Borgmann 1987) and temporal dynamics (e.g. Moloney & Field 1991) in the plankton community. However, in most natural plankton communities, individual body size changes fairly continuously and diversely (Sheldon et al. 1972). In addition, plankton predators in different taxonomic groups have different P:P ratios (Hansen et al. 1994). On the basis of these considerations, the food-web structure could be determined more precisely, which may reveal the effects of complexity and size diversity on the ecosystem function as a whole.

We examined the effects of complexity on food-web structure and carbon flux related to size diversity in the epipelagic plankton community of the Western Equatorial Pacific. The food-web structure of this community was determined using data on size-dependent predation by zooplankton, carbon-transfer efficiency, and data on the biomass and individual size of all plankton members. From the detailed food-web structure estimated for the community studied, we clarified general and specific aspects of the food-web structure in the equatorial epipelagic ecosystem.

MATERIALS AND METHODS

Data description. We examined data on the plankton community in the upper 200 m of the water column in the Western Equatorial Pacific (0° N, 175° E). The data were collected during 5 independent observations on 25 September 1990, 21 and 22 September 1991, 19 and 20 September 1992, 19 and 20 September 1993 and 28 and 29 April 1994 as a part of the 'NW Pacific Carbon Cycle Study' (NOPACCS). Plankton samples were collected from depths of 0 to 50 and 50 to 200 m with vertical tows of a modified NORPAC net (mesh sizes 30, 100 and 330 μm). Bottle-casts were conducted at 0, 10, 25, 40, 75, 100, 125, 150 and 200 m and at maximum chlorophyll fluorescence depth. Samples were fixed with 2 or 5% buffered formaldehyde. The collected organisms were identified to taxonomic group, and counted. The length and width of each organism, cell, individual, or colony, were also determined and converted into equivalent spherical diameters (ESD, μm). Carbon biomass (mg C m^{-2}) of each taxonomic group was estimated from the total volume of organisms integrated in the 0 to 200 m water-column using volume-specific conversion factors (Strathmann 1967, Parsons et al. 1984, Lee & Fuhrman 1987, Verity et al. 1992). The plankton community studied was expected to inhabit the euphotic and part of the disphotic zones, since 0.1% of the photosynthetic active radiation always reached depths shallower than 200 m, generally varying between 121 m and 169 m. Details of field sampling and biomass estimation are given in Kiyosawa et al. (1995) and Ishizaka et al. (1997).

Nitrate concentrations in the surface water at the study site were <0.1 μM in 1990 to 1993, and exceeded 2 μM in 1994, possibly due to equatorial upwelling (Ishizaka et al. 1997). The oligotrophic waters in 1990 to 1993 were above 50 to 75 m, below which nitrate gradually increased up to 13 to 17 μM at 200 m. Nitrate concentrations in 1994 gradually increased from 2 μM at the surface to a relatively constant concentration of 12 μM at 100 to 200 m. Chlorophyll *a* (chl *a*) in 1990 to 1993 had a subsurface maximum at 75 to 100 m, with concentrations 6 to 11 times higher than surface values. This depth corresponded to a rapid increase in nitrate concentration. There was no appreciable subsurface chl *a* maximum in 1994. The study site is located at the border between 2 regions called 'warm pool' with highly stratified water and 'high-nutrient, low-chlorophyll (HNLC)' (Le Borgne et al. 2002a). The observed vertical structure of nitrate and chlorophyll concentrations suggests that warm pool conditions prevailed in September 1990 to 1993, while HNLC conditions were evident in April 1994 (Ishizaka et al. 1997).

The plankton community was dominated by picoplankton such as *Prochlorococcus* spp. and hetero-

trophic bacteria in all 5 observation periods (Ishizaka et al. 1997). Such picoplankton dominance has typically been observed in tropical oligotrophic oceanic ecosystems (cf. Caron et al. 1995, Roman et al. 1995, Le Borgne & Landry 2003). The size spectrum of the plankton community displayed 3 peaks in pico-, nano- and mesoplankton biomass each year. The individual ESD of organisms in the 22 taxonomic groups classified by Ishizaka et al (1997) generally varied by 1 to 2 orders of magnitude. In addition, the community observed in 1994 contained a slightly larger relative contribution of large autotrophic cells compared with the other years (Ishizaka et al. 1997), corresponding with previous observations showing a clear contrast between the 2 microbial communities of the warm pool and HNLC regions of the tropical Pacific (Landry & Kirchman 2002, Le Borgne et al. 2002b).

The plankton data sets used in this study were largely the same as those examined by Ishizaka et al. (1997), but some classifications were changed. Dinoflagellates without photosynthetic pigments were reclassified as heterotrophs in this study. For 1990 and 1991, when microscopic observations were not conducted, 50% of the Gymnodiniales observed were assumed to be heterotrophs, since approximately half had displayed no chlorophyll fluorescence in microscopical analyses carried out in 1992 to 1994. The trophism of other taxonomic groups of dinoflagellates in 1990 and 1991 was verified according to Chihara & Murano (1997). We included organisms larger than 2000 µm, which were excluded from the analysis of Ishizaka et al. (1997). The ESD of heterotrophic bacteria was assumed to be 0.42 to 0.46 µm, in accordance with the observations of Ducklow et al. (1995) at 0° N, 140° W. Likewise, the ESD of *Prochlorococcus* spp. was defined as approximately 0.54 µm in 1990 to 1993 and as 0.73 µm in 1994, according to the ESD of *Prochlorococcus* spp. measured in the warm pool and HNLC regions, respectively (Blanchot et al. 2001).

Estimation of food-web and carbon flow structure. The 22 taxonomic groups described by Ishizaka et al. (1997) were roughly reclassified into 10 functional groups in this study (Table 1) according to trophism (autotrophic or heterotrophic), heterotrophism (ingestion of dissolved or particulate organic matter), range of individual body sizes, and average biomass. Non-dominant taxonomic groups of zooplankton were grouped with other dominant taxonomic groups in a similar size range, because the P:P ratio and prey items of minor taxonomic groups are not exactly known. Although this classification sorted organisms with different feeding habitats into functional groups such as 'chae' or 'cope', the non-dominant groups only slightly affected carbon-flux estimates. Therefore, our estimates of food-web complexity are mini-

mum estimates, and the carbon fluxes rough approximations.

We treated picophytoplankton (picop), nanophytoplankton (nanop), microphytoplankton (microp) and bacteria (bac) as 'basal' functional groups that never feed on particulate matter (Table 1). Heterotrophic bacteria were included in the basal group 'bac' because bacterial growth is dependent on dissolved organic carbon (DOC), produced by phytoplankton during photosynthesis or egested from zooplankton, rather than on living particles (Nagata 2000). In contrast, heterotrophic nanoflagellates (hnf), heterotrophic dinoflagellates (hdf), ciliates and other minor protozoans (ciliates), copepod nauplii (nauplii), crustaceans, mainly copepods (cope), and other metazoans, mainly chaetognaths (chae), were treated as heterotrophic predators that graze on living particulate matter while at the same time being grazed on by larger predators. Furthermore, the predatory groups were divided into 2 groups: (1) omnivores of hnf, hdf, 'ciliates', nauplii and cope, which were considered to prey on all organisms of suitable size, and (2) carnivores of chae that prey only on heterotrophs. Detritivores were not divided into special functional groups because we could not determine which zooplankton were strict detritivore specialists and how many generalists consumed detritus in addition to living particulates.

Organisms within functional groups were grouped into 20 size-class categories called 'compartments'. The smallest size class ranged from −1 to −0.75 (common logarithm of ESD/2) or 0.20 to 0.36 µm ESD with a median value of 2.7 µm ESD. The next 3 larger size classes ranged from −0.75 to −0.50, from −0.50 to −0.25 and from −0.25 to −0.00 (common logarithm of ESD/2), with median values of 0.47, 0.84 and 1.5 µm ESD, respectively. The other 16 size classes up to 20 000 µm were also similarly defined, and designated by the median value of the relevant size range. All compartments where any plankton was observed in the study community were coded with serial numbers from 1 to $k-1$ and from k to $l-1$ for basal functional groups of autotrophs and bacteria, respectively, and from l to m for predatory functional groups ($1 < k < l < m$).

A given predatory compartment j ($l < j < m + 1$) was assumed to prey on compartment i when the size ratio of the predator (P) to the probable prey (P) was within the range of the P:P ratios for each predatory functional group (Table 1). Following Hansen et al. (1994), who suggested that different P:P ratios are more appropriate for different taxonomic groups than the constant P:P ratio of 1:10, the P:P ratios were derived from literature values of grazing experiments for the relevant taxonomic groups. The binary food-web matrix for the study community can be estimated from:

Table 1. Major taxonomic groups in the studied community aggregated into functional groups, trophic level transfer efficiencies (TTE, Straile 1999), predation types and ranges of predator:prey size ratios (P:P ratios). Average biomass (mg C m^{-2}) of each taxonomic group in 5 observation periods is also shown. Parameters for ciliates, cope or chae were derived from empirical values for these dominant taxonomic groups. B: basal functional groups; P: predatory functional groups; O: omnivore; C: carnivore

Major taxonomic groups	Functional group code	Average biomass	Trophic type	TTE	Predation type	log P:P ratio range (Source)
Prochlorococcus spp.	picop	494	B			
Synechococcus spp.		38				
Autotrophic nanoflagellates	nanop	246	B			
Coccolithophorids	microp	43	B			
Autotrophic dinoflagellates		119				
Diatoms		30				
Bacteria	bac	1048	B			
Heterotrophic nanoflagellates	hnf	164	P	0.28	O	0.25–0.75 (Chrzanowski & Šimek 1990)
Heterotrophic dinoflagellates	hdf	82	P	0.26	O	0.00–0.50 (Jakobsen & Hansen 1997)
Ciliates	ciliates	40	P	0.3	O	0.75–1.25 (Hansen et al. 1994)
Radiolarians		10				
Foraminiferans		5				
Copepod nauplii	nauplii	11	P	0.22	O	1.00–1.50 (Hansen et al. 1994)
Eggs (mainly of copepods)		0.8				
Copepoda	cope	240	P	0.22	O	1.00–1.75 (Hansen et al. 1994)
Malacostraca		14				
Ostracoda		0.1				
Branchiopoda		3.7				
Carnivorous metazoans other than crustaceans: mainly chaetognaths, cnidarians and annelids	chae	124	P	0.23	C	0.50–1.00 (Pearre 1980)
Omnivorous metazoans other than crustaceans: fish larvae, gastropods, echinoderms, tunicates		12				

$$R_{ij} = \begin{cases} 1, S_j / S_i \in [\text{P:P ratio range}] \\ 0, \text{otherwise} \end{cases} \quad (1)$$

R_{ij} represents the existence or non-existence of prey–predator relationships between prey compartment i and predator j designated by 1 or 0, respectively. The symbols s_i and s_j express body size (ESD) of prey i and predator j. The P:P ratio range is a closed set, which contains its own boundary. In the estimated compartmental food web, predatory compartments belonging to different functional groups have different sets of prey even when they are in the same size class, because of differences in the allocated P:P ratios and predation types. Basal compartments in the same size class have an equivalent set of predators. Food selectivity other than body size was not taken into account in this study.

For estimation of carbon flux among the compartments of the food web, productivity of each basal compartment was previously determined from the allocation of net primary productivity (NPP) or bacterial productivity (BP) in proportion to measured biomass in

each compartment. NPP and BP were estimated following Ishizaka et al. (1997). NPP measured using the ^{13}C method in 1993 was 382 mg C m^{-2} d^{-1}, and in 1994 was 1210 mg C m^{-2} d^{-1}. The 3-fold greater NPP in 1994 can be explained by different oceanic conditions between the measurements in 1993 and 1994, with clear contrasts between warm pool and HNLC conditions in terms of primary productivity being reported (Barber & Chavez 1991, Le Borgne et al. 2002a). The NPP in 1994 was higher than the average primary productivity in the HNLC of 644 ± 15 mg C m^{-2} d^{-1} reported by Le Borgne et al. (2002a), but within the range of 720 to 1528 mg C m^{-2} d^{-1} reported by Barber et al. (1996). The NPP of 382 mg C m^{-2} d^{-1} was similar or slightly higher than the 316 ± 13 mg C m^{-2} d^{-1} observed in the warm pool region (Le Borgne et al. 2002a). The NPP measured in 1993 was also applied to 1990 to 1992, since NPP measurements were not available for these years. BP was given by the following log-log relationship to NPP ($r^2 = 0.56$, Cole et al. 1988):

$$\log BP = 0.75 \log NPP + 0.093 \quad (2)$$

The estimated BP was 107 mg C m^{-2} d^{-1} in 1990 to 1994 and 254 mg C m^{-2} d^{-1} in 1994, and the ratio of BP to NPP was 28% in 1990 to 1993 and 21% in 1994.

In the predatory compartments, predators were assumed to share prey productivity in proportion to their biomass. Thus, the daily carbon supply rate for predatory compartment j from prey i (F_{ij}, mg C m^{-2} d^{-1}) was calculated from the ratio of the predator j biomass (b_j) to the total biomass of potential predators of prey i multiplied by the productivity of the prey i (p_i):

$$F_{ij} = \frac{R_{ij} \cdot b_j}{\sum_{k=1}^{m} R_{kj} \cdot b_k} \times p_i \ (j > l-1) \quad (3)$$

The daily total carbon supply rate to the predatory compartment j (f_j, mg C m^{-2} d^{-1}) was the sum of food sources from multiple prey items:

$$f_j = \sum_{k=1}^{m} F_{kj} \ (j > l-1) \quad (4)$$

Reproduction by predatory compartment j (p_j) was estimated from f_j multiplied by the trophic level transfer efficiency (TTE) as:

$$p_j = \text{TTE} \times f_j = \text{consumption efficiency} \times \\ \text{gross growth efficiency} \times f_j \ (j > l-1) \quad (5)$$

TTE, the fraction of the consumer productivity to the productivity of its prey, is the multiplier of gross growth efficiency (fraction of carbon used for growth:total ingested carbon) and consumption efficiency (fraction of actually consumed carbon of prey:total available productivity of prey) (Begon et al. 1996). In this study, we assumed that consumption efficiency is 100% because grazing rates of predators and production rates by phytoplankton are known to be roughly balanced in the tropical plankton community. The gross growth efficiency was assumed to be 0.21 to 0.30 from Straile (1997) (Table 1).

For evaluation of food-web functions, we calculated dependent coefficients, net transfer efficiencies and average food-chain length with respect to cope, the representative mesozooplankton for the plankton community. The dependency coefficient describes the extent to which each predator depends upon other components for its carbon supply either by direct or indirect flows (Wulff et al. 1989). We calculated dependent coefficients on different basal functional groups with respect to carbon supply for cope. Using the dependency coefficient (dep. coef.), net carbon transfer efficiency (NTE) from a focused basal group — the percentage of total productivity of a focused basal functional group reaching cope — can be estimated (est.) as:

$$\text{NTE from a focused basal group } (X) = \\ \frac{\text{dep. coef. of cope on } X \times \text{est. total carbon supply to cope}}{\text{total productivity of } X} \quad (6)$$

The NTE can then be expressed as:

$$\text{NTE from } X = \text{TTE}_{ave}{}^{\text{AFL-1}} \quad (7)$$

where AFL is the average food-chain length between cope and X, and TTE$_{ave}$ is the average TTE (weighted by productivity) of all consumers at intermediate trophic levels between X and cope.

From Eq. (7), we calculated AFL between X and cope as:

$$\text{AFL} = \frac{\log(\text{NTE from } X)}{\log(\text{TTE}_{ave})} + 1 \quad (8)$$

Whereas food-chain length to cope from bac, picop, nanop and microp can be calculated as integers 3, 3, 2 and 1, respectively, in a conceptual food web such as that in Fig. 1, AFL can be a decimal value that represents a diverse carbon pathway from the basal functional groups to cope. Note that the dependent coefficients and NTE depend mainly on TTE and relative productivity of the basal functional groups, but not on exact values of NPP and BP, and AFL is independent of the assumed TTE, NPP and BP.

Daily growth rates per unit biomass (d^{-1}) of protozoans were also calculated from the estimated productivity by each protozoan compartment per unit biomass for comparison with the allometric relationship between their body size and the carbon-specific maximum growth rates reported by Hansen et al. (1997). In the same way, the daily carbon supply rates per unit biomass (d^{-1}) estimated in metazoan compartments
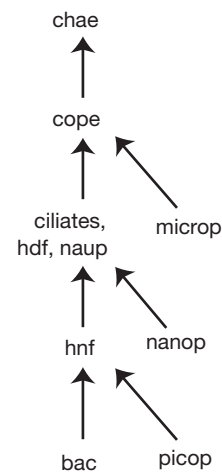

Fig. 1. Conceptual microbial food-web structure after Azam et al. (1983), reorganized by Ishizaka et al. (1997). Arrows show direction of carbon flow. Definition of functional groups and abbreviations as in Table 1

were compared with the potential carbon demand calculated by multivariate regression explaining respiration rates as a function of animal body weight and water temperature (Ikeda 1985). For conversion from respiration rates to potential carbon demands, we assumed a respiration efficiency of 33% (Dam et al. 1995). Water temperature of 25°C was used because the integrated 0 to 200 m average water temperature in the study region was 24.3 to 27°C in the 5 observations, with an average of 25.4°C.

RESULTS

Total carbon biomass of the plankton community varied from 2002 to 3439 mg C m^{-2}, with a coefficient of variation (CV) of 0.2 during 1990 to 1994 (Table 2). Total phytoplankton and bacterial biomass was 582 to 1505 mg C m^{-2} and 968 to 1198 mg C m^{-2}, respectively. Their biomass always exceeded that of total zooplankton (381 to 952 mg C m^{-2}). The total biomass of phytoplankton and zooplankton showed changes correlated with each other (r = 0.920, p < 0.01).

Among the autotrophic functional groups, picop dominated at 42 to 60% of the total phytoplankton biomass, while nanop and microp contributed 19 to 34% and 13 to 28%, respectively (Table 2). Protozoans (hnf, hdf and ciliates) accounted for 20 to 53% of the total zooplankton biomass. Hnf was the dominant group by biomass in the protozoan functional groups, and cope the dominant in the metazoan group. In addition, ciliates in 1992, hdf in 1991 to 1992 and chae in 1991 showed large biomass. The biomass of the protozoan functional groups was highly variable with a CV of

0.73 to 1.00 compared with functional groups of metazoans and phytoplankton with a CV of 0.16 to 0.55. The biomass of every functional group in 1994 (except for picop) was within the range observed in 1990 to 1993, regardless of the differences between vertical structures in 1990 to 1993, and 1994, probably because integrated biomass in the water column of 0 to 200 m was considered. The only exception was a lower percentage contribution of picop to the total phytoplankton biomass in 1994 (42%) compared to the other years (53 to 60%).

All functional groups except for bac contained a variety of individual sizes covering 1 to 2 orders of magnitude of ESD, and their size–biomass distributions revealed biomass peaks at different sizes in different years (Fig. 2). The observed functional groups of phytoplankton centered their major biomasses at 0.47 to 0.84 µm for picop, at 1.5 to 4.7 µm for nanop, and at 8.4 to 47 µm for microp. A biomass peak for picop was observed at 0.47 µm in 1990 to 1993 and at 0.84 µm in 1994, both peaks being composed of *Prochlorococcus* spp. Biomass peaks of nanop that contributed 51 to 71% to the total nanop biomass were present at 4.7 µm in 1991 and at 2.7 µm in the other years. Microp had the largest size ranges (over 2 orders of magnitude) and relatively uniform biomass distributions compared with the other basal groups, while slight peaks in biomass were observed at 27 µm for coccolithophorids in 1990 and at 8.4 µm (mainly for Gymnodiniales) in 1991 to 1994. Protozoans ranged from 0.84 to 470 µm ESD, with hnf occupying smaller and narrower size ranges of 0.84 to 15 µm compared with 4.7 to 150 µm for hdf and 4.7 to 470 µm for ciliates. For Hnf, organisms of 1.5 µm contributed 75% of the total hnf biomass in 1990 and 25% in 1991, but none in 1992 to 1994. More than 70% of hdf centered at 8.4 µm every year except in 1990. In ciliates, there were clear biomass peaks at 15 µm in 1992 and at 47 µm in 1990 and 1991, while the biomass had relatively uniform distributions in 1993 and 1994. Both the individual size and size ranges of metazoans increased in the order nauplii (47 to 270 µm), cope (47 to 8400 µm), chae (47 to 4700 µm). The occurence of compartments larger than 2000 µm was highly variable among years, probably due to the sampling and analytical errors connected with lower abundance (Landry et al. 2001).

Compartmental food webs estimated from the observed size-biomass distributions were characterized by many trophic links between compartments,

Table 2. Total integrated biomass (mg C m^{-2}) at 0 to 200 m depth for each functional group in the Equatorial Pacific (0° N, 175° E) in September 1990 to 1993 and April 1994. Values in parentheses are percentage contributions to total biomass of phytoplankton or zooplankton. CV is the coefficient of variation in biomass for the 5 yr. Other abbreviations as in Table 1

Group	1990	1991	1992	1993	1994	CV
Plankton	2617	3439	3010	2002	2580	0.20
Phytoplankton	878	1505	1175	582	710	0.38
picop	469 (53)	901 (60)	687 (58)	307 (53)	298 (42)	0.49
nanop	298 (34)	354 (24)	223 (19)	143 (25)	212 (30)	0.33
microp	111 (13)	250 (17)	266 (23)	132 (23)	200 (28)	0.36
Bacteria (bac)	1051	982	968	1040	1198	0.09
Zooplankton	688	952	867	381	672	0.31
hnf	329 (48)	249 (26)	105 (12)	42 (11)	95 (14)	0.73
hdf	17 (3)	164 (17)	123 (14)	22 (6)	86 (13)	0.77
ciliates	21 (3)	51 (5)	150 (17)	13 (3)	42 (6)	1.00
nauplii	9 (1)	5 (1)	15 (2)	10 (3)	20 (3)	0.48
cope	265 (39)	236 (25)	316 (36)	206 (54)	267 (40)	0.16
chae	46 (7)	247 (26)	158 (18)	88 (23)	163 (24)	0.55

even within the same functional groups, and with a variety of food-chain lengths from basal compartments to top predators (Fig. 3). In the longest food-chain, there were 6 to 10 intermediate trophic levels between the smallest basal compartments (bac or picop) at 0.47 µm and the largest top predators (e.g. chae) at 2700 µm (Fig. 3a). In the shortest food-chain, top predators such as cope at 8400 µm directly grazed on phytoplankton (Fig. 3b). The estimated carbon fluxes in the compartmental food webs are summarized as carbon fluxes among functional groups in Appendix 1.

Pyramid structures of estimated secondary productivity relative to the total NPP were approximately constant through the 5 yr (Fig. 4), regardless of differences between total fluxes in the warm pool and HNLC conditions and variability in food composition in each predatory functional group (Appendix 1). This was due to the fact that identical TTEs were applied in all cases. In the food webs, hnf was the main contributor to productivity at both the second and third trophic levels, since it was the major predator on the dominant basal groups picop and bac. Hdf, ciliates and naup mainly grazed on nanop as first-consumers and on hnf as second-consumers. Consequently, protozoans grazed 73 to 87 % of total NPP and 27 to 67 % of the total secondary productivity. In contrast, cope fed on microp as the first-consumers, and on ciliates and hdf as the second-consumers. These patterns of the main carbon pathways were consistent with the conceptual food web in Fig. 1. Although the longest food chain included 10 intermediate trophic levels in the compartmental food webs, due to the exponential decrease in food supply through the sequential trophic levels, the carbon actually reaching further than the 4th trophic level was <1 % of the total NPP. The relative percentage contribution of estimated secondary productivity to total NPP can vary as a function of the assumed TTE, but the relative composition of the functional predatory groups within each trophic level and the main carbon pathways cannot vary with the assumed TTE.

At the compartmental level, the estimated daily growth rates for protozoans or carbon supply rates for metazoans per unit biomass were scattered (Fig. 5), since almost every predatory compartment had a different set of prey within the food-web. In addition,
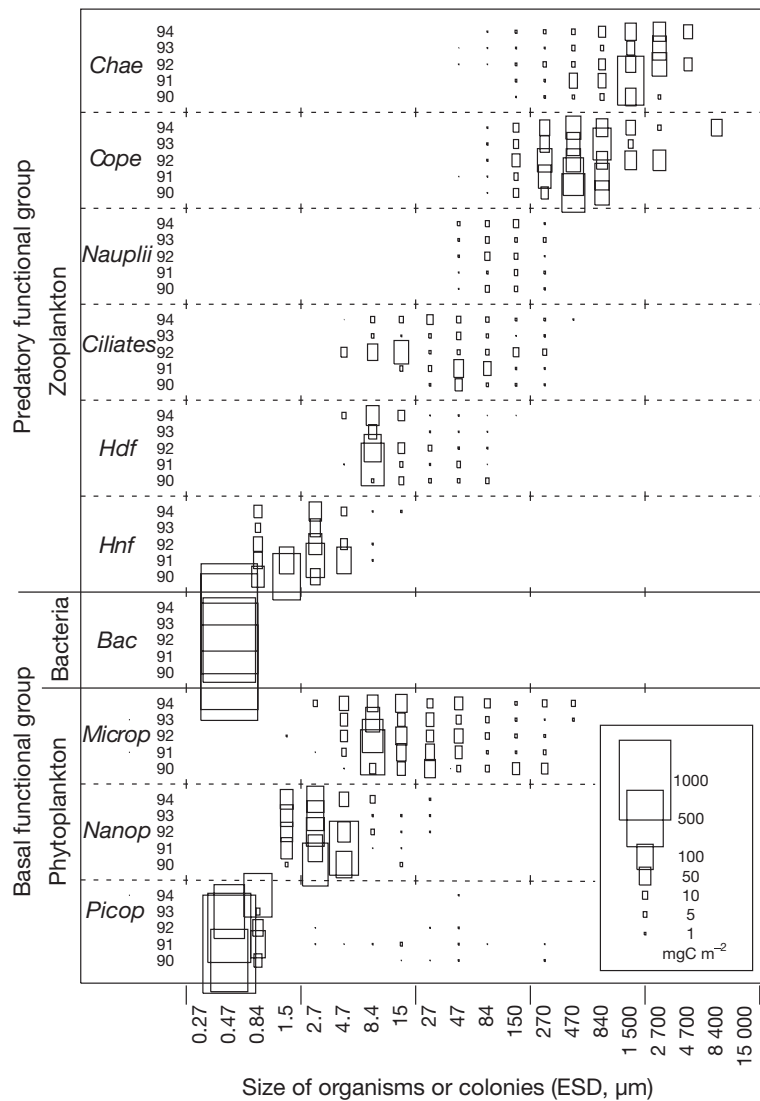

Fig. 2. Size distribution of compartments and their carbon biomass for each functional group at 0 to 200 m depth in the equatorial Pacific, September 1990 to 1993 and April 1994. Functional group abbreviations as in Table 1. ESD: equivalent sperical diameter

there were clear differences between the HNLC conditions in 1994 and the warm pool conditions in the other years. The estimated growth rates of protozoans were mostly below the empirical prediction of maximum growth rate in 1990 to 1993, but were approximately similar to or only slightly lower than the empirical value in 1994. The fact that most growth rates estimated from carbon supply from the grazing food web did not exceed the upper limit of the protozoans' potential growth suggests that almost all protozoans were limited by food supply (as we assumed in this model) rather than grazing by predators. Except for 1994 the estimated carbon supply rates of metazoans were also lower than the predicted carbon-demand
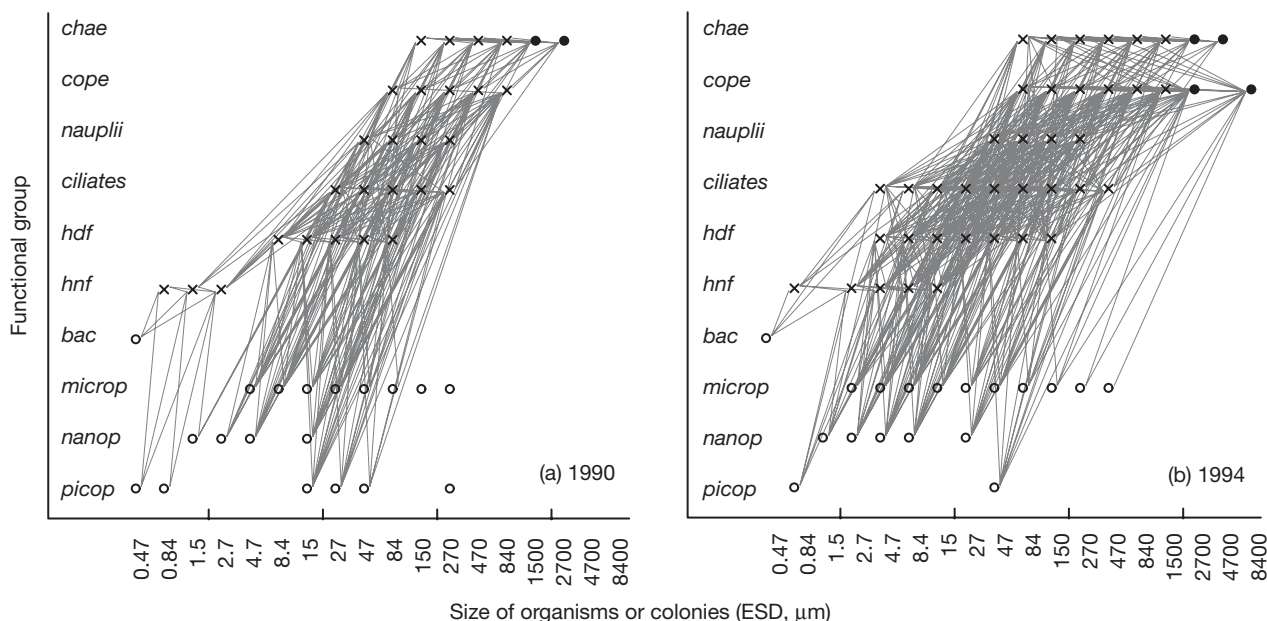
Fig. 3. Representative compartmental food webs based on the assumption of size-dependent predation and data collected in (a) 1990 and (b) 1994. The food webs of (a) 1990 and (b) 1994 show minimum and maximum numbers of compartments and trophic links (lines) estimated in the plankton community studied, respectively. Each data point represents basal compartment (○), compartment of top predator (●), or other predatory compartment (✕). Abbreviations as in Table 1. ESD: equivalent sperical diameter

rates. In particular, some compartments with small biomass and <200 µm ESD had very low carbon supplies compared to the predicted demand. Because the predicted carbon demand represents the minimum carbon required for survival (Ikeda 1985), this result might suggest a possible shortage of food sources for metazoans in warm pool conditions.

Differences in both taxonomic and size–biomass compositions among the 5 observation periods resulted in different carbon-flow structures not only between warm pool and HNLC conditions but also among the 4 observations during warm pool conditions (Fig. 6). For example, hnf of 1.5 and 2.7 µm (Fig. 6a) grazed on smaller hnf at 0.84 and 1.5 µm in addition to picop and bac, while such grazing among hnf was minor in 1992 (Fig. 6b) and 1994 (Fig 6c). This arose because large and small hnf occurred simultaneously in the community in 1990, but not in 1992 and 1994. In the same way, ciliates of 4.7 and 8.4 µm consumed picop and bac in 1992 (Fig. 6b), but this trophic pathway was rare in the other years. Hdf was a minor consumer of microp and nanop in 1990, but became a major consumer in 1992. Because the biomass of hdf (a competitor of cope for nanop and mircop) was small in 1990, direct grazing of cope on nanop and microp in 1990 was relatively greater than in the other years (Appendix 1).
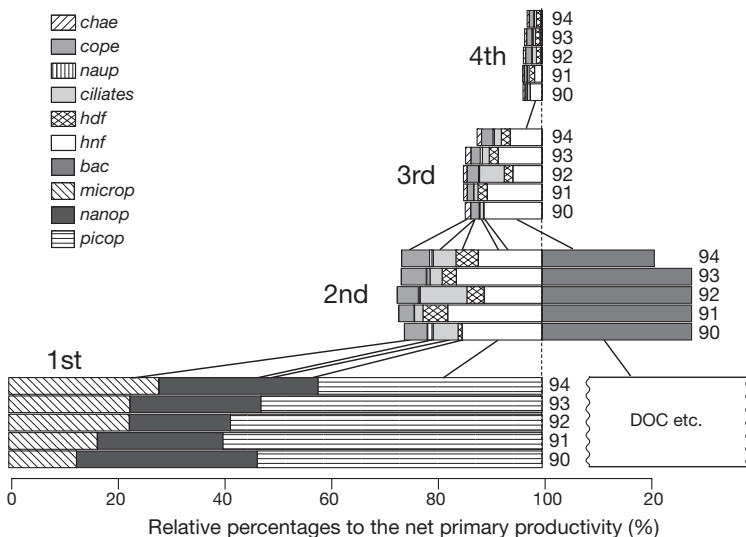

Fig. 4. Trophic structure and relative contribution of functional groups to total net primary productivity, based on data collected in 1990 to 1994. Trophic level of bac was assumed to be 2 (after Gaedke et al. 1996). Lines connecting functional groups show suggested main predator–prey relationships. 1st to 4th: trophic levels; DOC: dissolved organic carbon. Other abbreviations as in Table 1

The average food chain length connecting basal functional groups to cope also showed variability among the 5 different years, corresponding to the variability in carbon flows (Table 3). The carbon productivity of picop reached cope via food chains with an AFL of 2.7 to 3.5 and NTE of 4 to 13%. Then picop productivity contributed 8 to 21% of total available carbon of cope. Intermediate trophic levels between picop and cope were occupied by hnf, ciliates and/or hdf. The food chain length from picop to cope was sometimes shortened by small ciliates of <10 μm grazing on picop (especially in 1992), and lengthened by intra-functional predation within hnf (especially in 1990 and 1991). Bac productivity was utilized by cope through almost the same routes as picop productivity via food chains with an AFL of 2.7 to 3.5. When biomass peaks of picop shifted to a larger size of 0.84 μm in 1994, AFL of picop (2.7) was slightly shorter than that of bac (2.8), although the effect was very minor compared with the variability in AFL among the 5 observation periods.

Nanop supplied their carbon productivity via food chains with an AFL of 1.6 to 1.9; the basal nanop productivity of 29 to 49% was utilized by cope, and their contribution to total cope's grazing was 19 to 57%. The intermediate trophic levels from nanop were comprised mainly of hdf or ciliates. In addition, some nanop at 4.7 μm was directly consumed by cope at 270 μm (Fig 6a). Because most of the microp was consumed directly by cope, the AFL between microp and cope was the shortest in all 4 basal functional groups. The efficient carbon transfer of 67 to 95% from microp to cope resulted in a large dependency coefficients of cope on microp (31 to 54% during warm pool and 60% during HNLC conditions). Consequently, despite the predominant contributions of picop and bac to total basal productivity, the dependency coefficients of cope on picop and bac were generally low compared to those on nanop and microp, because the food-chain lengths from picop and bac to cope were very long (via 2 to 3 intermediate trophic levels). All indices in Table 3, except for the dependency coefficient of microp in 1994, were within the range in 1990 to 1993 owing to the large variability of the indices in the latter period. Therefore, the contrast between food-web structure in 1990 to 1993 and that in 1994 was not as clear as differences in the total carbon flux.
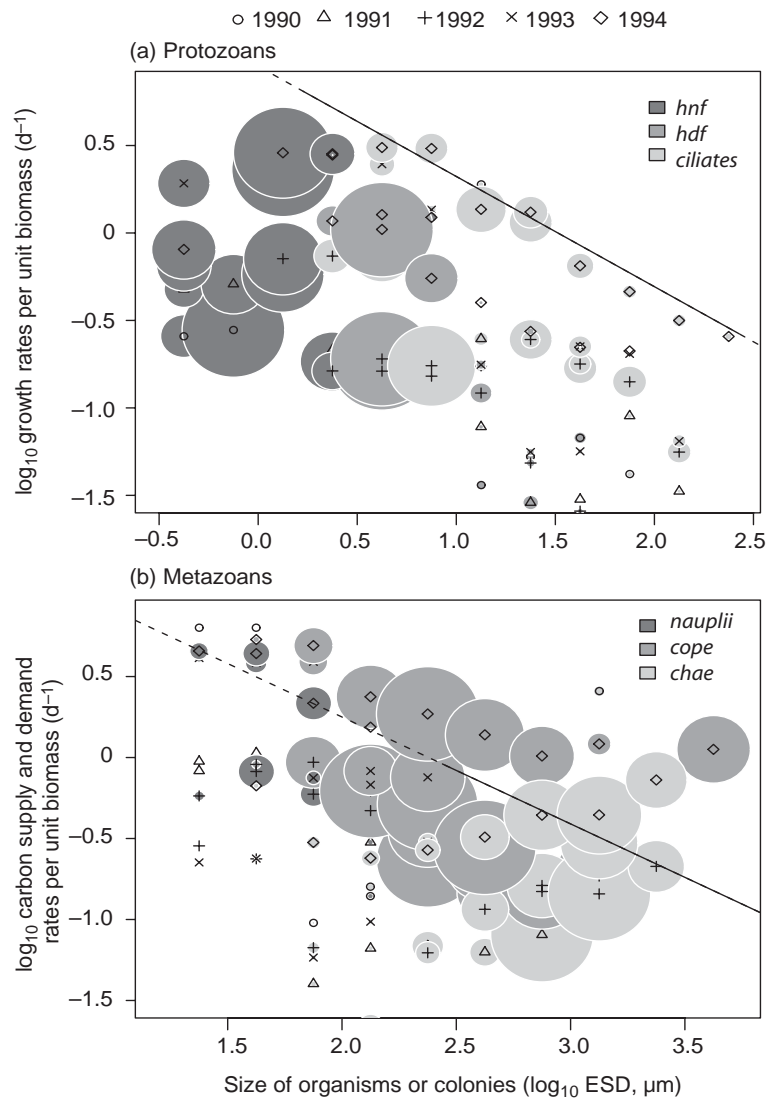

Fig. 5. Estimated rates (symbols, present study) of (a) daily growth in protozoans and (b) total carbon supply for metazoans, each compared to empirical allometric relationships — (a) maximum growth rate at 25°C (Hansen et al. 1997) and (b) carbon demand (Ikeda 1985) — with size of organisms/colonies (continuous and dashed lines, the latter representing extrapolated ranges). Area of each circle is proportional to biomass of each compartment. Abbreviations as in Table 1. ESD: equivalent spherical diameter

DISCUSSION

The food webs described in this study were characterized by variable food-chain lengths dependent on community size–biomass composition and by large variations in carbon supply rates from different types of prey to the predatory compartments. In addition, while the total amounts of carbon flux from NPP and BP differed between warm pool and HNLC conditions, the food-web structure (e.g. the main carbon pathway and average food chain length from specific basal functional groups to cope) did not show obvious
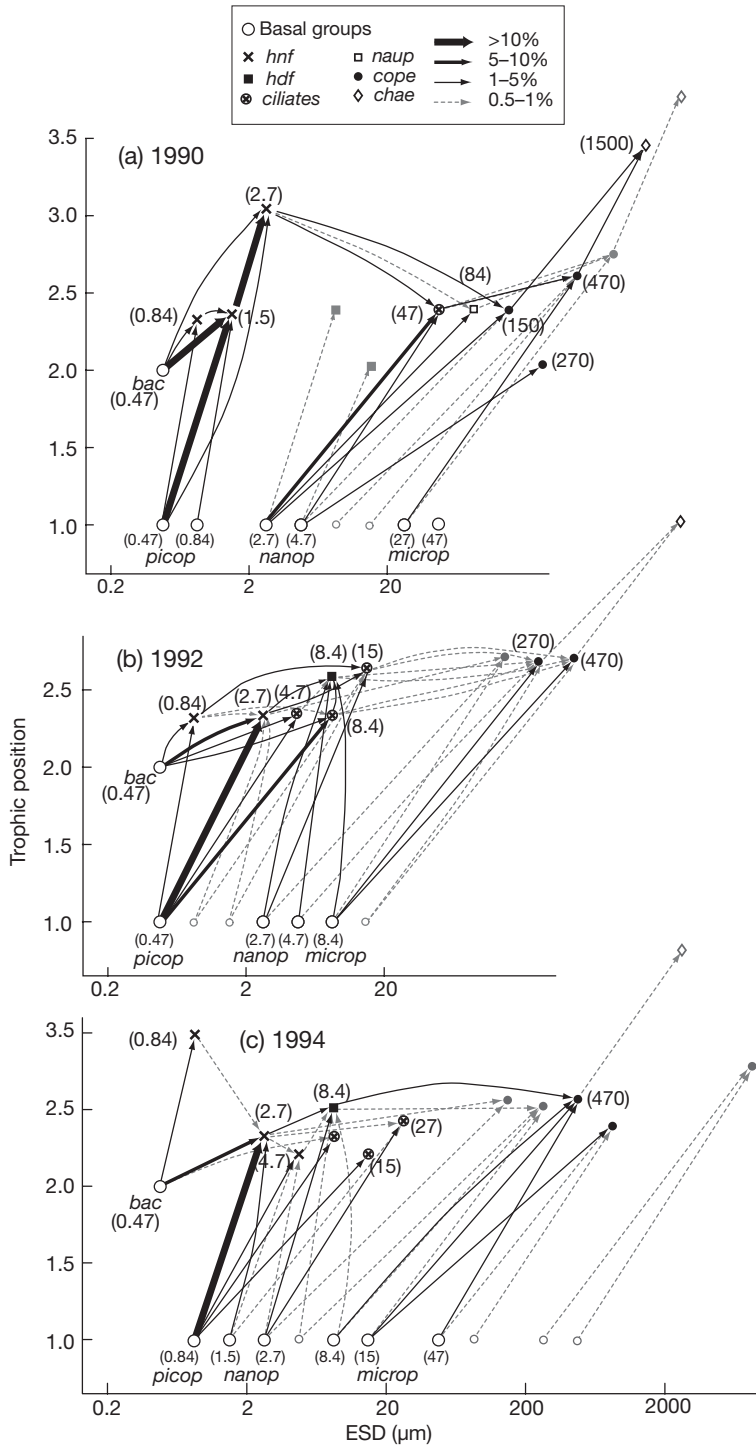
Fig. 6. Major carbon flow structure estimated in (a) 1990 and (b) 1992 (warm pool conditions) and (c) 1994 (high-nutrient, low-chlorophyll condition). The carbon flow only shows trophic links accounting for >1% (black arrows) and 0.5 to 1% (dashed arrows) of total carbon flux. Collectively, trophic links shown contributed 93, 81 and 73% of total carbon flux in 1990, 1992 and 1994, respectively — estimated carbon flux among compartments was centered around a few trophic links due to uneven biomass distributions. Numbers in parentheses indicate equivalent spherical diameter (ESD) in μm. The *y*-axis represents trophic position of each compartment (after Ulanowicz & Kemp 1979). Abbreviations as in Table 1

difference between the two environmental states.

The main carbon pathway estimated for the plankton food web was roughly consistent with the conceptual microbial food web in Fig. 1. The extra trophic links that the conceptual food web did not describe characterized food webs in 5 different observation periods, and determined deviations in AFL (Fig. 6). These extra links have been reported as predation of large hnf on small hnf (Calbet & Landry 1999, Calbet et al. 2001) and as grazing of small ciliates on bacteria (Sherr & Sherr 1987). The fact that the percentage consumption of protozoans on NPP (73 to 87%) was similar to that actually determined in a tropical oceanic region (75 ± 2%, Calbet & Landry 2004) supports our estimate.

Large variations in daily growth rates of protozoans and carbon supply rates of metazoans per biomass (Fig. 5) indicated that the food webs were not at steady-state at the compartmental level, since organisms receiving a larger supply of carbon are likely to increase their biomass at a greater rate than those receiving a smaller carbon supply. Therefore, the individual food webs based on 5 independent observation periods could be snapshots of short-term and/or local-scale structure rather than representatives of annual variability. Community variability similar to that observed among the 5 separate years in the present study was reported over a period of a few days during field observations in the equatorial Pacific, in terms of growth rate and abundance of phytoplankton, grazing impact and biomass of microzooplankton (Verity et al. 1996). Sampling and analytical errors (especially of larger organisms) (Landry et al. 2001) can also result in variations in estimated biomass.

Why did a plankton community comprised of compartments with non-steady-state dynamics show relatively stable biomass structure at the level of functional groups through 5 independent observation periods? Microbial communities in the tropical pelagic ecosystems are known to display apparent constancy in biomass structure (Landry 2002, Landry & Kirchman 2002), although some field experiments have found evidence of trophic cascades between bacteria and intraguild

Table 3. Estimated average food-chain length (AFL), net carbon transfer efficiency (NTE) and dependency coefficients with respect to cope. Estimates from the conceptual food web in Fig. 1 using the same assumption of trophic level transfer efficiency are also shown. Abbreviations as in Table 1

		AFL				NTE (%) from				Dependency coefficient (%) upon		
	bac	picop	nanop	microp	bac	picop	nanop	microp	bac	picop	nanop	microp
1990	3.5	3.5	1.5	1.0	4	4	49	95	5	8	57	31
1991	3.5	3.4	1.9	1.3	4	5	31	67	6	12	33	50
1992	2.7	2.7	1.8	1.2	12	13	34	76	10	21	19	50
1993	2.8	2.8	1.9	1.1	10	10	31	85	8	16	22	54
1994	2.8	2.7	1.9	1.1	10	11	29	82	5	12	23	60
Average	3.0	3.0	1.8	1.2	8	9	35	81	7	14	31	49
Estimates	3.0	3.0	2.0	1.0	7	7	25	100	6[a]	12[a]	21[a]	61[a]

[a]Average for 5 yr period

predation of heterotrophic nanoflagellates (Calbet & Landry 1999, Calbet et al. 2001) that could cause large dynamical changes in microbial community structure. Although May (1973) suggested that increasing complexity in food-web structure might decrease the stability of the system as a whole, recent studies have supported the importance of food-web complexity in enhancing community stability through various mechanisms such as aggregation effects in random population dynamics (King & Pimm 1983), weak interactions due to a 'noise-dampening role' (McCann et al. 1998a, Neutel et al. 2002) and adaptive foraging (Kondoh 2002). In particular, intraguild predation could contribute to the fact that the effects of trophic cascades are unpredictable in some aquatic ecosystems (McCann et al. 1998b, Hart 2002). Therefore, the apparent stability of community structure as a whole might be because random or compensated fluctuations caused by complex interactions in the food webs stabilizes the total community. The mechanisms that stabilize complex plankton food webs should be revealed by future research.

The grazing food webs in warm pool conditions could not explain 54 % of the total carbon demand of cope in 1990 to 1993 and 63 % of chae in 1991 to 1993 (Table 4). Estimation errors involving uncertainty of parameters such as NPP, BP and TTE were not likely to cause this shortage of carbon supply for mesozooplankton. NPP would have to be 557 to 1129 mg C m^{-2} d^{-1}, (1.5 to 3.0 times higher than our estimate) in order to satisfy the estimated carbon demand of cope, but such high rates of NPP have rarely been observed in the equatorial warm pool (Le Borgne et al. 2002a). Furthermore, increasing BP and TTE (2-fold higher BP and TTE plus 0.05) accounted only slightly for 3 and 5 % of the estimated carbon demand of cope, respec-

Table 4. Comparison of carbon supply and demand rates estimated for mesozooplankton. Carbon supply rates estimated using different parameters of bacterial productivity (BP) and trophic level transfer efficiency (TTE) averaged in 1990 to 1993 are also shown. TTE 0.05: using TTE of the base case plus 0.05; 2 BP: assuming 2 times larger BP than the base case. Carbon demands were estimated from empirical equation with body size (Ikeda 1985). S/D is the contribution percentage of each carbon source to the total carbon demand. HNLC: high nutrient, low chlorophyll. Functional group abbreviations as in Table 1

Functional group	HNLC in 1994		Warm pool in 1990 to 1993									
			1990	1991	1992	1993	Avg.		TTE 0.05		2 BP	
	mg C m^{-2} d^{-1}	S/D (%)	mg C m^{-2} d^{-1}				mg C m^{-2} d^{-1}	S/D (%)	mg C m^{-2} d^{-1}	S/D (%)	mg C m^{-2} d^{-1}	S/D (%)
Cope												
Total carbon demand	227		264	246	302	194	251		251		251	
Supply from direct grazing on phytoplankton	288	127	74	50	68	81	68	27	68	27	68	27
Supply from indirect predation on phytoplankton	155	68	32	30	50	42	38	15	48	19	38	15
Supply from indirect predation on bacteria	25	11	5	5	13	11	8	3	11	4	17	7
Unknown (100−S/D, %)		−106						54		49		51
Chae												
Total carbon demand	73		25	132	69	36	66		66		66	
Supply from indirect predation on phytoplankton	72	99	25	18	21	26	22	34	30	45	22	34
Supply from indirect predation on bacteria	4	6	1	1	3	2	2	3	3	5	4	5
Unknown (100−S/D, %)		− 5						63		50		61

tively (Table 4). In addition, considering the observation of Le Borgne et al. (2003) that 75% of the total mesozooplankton biomass in the 0 to 400 m depth range resided at depths shallower than 100 m during the daytime, the carbon demand of cope and chae might still be underestimated, since estimated carbon demand at the mean temperature of 28 to 30°C at 0 to 100 m would be higher than our estimate at 25°C.

The shortage of carbon could reflect dynamic aspects of the food-web structure and the importance of detritus and detritivore feeding, since there was an adequate food supply under HNLC conditions (Table 4). The large difference between the carbon budget in 1990 to 1993 and 1994 is simply because the NPP in 1994 was approximately 3 times higher than that in 1990 to 1993, while cope biomass in 1994 (267 mg C m^{-2}) was intermediate in the 1990 to 1993 range (206 to 316 mg C m^{-2}). The possibility of carbon shortage for omnivorous mesozooplankton has also been indicated by previous field observations in the equatorial pelagic ocean. Using gut-fluorescence measurements, Dam et al. (1995) showed that grazing of omnivorous mesozooplankton on phytoplankton satisfied <20% of the total carbon demand at a respiration efficiency of 33%. This estimation was similar to our estimation for direct grazing of cope on phytoplankton at 25°C in 1990 to 1993 (27% on average, Table 4), but not in 1994 (127%). Roman & Gauzens (1997) also reported a similar result that indicated the importance of food sources other than phytoplankton. Both of the 2 previous studies concluded that insufficient carbon supply must be compensated for by carbon supply from microzooplankton, which graze on bacteria and other small phytoplankton or detritus, or the direct grazing on detritus by the mesozooplankton. In our estimates, neither bacteria nor small phytoplankton that were indirectly grazed by cope could compensate for the remaining carbon demand in 1990 to 1993, since both only contributed 15 to 19% and 3 to 7%, respectively, of the total carbon demand of cope. Considering these facts, detritus must be important as a carbon source for heterotrophic organisms. In addition, temporal variability between HNLC and warm pool conditions in the study region might result in temporal offsets in storage and utilization of carbon sources such as detritus, although this effect could not be determined from our data.

In addition to possible detritivory, there may be other ecological processes not considered in this study. For example, different nutrient utilization efficiencies among phytoplankton taxonomic groups may result in variable growth rates among taxa (Landry et al. 2003). Furthermore, vertical and spatial distributions of plankton (Roman et al. 1995, Blanchot et al. 2001), utilization of marine snow as microhabitats by protozoans

(Azam & Long 2001) and fluctuations of physical and chemical environmental factors might play a role. In future studies of the Equatorial Pacific, such ecological processes, in addition to the food-web complexity examined in this study, should be considered as possible important mechanisms for sustaining plankton-community stability.

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Appendix 1. Net primary productivity (NPP) and bacterial productivity (BP) used carbon flow to estimate, and estimated carbon flux among functional groups. Food composition (%) of each predator is also shown below each predatory functional group. HNLC: high nutrient, low chlorophyll. 'Microzoo' includes hdf, ciliates and naup. Other abbreviations as in Table 1

		1990	1991	1992	1993	Avg.	HNLC 1994
Basal productivity (mg C m^{-2} d^{-1})							
NPP		382	382	382	382	382	1210
BP		107	107	107	107	107	254
Estimated carbon supply (mg C m^{-2} d^{-1})							
hnf		392	404	227	337	340	787
(%)	picop	52	56	61	57	57	55
	nanop	0	3	4	8	4	11
	bac	27	26	30	30	29	30
	hnf	20	14	4	5	11	4
hdf		14	112	86	78	72	315
(%)	nanop	0	0	0	0	0	0
	microp	73	43	30	38	46	42
	hnf	10	18	26	13	17	20
	Microzoo	17	39	44	49	37	38
ciliates		76	37	182	51	86	241
(%)	picop	0	1	46	19	16	33
	nanop	78	38	13	29	39	31
	microp	1	16	3	8	7	7

		1990	1991	1992	1993	Avg.	HNLC 1994
ciliates (continued)							
	bac	0	0	21	10	8	7
	hnf	21	30	14	31	24	18
	Microzoo	0	16	3	3	5	3
nauplii		25	3	11	25	16	62
(%)	nanop	79	38	26	34	44	35
	Others	21	62	74	66	56	65
cope		110	84	131	134	115	468
(%)	nanop	36	15	9	10	18	9
	microp	30	43	43	50	42	52
	hnf	7	4	4	12	7	6
	Microzoo	26	37	39	26	32	27
	cope	0	0	5	2	2	6
chae		26	19	24	28	24	77
(%)	cope	93	86	86	94	90	84
	Others	7	14	14	6	10	16
Total grazing		642	659	660	653	654	1950