



Planktonic trophic structure in a coral reef ecosystem – Grazing versus microbial food webs and the production of mesozooplankton



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ABSTRACT

The relative contributions of grazing versus microbial food webs to the production of mesozooplankton communities in coral reef ecosystems remains an important and understudied field of inquiry. Here, we investigated the biomass and production of component organisms within these two food webs, and compared them to those of mesozooplankton on a coral reef in Okinawa, Japan throughout four seasons in 2011–2012. The relative production of grazing (phytoplankton) and microbial (nano and microzooplankton) food webs were on average 39% (7–77%) and 37% (19–57%), respectively, of the food requirements of particle-feeding mesozooplankton. Carbon flows within this planktonic food web suggested that primary production from the grazing food web could not satisfy the nutritional demands of mesozooplankton, and that the microbial food web contributed a significant amount of nutrition to their diets. These results also show that the heterotrophic components of the microbial food web (nano and microzooplankton) and mesozooplankton consume the equivalent of the entire phytoplankton production (particulate net production) each day, while the microzooplankton were almost entirely eaten by higher trophic levels (mesozooplankton) each day. However, even the combined production from both the grazing and microbial food webs did not fulfill mesozooplankton food requirements in some seasons, explaining 26–53%, suggesting that detritus was used to compensate for nutritional deficiencies during these periods. Understanding the flow of energy throughout coral reefs requires a detailed accounting of pelagic sources and sinks of carbon. Our results provide such an assessment and indicate that detailed investigation on the origin and production of detritus is necessary to better understand pelagic trophodynamics in coral ecosystems.

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1. Introduction

Understanding the ecological dynamics of mesozooplankton communities (the zooplankton that can be collected by a common plankton net such as a 200 μm mesh net) is critical for understanding the ecological dynamics of marine and freshwater pelagic ecosystems because they facilitate major energy and material transfers from primary producers to higher trophic levels such as fishes and benthic planktivorous animals (Hardy, 1924). Therefore, the amount of organic matter produced by primary producers that is transferred to mesozooplankton has been a long-term question

for ecologists working in marine and freshwater ecosystems (Berglund et al., 2007; Hayashi and Uye, 2008; Kankaala et al., 1996; Kobari et al., 2016; Pagano et al., 2006).

Mesozooplankton are often classified into two functional groups by feeding behavior characteristics: predatory-feeders and particle (or suspension)-feeders (Ohtsuka and Nishida, 1997) (Fig. 1). The former consists of relatively large carnivorous mesozooplankton (such as chaetognaths) that are capable of capturing organisms of relatively higher swimming ability, while the latter includes herbivores, omnivores, and detritivores obtaining energy and organic matter from three different pathways: grazing, microbial and detrital food webs (Legendre and Rassoulzadegan, 1995; Ohtsuka and Nishida, 1997). The grazing (or herbivorous) food web is based mainly on microphytoplankton that are consumed

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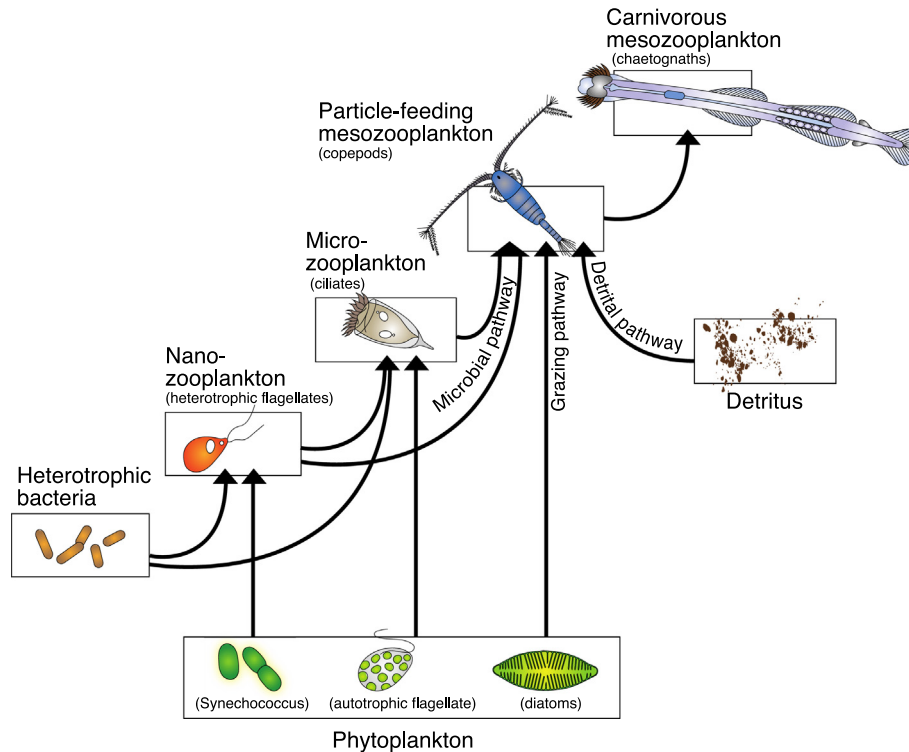


Fig. 1. Schematic carbon-flow diagram of planktonic food webs in marine waters. Names in parentheses provide one example of an organism in each category.

directly by mesozooplankton (Lignell, 1993). In contrast, the microbial food web starts with heterotrophic bacteria and/or pico- and nanophytoplankton that are transferred to mesozooplankton via nano- and microzooplankton such as protists and copepod nauplii (Azam et al., 1983; Calbet and Saiz, 2005; Nakamura and Turner, 1997; Pomeroy, 1974; Sherr and Sherr, 1987; Stoecker and Capuzzo, 1990). Meanwhile, the detrital food web is based on detritus originating from non-living organic matter such as dead animals, plants and feces as well as attached microorganisms (Meyer and Bell, 1989; Roman, 1984, 1977). These different food webs often co-exist spatiotemporally in aquatic ecosystems (Berglund et al., 2007; Koshikawa et al., 1996), and assessing the relative importance of the different pathways has been a goal for understanding the ecological dynamics of marine and freshwater ecosystems. The most productive situations may involve a multivorous web, in which each different food web plays significant roles (Legendre and Rassoulzadegan, 1995). In marine ecosystems, most investigations on these relative dominances of different food webs have been conducted in temperate regions (Ara and Hiromi, 2009; Giering et al., 2014; Kobari et al., 2016; Koshikawa et al., 1996; Lopes et al., 2016; Minutoli and Guglielmo, 2012; Shinada et al., 2001; Wylie and Currie, 1991). For instance, in the Oyashio region off Japan, transferred organic matter through the grazing food chain is a significant pathway to mesozooplankton during spring while that in the microbial food chain is the important pathway during winter and summer (Shinada et al., 2001). However, relatively fewer studies have been done in tropical and subtropical regions, and little is known in coral reef ecosystems (Dupuy et al., 2016; Sakka et al., 2002).

Coral reef ecosystems are distributed in shallow oligotrophic waters in the inter-tropical regions (30°N–30°S) in the oceans (Salvat, 1992). In coral reef ecosystems, mesozooplankton play a significant role in trophodynamics, serving as one of the important food sources to various reef fish and benthic planktivores including scleractinian (reef-building) corals (Coma et al., 1999; Glynn, 1973;

Houlbrèque et al., 2004; Sebens et al., 1996). Approximately half of the benthic animals on coral reefs are filter feeders, or particle feeders, which feed on zooplankton and particulate organic matter (POM) (Houlbrèque et al., 2004; Sorokin, 1995); and larvae and juveniles of many species of reef fishes grow by feeding specifically on mesozooplankton (Sampey et al., 2007). Therefore, mesozooplankton are critically important components in coral reef ecosystems, and their ecological dynamics are of major interest for understanding the reef ecological dynamics. To date, the abundance and biomass of mesozooplankton communities have been examined in coral reefs worldwide for more than five decades (Table 1). However, the production rates that are crucial for understanding the material and energy flow from lower to higher trophic levels are still comparatively sparse on coral reefs, making it difficult to understand the ecological dynamics of this ecosystem.

The trophic environment of mesozooplankton in coral reef ecosystems remains paradoxical. The biomass of phytoplankton is generally low in coral reef waters with typical concentrations of chlorophyll-*a* (chl-*a*) at approximately 0.2–0.6 µg chl-*a* l⁻¹ (Nakajima et al., 2016) due to a low concentration of inorganic nutrients (e.g., dissolved inorganic P < 0.3 µmol l⁻¹; N 0.05–0.5 µmol l⁻¹, (Hearn et al., 2001). Picophytoplankton (<2–3 µm) comprise the majority (>50%) of the phytoplankton assemblage in such oligotrophic environments (Furnas et al., 1990; Tada et al., 2001) because a large surface area to volume ratio is an advantage over larger cells for nutrient uptake (Chisholm, 1992; Dufour et al., 1999). Although primary production of coral reef phytoplankton can sometimes be comparable to that in temperate water, the majority of the production is achieved by picophytoplankton (Charpy and Blanchot, 1999; Pagano et al., 2012). These small picophytoplankton cells are not readily utilized by many particle-feeding mesozooplankton because they are too small to be captured (Bartram, 1981; Berggreen et al., 1988; Landry and Lehner-Fournier, 1988; Ohtsuka and Kubo, 1991; Ohtsuka and Nishida, 1997), and microzooplankton selectively and efficiently

Table 1

Summary of coral reef mesozooplankton abundance, biomass, and production. N, net-tow; P, pump; M, moored net; B, bucket; D/N, day/night; FR, French Polynesia; GBR, Great Barrier Reef. Values in parenthesis indicate the average.

Site	Reference	Specific sampling site	Method	Time	Mesh	Abundance	Biomass	Production
					(μm)	(ind. m^{-3})	(mg C m^{-3})	($\text{mg C m}^{-3} \text{ day}^{-1}$)
<i>Atlantic Ocean</i>								
San Blas Island (Panama)	Porter (1974)	–	N	Night	160	4003	–	–
		–	N	Night	160	1184–1343 (1264)	–	–
Barbados	Moore and Sander (1976)	–	N	Day	239	345	0.6 ^{a,b}	–
Limon (Costa Rica)	Alvaro Morales and Murillo (1996)	Lagoon/off reef	N	Day?	280	232–1035 (644)	–	–
	Carrillo-Baltodano and Morales-Ramírez (2016)	Lagoon	N	Day	200	3082–42,402 (12,847)	0.4–7.3 ^{a,b}	–
Kingston (Jamaica)	Moore and Sander (1979)	–	N	Day	203	1698	1.6 ^{a,b}	–
Discovery Bay (Jamaica)	Heidelberg et al. (2004)	Forereef	P	Night	40	1252–5059 (3172)	1.0–15.6 (4.7)	–
Laurel Reef (Puerto Rico)	Glynn (1973)	Reef flat/lagoon	B	Day	76	<25,000	–	–
		Reef flat/lagoon	B	Night	76	>25,000	–	–
Mahahual Reef (Mexico)	Suárez-Morales and Gasca (2000)	Lagoon	N	Dusk	300	3161–6657 (4777)	–	–
		Lagoon	N	Day	300	149–5272 (2000)	–	–
Virgin Island (USA)	McFarland et al. (1999)	–	–	D/N	–	<10–1163	–	–
Florida Keys (USA)	Leichter et al. (1998)	Reef slope	N	Day	105	~124	0.1–1.4 (0.4) ^{a,b,d}	–
		Reef slope	N	Day ^g	105	~1714	0.6–3.2 (1.6) ^{a,b,d}	–
	Heidelberg et al. (2010)	Reef flat	P	Day	40	1805–4805 (2946)	3.5–8.7 (5.1)	–
		Reef flat	P	Dawn/Dusk	40	3,922–5489 (4459)	11.9–19.2 (14.9)	–
		Reef flat	P	Night	40	3370–6333 (4474)	11.8–23.4 (16.5)	–
<i>Indian Ocean</i>								
Eilat (Israel)	Yahel et al. (2002)	Forereef	P	Day	100	811	–	–
		Forereef	P	Night	100	1622	–	–
	Yahel et al. (2005a)	Forereef	P	Day	500	10	–	–
		Forereef	P	Night	500	59	–	–
	Yahel et al. (2005b)	Forereef	P	Day	100	793	0.6 ^a	–
		Forereef	P	Night	100	1940	1.0 ^a	–
Kavaratti Atoll (India)	Tranter and George (1972)	Lagoon	N	Night	200	565	–	–
	Goswami (1983)	Lagoon	N	Day	330	–	–	5.3 ^h
	Suresh and Mathew (1997)	Lagoon	B	Day	Silk	61–1987	–	–
		Lagoon	B	Night	Silk	1404–5762	–	–
	Goswami and Goswami (1990)	Lagoon	N	D/N	335	–	0.04–2.0 ^{a,b,d}	–
Minocoy Atoll (India)	Goswami and Goswami (1990)	Lagoon	N	D/N	335	–	0.3–1.8 ^{a,b,d}	–
Iles Eparses	Bouvy et al. (2016), Dupuy et al. (2016)	Lagoon	N	?	80	33–6008 (2514)	–	–
<i>Pacific Ocean</i>								
Princess Charlotte Bay (GBR, Australia)	McKinnon et al. (2005)	Reef flat/lagoon	N	D/N	73	25,400	7.4 ^{a,b}	–
Cairns-Innisfail sector (GBR, Australia)	McKinnon et al. (2005)	Reef flat/lagoon	N	D/N	73	8700	8.2 ^{a,b}	–
Lizard Island (GBR, Australia)	Allredge and King (1977)	Sand flat	N	Day	235	61	–	–
		Sand flat	N	Night	235	636	–	–
Low Isles (GBR, Australia)	Sorokin and Sorokin (2010)	Off deep lagoon	N	Day	120	4000–10,000	3.9–7.8 (6.3) ^{a,b,c}	–
		Off deep lagoon	N	Night	120	9000–20,000	13.7–17.4 (15.7) ^{a,b,c}	–
Davies Reef (GBR, Australia)	Hamner et al. (1988)	Reef crest	N	Day	250	–	0.1–0.9 (0.4) ^a	–
		Reef crest	N	Day	250	–	0.2–0.6 (0.6) ^a	–
	Roman et al. (1990)	Lagoon	N	Day	200	8–100 (42)	0.2–0.5 (0.2)	–
		Lagoon	N	Night	200	7–141 (88)	0.1–0.8 (0.4)	–
Heron Island (GBR, Australia)	Sale et al. (1976)	Reef slope	N	Night	210	300	–	–
		Lagoon	N	Night	210	200	–	–
	Sorokin and Sorokin (2009)	Off reef	N	Day	220	–	1.7–26.8 (12.0) ^{a,b,c}	–
		Off reef	N	Night	220	–	6.7–31.2 (17.4) ^{a,b,c}	–
North West Cape (Australia)	McKinnon and Duggan (2003)	Lagoon	N	?	73	2400–33,000 (7800) ^f	0.33–5.06 ^f	0.11–1.0 (0.42) ^f
Uvea Atoll (New Caledonia)	Le Borgne et al. (1997)	Lagoon	N	D/N	200	–	3.6	4.1
Taiaro Atoll (French Polynesia)	Carleton and Doherty (1998)	Lagoon	N	Night	500	50–110 (68)	–	–
		Ocean	N	Night	500	10–23 (17)	–	–

Table 1 (continued)

Site	Reference	Specific sampling site	Method	Time	Mesh (μm)	Abundance (ind. m^{-3})	Biomass (mg C m^{-3})	Production ($\text{mg C m}^{-3} \text{ day}^{-1}$)
Takapoto Atoll (French Polynesia)	Sakka et al. (2002)	Lagoon	N	Morning	250	–	6.6 ^b	8.2 ^{e,h}
Tikehau Atoll (French Polynesia)	Le Borgne et al. (1989)	Lagoon	N	D/N	200	–	5.6–7.0 (6.3)	–
Moorea (French Polynesia)	Lefevre (1985)	Lagoon	N	Day	200	5–1125 (298)	–	–
	Alldredge and King (2009)	Back reef	P	Day	200	59	–	–
		Back reef	P	Night	200	58–119 (89)	–	–
Ahe Atoll (French Polynesia)	Pagano et al. (2012)	Lagoon	N	?	80	5058–23,324	2.6–10.4 ^{a,b}	–
Enewetak Atoll (Marshall Islands)	Gerber and Marshall (1982)	Lagoon	N	Day	158/239	460–1769 (945)	2.2–5.7 (4.0)	–
Palau Islands	Motoda (1994; 1940)	Bay	N	Day	330	385	0.03 ^{a,b}	0.2
		Lagoon	N	Day	330	835	0.1 ^{a,b}	0.4
		Ocean	N	Day	330	371	0.03 ^{a,b}	0.2
Lighthouse Reef (Palau)	Hamner et al. (2007)	Near back reef	M	Night	305	–	0.8–1.0 (0.9) ^{a,b,c}	–
		Forereef	M	Night	305	–	0.7–5.8 (4.0) ^{a,b,c}	–
Redang Island (Malaysia)	Nakajima et al. (2008)	Reef flat	N	Day	100	2619	5.8	–
		Reef flat	N	Night	100	8846	18.5	–
Tioman Island (Malaysia)	Nakajima et al. (2009b)	Reef flat	N	Day	100	3168	2.2	–
		Reef flat	N	Night	100	4629	4.6	–
	Nakajima et al. (2014)	Reef flat	N	D/N	100	5922–8363 (7261)	2.3–3.3 (2.7)	0.93–1.8 (1.3)
Akajima Island (Okinawa, Japan)	Omori et al. (2015)	Outer reef	N	Day	100	58–962 (332) ^f	–	–
Ishigaki Island (Okinawa, Japan)	Fukuoka et al. (2015)	Forereef	N	Day	100	3314 ^f	–	–
		Offshore	N	Day	100	677 ^f	–	–
Sesoko Island (Okinawa, Japan)	Go et al. (1997)	Reef flat/edge/slope	N	Day	94	196–405	0.3–1.2 ^{a,b,c}	0.30–3.42 (1.40)
		Reef edge	N	Day	94	347	0.7 ^{a,b,c}	–
		Reef slope	N	Day	94	405	1.2 ^{a,b,c}	–
	This study	Reef flat	N	Night	180	1243–6689 (3554)	7.0–36.5 (20.3)	1.8–9.1 (4.8)

Biomass was calculated assuming (a) carbon weight (CW) = 0.37 ash free dry weight (AFDW) ([Nagao et al., 2001](#)); (b) AFDW = 0.53 dry weight (DW) ([Nagao et al., 2001](#)); (c) DW = 0.1 wet weight (WW) ([Odate and Maita, 1988](#)); and (d) DW = 18.6 settling volume (SV) ([Grindley and Wooldridge, 1974](#)). (e) Assuming a daily production/biomass ratio of 124% day^{-1} ([Sakka et al., 2002](#)); (f) copepod only; (g) during internal breaking waves; (h) calculated from areal value by depth (m).

graze on the larger phytoplankton cells (Sakka et al., 2000; Zhou et al., 2015). Particle-feeding mesozooplankton communities (both on coral reefs and in adjacent oceanic waters), therefore, can utilize only a small fraction of phytoplankton production from the grazing food web. Nevertheless, mesozooplankton communities on coral reefs are highly abundant compared to adjacent oceanic waters (Carleton and Doherty, 1998; Fukuoka et al., 2015). For example, on an atoll of Tuamotu Archipelago (French Polynesia), the abundance of mesozooplankton within coral reef lagoons is ca. 6-fold greater than those at the surrounding oceanic water (Carleton and Doherty, 1998). These large differences between in-reef and out-reef mesozooplankton communities have fueled much debate regarding trophic transfer and the quantitative balance of phytoplankton and mesozooplankton in coral reef ecosystems (Le Borgne et al., 1997; Nakajima et al., 2014; Roman et al., 1990; Sakka et al., 2002).

To make up for this paradox, detrital and microbial food webs may play significant roles on the nutrition cascades or pathways in the coral reef ecosystem (Pagano et al., 2012). Indeed, previous studies have reported that detritus (as opposed to phytoplankton) might be the main food source for particle-feeding mesozooplankton on coral reefs, given the low contribution of phytoplankton to particulate organic matter (POM) (Roman et al., 1990) and observations of gut contents (Gerber and Marshall, 1974). However, these studies did not fully consider the production and potential contributions of the microbial food web (components such as nano and microzooplankton). Coral reef waters are dominated by picoplankton (heterotrophic and autotrophic bacteria), which channel through the microbial food web (Ferrier-Pagès and Furla, 2001), and may explain the high production of mesozooplankton despite low available phytoplankton production. However, few studies have considered the contributions of the microbial food web to reef mesozooplankton production (Sakka et al., 2002), and the relative importance of grazing versus microbial food webs to the diets of mesozooplankton on coral reefs remains unclear in a quantitative perspective. Similarly, the relative contributions of detritus to mesozooplankton production is also of great interest and not well-described. If the summed production of the grazing and

microbial food webs does not satisfy mesozooplankton food requirements, then the detrital pathway may also be an important component for mesozooplankton as well.

Here, we examined production within grazing and microbial food webs on a coral reef, and compared these values with the food requirements of the associated mesozooplankton community. Specifically, our study addressed three key topics regarding mesozooplankton production: (1) whether phytoplankton production, alone, could satisfy food requirements of the mesozooplankton, (2) the relative production from microbial versus grazing food webs available for mesozooplankton production, and (3) the importance of the detrital pathway as a function of other sources of nutrition.

2. Materials and methods

2.1. Study site and periods

This study was carried out on a coral reef along southeastern Sesoko Island, at the Sesoko Station of the Tropical Biosphere Research Center (University of the Ryukyus), Okinawa, Japan (26°38'N, 127°52'E) (Fig. 2). The reef covers an area of ca. 2500 m² and the reef flat is ca. 100 m wide and ca. 1 m deep at low tide and 2 m deep at high tide (Van Woesik et al., 2011). The study site is a protected zone, managed by the research station, where unauthorized collection of animals is prohibited and artificial light (e.g., from street and building lights) does not affect the ambient light field on the reef at night. Sampling was conducted during four seasons: May 2011 (spring), August 2011 (summer), November 2011 (fall), and January 2012 (winter) at Sesoko Island. Water temperatures (mean ± SD) vary from 19.5 ± 1.1 °C in winter to 29.4 ± 1.0 °C in summer with an overall mean of 24.3 ± 4.1 °C.

2.2. Sample collection

We collected zooplankton samples at nighttime (20:00–22:00 h) during high tide for three consecutive days during each

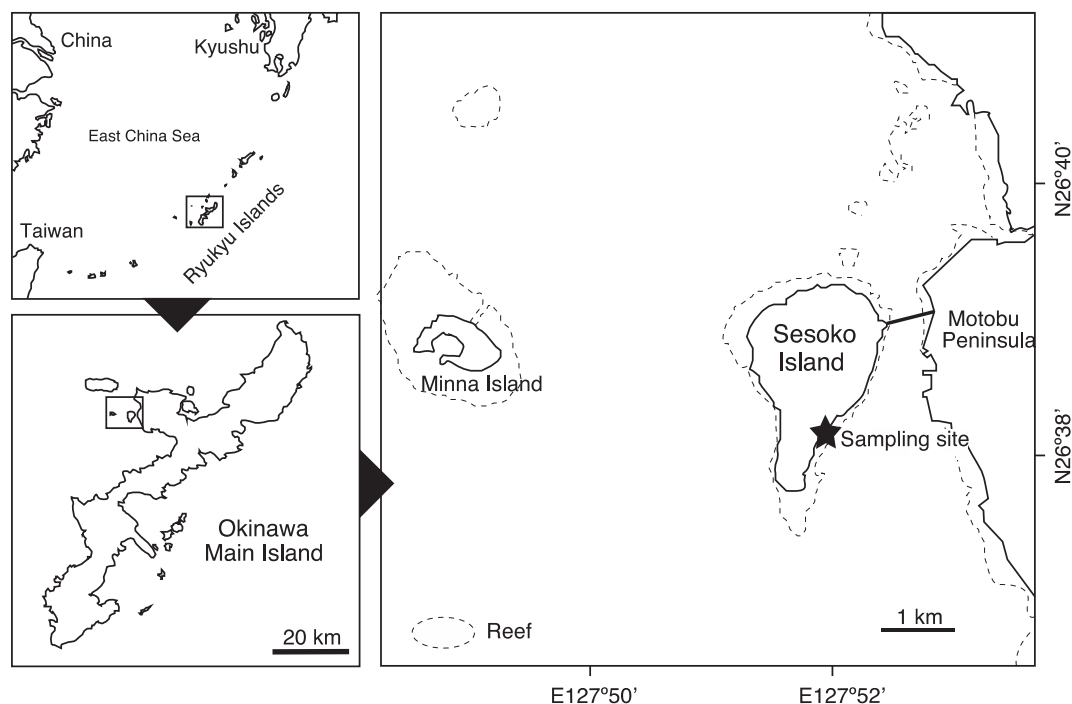


Fig. 2. Map of the study site, Sesoko Island, Okinawa Japan (modified from (Hohenegger et al., 1999)). Dashed lines correspond to the reef edge.

study period. The timing of sunset was 19:12, 19:16, 17:42 and 18:05 h in May, August, November and January, respectively. Mesozooplankton were sampled by pooling five oblique tows of a plankton net (mesh size, 180- μ m; diameter, 30 cm; length, 90 cm) equipped with a pre-calibrated flow-meter (model 2030, General Oceanics) from the seafloor to the surface. The pooled samples were immediately brought back to the laboratory within 5 min, and fixed with buffered formalin to a final concentration of 5% for subsequent microscopic observation.

Prior to mesozooplankton collections, surface seawater was collected using a bucket (inner volume: 10 L). The water was pre-filtered through a 180- μ m mesh screen to remove mesozooplankton and brought back to the laboratory for the measurement of the concentrations of chlorophyll-*a* (chl-*a*), and particulate organic carbon (POC) and nitrogen (PON). Seawater was also sampled by a 5-l acid-washed Van Dorn bottle at 0.5 m depth below the surface for the enumerations of heterotrophic bacteria (hereafter called bacteria), nanozooplankton (heterotrophic nanoflagellates or HNF), and microzooplankton (ciliates and copepod nauplii). The collected seawater in the Van Dorn bottle was gently transferred to an acid-washed container (inner volume: 10 L) using a silicone tube attached to the sampling bottle to avoid air bubbles, which may break up fragile cells of protists. The container was filled with the sampled water from the sampler and rendered free of air space by the use of a tight cover and immediately brought back to the laboratory.

2.3. Sample analysis

For POC/N analysis, triplicate subsamples (2 L each from bucket) were filtered onto pre-combusted (500 °C; 4 h) GF/F filters (25 mm, Whatman), rinsed with 1 N HCl followed by distilled water to remove carbonates, and then dried for 24 h at 60 °C and stored in a desiccator until analysis. The POC/N concentration was measured using a CN analyzer (Flash EA-1112, Thermo Finnigan). For chl-*a* analysis, triplicate subsamples (1 L each from bucket) were filtered onto GF/F filters (25 mm), then immersed in *N,N*-dimethylformamide (DMF) and stored frozen at -20 °C until analysis (Suzuki and Ishimaru, 1990). Chl-*a* concentrations were determined using a fluorometer (10-AU, Turner Designs) (Welschmeyer, 1994).

For bacterial counts, triplicate subsamples (15 ml each from Van Dorn bottle) were transferred into sterilized Corning tubes and fixed with buffered formalin (1% final conc.) and stored at 5 °C for 3–5 days, then stored frozen at -20 °C until analysis. Triplicate subsamples (200 ml each from Van Dorn bottle) for enumeration of HNF were transferred into dark polycarbonate bottles and fixed in 1% glutaraldehyde seawater and stored at 5 °C until analysis. To enumerate bacteria, 1.6–2 ml of the formalin fixed sample was filtered onto a 0.2 μ m black membrane filter (Isopore, Millipore) and stained with SYBR Gold (Molecular Probes) (Shibata et al., 2007). For HNF, 100 ml of the glutaraldehyde fixed sample was filtered onto a 0.8 μ m black membrane filter (Isopore, Millipore), and the filter was stained with primulin (Sigma) (Sherr et al., 1993). Bacteria and HNF were counted with an epifluorescence microscope (Axioskop 2 plus, Zeiss) using UV and blue light excitations at $\times 1000$ magnification. Autotrophic plankton were distinguished from non-pigmented heterotrophic bacteria or flagellates by autofluorescence signals. For bacteria, at least 400 cells were counted per filter, and 20–50 microscope fields per filter were scanned for flagellates. Heterotrophic bacterial numbers might have been overestimated due to the possibility of lowered autofluorescence signals of picophytoplankton due to our preservation protocols (see above).

For microzooplankton enumeration, triplicate subsamples (500 ml each from the Van Dorn bottle) were transferred into dark

polycarbonate bottles and fixed with acid Lugol's solution (3% final conc.) and stored at 5 °C until analysis. Microzooplankton samples (500 ml) were concentrated by settling to a final volume of 50 ml, and then transferred to an Utermöhl settling chamber (Hydro-Bios) for further sedimentation, which were counted under an inverted microscope (Axiovert 25, Zeiss). In this study, tintinnid and naked ciliates and copepod nauplii were assigned to the microzooplankton.

Mesozooplankton were identified to the lowest taxonomic level possible and counted under a dissecting microscope (SZX16, Olympus). Large zooplankton species (e.g. mysids and larval decapods) were first counted and sorted, then the remaining sample was split (1/1–1/4), from which all zooplankton were characterized and enumerated. At least 300 zooplankton were enumerated in each sample. Copepods were identified to species whenever possible. After the counting of individuals in each sample, individual abundances per cubic meter were calculated from the filtered volumes measured by the flowmeter and the frequency of sample split.

2.4. Biomass estimation

The carbon biomass of total phytoplankton was estimated from chl-*a* concentration using a C:Chl-*a* ratio. The C:Chl-*a* ratio varies from ca. 12 to >200 in phytoplankton cultures (Taylor et al., 1997), and the choice of these factors may affect the relative importance of phytoplankton biomass to POM. The ratios are highly regulated in response to irradiance, nutrient availability and temperature. It is minimal at high temperature (>25 °C) and low irradiances (<20 μ mol photons $m^{-2} s^{-1}$) under nutrient-replete conditions and increases at high irradiances especially at low temperature and under nutrient-limiting conditions (Taylor et al., 1997). In this study, we used a C:Chl-*a* ratio of 50, as our coral reef experiences high irradiances in an oligotrophic environment at relatively high temperatures. A C:Chl-*a* ratio of 50 has often been used for calculate phytoplankton C biomass in other coral reefs (Charpy-Roubaud et al., 1989).

The biomass (B , $mg C m^{-3}$) of a given taxonomic group was estimated based on its abundance (A , inds. m^{-3}) and individual carbon weight (CW , $mg C$): $B = A \times CW$. Individual carbon weight (CW , $mg C$) of bacteria, nano-, micro- and mesozooplankton was estimated as follows. Bacterial cell numbers or cell volumes (μm^3) of HNF were converted to carbon units using conversion factors (Table 2). The cell volumes of HNF were calculated from the length and width measured by an image analysis software (AxioVision, Zeiss) and a digital camera (Zeiss AxioCam MRC5, Zeiss) mounted on the microscope. For microzooplankton, the length and width of tintinnids and naked ciliates were measured to determine their lorica or cell volumes (μm^3), respectively. The lorica volume (LV , μm^3) of tintinnids and cell volume of naked ciliates were converted to carbon

Table 2

Conversion factors or formulae to estimate carbon weight (CW) for the planktonic microorganisms. LV: lorica volume (μm^3); BL: body length (μm); HNF, heterotrophic nanoflagellates.

Taxonomic groups	Conversion factor/equation	Reference
Heterotrophic bacteria	$CW (fg) = 20 \text{ cell}^{-1}$	Lee and Fuhrman (1987)
HNF	$CW (fg) = 183 \mu m^{-3}$	Caron et al. (1995)
Tintinnid ciliates	$CW (pg) = 444.5 + 0.053 LV (\mu m^3)$	Verity and Lagdon (1984)
Naked ciliates	$CW (fg) = 190 \mu m^{-3}$	Putt and Stoecker (1989)
Copepod nauplii	$\log CW (ng) = 2.94 \times \log BL (\mu m) - 4.82$	Uye et al. (1996)

Table 3

Length-weight regression equations used for biomass calculation of different mesozooplankton taxa. DW, dry weight; AFDW, ash free dry weight; D, body diameter; BL, full body length; PL, prosome length; CL, carapace length; TL, trunk length; Log, common logarithm (\log_{10}); ln, natural logarithm (\log_e).

Taxonomic group	Equation	Reference
Medusae	$\log CW (\mu g) = -8.71 + 2.75 \times \log D (\mu m)$	Hirota (1986)
Gastropod veliger	$\log CW (\mu g) = -5.85 + 2.46 \times \log BL (\mu m)$	Hirota (1986)
Bivalve veliger	$\log CW (\mu g) = -3.45 + 1.47 \times \log BL (\mu m)$	Hirota (1986)
Polychaete larvae	$\log CW (\mu g) = -5.97 + 2.10 \times \log BL (\mu m)$	Hirota (1986)
Ostracods	$\ln CW (\mu g) = 1.03 + 1.46 \times \ln BL (mm)$	Heidelberg et al. (2010)
Copepods		
Acartia	$\ln DW (\mu g) = -19.19 + 3.09 \times \ln PL (\mu m)$	Chisholm and Roff (1990)
Centropages	$\ln DW (\mu g) = -22.86 + 3.68 \times \ln PL (\mu m)$	Chisholm and Roff (1990)
Clausocalanus	$\ln DW (\mu g) = -19.65 + 3.25 \times \ln PL (\mu m)$	Chisholm and Roff (1990)
Euchaeta	$\ln DW (\mu g) = -17.82 + 3.00 \times \ln PL (\mu m)$	Webber and Roff (1995)
Paracalanus	$\ln DW (\mu g) = -19.65 + 3.25 \times \ln PL (\mu m)$	Chisholm and Roff (1990)
Calanopia	$\ln DW (\mu g) = -15.47 + 2.67 \times \ln PL (\mu m)$	Chisholm and Roff (1990)
Scolecithrix	$\ln DW (\mu g) = -21.36 + 3.57 \times \ln PL (\mu m)$	Webber and Roff (1995)
Temora	$\ln DW (\mu g) = -19.59 + 3.34 \times \ln PL (\mu m)$	Chisholm and Roff (1990)
Other calanoids	$\ln DW (\mu g) = -15.93 + 2.73 \times \ln PL (\mu m)$	Webber and Roff (1995)
Oithona simplex	$\log AFDW (\mu g) = -8.76 + 3.47 \times \log PL (\mu m)$	Hopcroft et al. (1998b)
Other Oithonidae	$\log AFDW (\mu g) = -8.18 + 3.16 \times \log PL (\mu m)$	Hopcroft et al. (1998b)
Corycaeidae	$\log AFDW (\mu g) = -7.17 + 2.80 \times \log PL (\mu m)$	Hopcroft et al. (1998b)
Farranula	$\ln DW (\mu g) = -16.19 + 2.72 \times \ln PL (\mu m)$	Webber and Roff (1995)
Oncaea	$\ln DW (\mu g) = -11.63 + 2.10 \times \ln PL (\mu m)$	Webber and Roff (1995)
Other cyclopoids	$\ln DW (\mu g) = -11.64 + 1.96 \times \ln PL (\mu m)$	Chisholm and Roff (1990)
Harpacticoids	$\log DW (\mu g) = -8.51 + 3.26 \times \log BL (\mu m)$	Hirota (1986)
Copepod nauplii (all species)	$\log CW (ng) = -4.82 + 2.94 \times \log BL (\mu m)$	Uye et al. (1996)
Isopods	$\ln CW (\mu g) = 1.03 + 1.46 \times \ln BL (mm)$	Heidelberg et al. (2010)
Amphipods	$\ln CW (\mu g) = 1.03 + 1.46 \times \ln BL (mm)$	Heidelberg et al. (2010)
Cumaceans	$\ln CW (\mu g) = 1.03 + 1.46 \times \ln BL (mm)$	Heidelberg et al. (2010)
Mysids	$\log CW (\mu g) = -0.167 + 3.10 \times \log BL (mm)$	Uye (1982)
Decapods		
Brachyuran zoea	$\log CW (\mu g) = -8.68 + 3.39 \times \log CL (\mu m)$	Hirota (1986)
Brachuran megalopa	$\log CW (\mu g) = -4.59 + 2.19 \times \log CL (\mu m)$	Hirota (1986)
Other decapod larvae	$\ln CW (\mu g) = 1.03 + 1.46 \times \ln BL (mm)$	Heidelberg et al. (2010)
Tanaids	$\ln CW (\mu g) = 1.03 + 1.46 \times \ln BL (mm)$	Heidelberg et al. (2010)
Cirriped nauplii	$\log CW (\mu g) = -6.90 + 2.65 \times \log BL (\mu m)$	Hirota (1986)
Cirriped cypris	$\log CW (\mu g) = -8.64 + 3.0 \times \log BL (\mu m)$	Japan Fisheries Agency (1987)
Chaetognaths	$\log CW (\mu g) = -0.93 + 2.79 \times \log BL (mm)$	Hirota (1986)
Appendicularians	$\log DW (\mu g) = -6.10 + 2.47 \times \log TL (\mu m)$	Hopcroft et al. (1998a)

weight (CW) using a regression equation or a factor, respectively (Table 2). The carbon weight of copepod nauplii was calculated from the body length measurements (Table 2).

For mesozooplankton biomass estimation, the length of an appropriate body portion, e.g., prosome length for copepods and full body length for amphipods, was measured using an eyepiece micrometer (Hirota, 1986). The length measurements were converted to carbon weight of zooplankton individuals (CW, mg C) using previously reported length-weight regression equations (Table 3). Regressions for copepods are modified assuming either $CW = 47\% DW$ (Hirota, 1981) or ash free dry weight (AFDW) = $89\% DW$ (Båmstedt, 1986). Regression for appendicularians are modified assuming $CW = 44.2\% DW$ (Hirota, 1986). Reported length-weight regressions of many species that occur at the sampling site are not available, but we used regressions according to similarity in genus or shape. Regressions for copepods of the same genus were employed whenever possible. Regressions established in tropical or subtropical seas were also employed as much as possible. Upon estimation of body weight, we considered the reported values of formalin shrinkage for the soft-bodied organisms; i.e., 5% length shrinkage in chaetognaths (Szyper, 1976), 20% body length shrinkage in cnidarians (Wang et al., 1995) and 30% shrinkage in polychaete larvae (White and Roman, 1992).

2.5. Production measurement and estimation

While the production rate (P , $mg C m^{-3} d^{-1}$) of phytoplankton was directly measured using stable isotope tracer method, those

of bacteria, nano-, micro-, and mesozooplankton were obtained based on their biomass (B , $mg C m^{-3}$) and specific growth rates (G , d^{-1}): $P = B \times G$. The growth rate (G , d^{-1}) of bacteria and HNF were measured by *in situ* incubation and those of microzooplankton (nauplii) and mesozooplankton were estimated using temperature-body weight related regressions in the present study.

Net primary production rate (P , $mg C m^{-3} d^{-1}$) of phytoplankton was determined by the *in situ* ^{13}C tracer method (Hama et al., 1983). The ^{13}C method with incubation for >12 h estimates primary production similar to that determined by the ^{14}C method, and this method with incubation for 24 h provides close to actual daily net primary productivity in natural environments (Hama et al., 1983). We collected seawater samples at 0.5 h before sunrise using a bucket, which was pre-filtered through a 180 μm -mesh to remove mesozooplankton. Quadruplicate subsamples (2 L each) of the collected seawater were dispensed into separate acid washed polycarbonate bottles (inner volume, 2 L), three for clear and one for dark, and incubated *in situ* at a depth of 1 m for 24 h after the addition of ^{13}C -sodium bicarbonate (Hama et al., 1983). Final ^{13}C atom% of dissolved inorganic carbon (DIC) was ca. 10% of that in the ambient water. DIC concentration in the seawater was determined in advance using a total organic C analyzer (Shimadzu, TOC-5000). After incubation, the samples were filtered onto pre-combusted (500 $^{\circ}C$; 4 h) GF/F filters. These filters were rinsed with 1N HCl followed by distilled water to remove carbonates, and then dried at 60 $^{\circ}C$ and stored in a desiccator until analysis. The isotopic ratios of ^{13}C to ^{12}C were determined by a mass spectrometer (Thermo Scientific Flash, EA1112) to determine the bulk carbon fixation rate.

Table 4Regression equations for estimating instantaneous growth rate (G , day^{-1}). Log, common logarithm (\log_{10}); T , water temperature ($^{\circ}\text{C}$); CW , body carbon weight (μg).

Taxonomic group		Equation	Reference
Hydrozoans Polychaetes Copepods		$\log G = -0.423 - 0.219 \times \log CW$	Hirst et al. (2003)
		$\log G = -0.630 + 0.409 \times \log CW$	Hirst et al. (2003)
	Broadcast-spawner ^a		
	Adult	$\log G = 0.0232 \times T - 0.285 \times \log CW - 1.196$	Hirst et al. (2003)
	Copepodites	$\log G = 0.0352 \times T - 0.233 \times \log CW - 1.230$	Hirst et al. (2003)
	Sac-spawner ^b		
	Adult	$\log G = 0.0223 \times T + 0.177 \times \log CW - 1.644$	Hirst et al. (2003)
	Copepodites	$\log G = -1.545 + 0.0408 \times T$	Hirst et al. (2003)
	Nauplii	$\log G = 0.0370 \times T - 0.0795 \times \log CW - 1.3840$	Hirst and Lampitt (1998)
Other crustaceans		$\log G = 0.0263 \times T - 0.327 \times \log CW - 0.919$	Hirst et al. (2003)
Chaetognaths		$\log G = -1.851 + 0.0367 \times T$	Hirst et al. (2003)
Appendicularians		$\log G = -0.495 + 0.0285 \times T$	Hirst et al. (2003)

^a Copepods which shed eggs freely, i.e. calanoids observed in the present study except for *Clausocalanus* and *Pseudodiaptoms*.^b Copepods which carry their eggs externally on the body, i.e. *Clausocalanus*, *Pseudodiaptoms*, all cyclopoids, and all harpacticoids observed in the present study.

The specific growth rate (G , d^{-1}) of bacteria and HNF was measured using the dialysis membrane method (Herndl and Velimirov, 1986). Seawater sampled by Van Dorn bottle as described above was immediately filtered either through $10\ \mu\text{m}$ mesh screens by reverse filtration or $2\ \mu\text{m}$ membrane filters (Millipore) by gravity filtration in order to obtain the seawater containing only bacteria ($<2\ \mu\text{m}$) or bacteria + HNF ($<10\ \mu\text{m}$). Triplicate subsamples ($1000\ \text{ml}$ each) of the filtrate ($<2\ \mu\text{m}$ or $<10\ \mu\text{m}$) were dispensed into separate cellulose dialysis membrane tubes (Spectra/Por, cut off 12,000–14,000 Da), which have proven to be sufficiently permeable to inorganic and organic nutrients (diffusive exchange of $<1\ \text{h}$) (Ferrier-Pagès and Furla, 2001). The dialysis tubes were incubated where the sample water was originated for 24 h. Incubation was started within 2 h of sample collection. Cell numbers of bacteria and HNF at the beginning and the end of the incubation were measured as described above. Growth rates (G , d^{-1}) of bacteria and HNF were obtained according to the following equation: $G = (\ln N_f - \ln N_i) (T_f - T_i)^{-1}$, where N_f and N_i are cell numbers (cells ml^{-1}) at the beginning (T_i) and end (T_f) of the incubation period. The specific growth rates (G , d^{-1}) of ciliates were estimated using the previously reported growth rate ($1.01\ \text{d}^{-1}$ at $28\ ^{\circ}\text{C}$) in the coral reefs of Miyako Island, Okinawa, relatively near to the present sampling site (Ferrier-Pagès and Gattuso, 1998). A Q_{10} of 2.5 was adopted for temperature correction (Caron et al., 1995).

The specific growth rates (G_z , d^{-1}) of mesozooplankton (copepods, other crustaceans, chaetognaths, cnidarians, appendicularians and polychaete larvae) were estimated from previously reported regression equations (Table 4). The biomass and production of particle-feeding and predatory mesozooplankton were calculated separately on the basis of the feeding habits of each group based on literatures (Table S1).

2.6. Detritus mass estimation

The amount of detritus (mg C m^{-3}) was estimated by subtracting the organic C value of organisms (i.e. sum of the carbon biomass of bacteria, nano- and microzooplankton and phytoplankton) from that of POC (Anderson and Rudehäll, 1993). Since our POC was collected on GF/F glass fiber filter (Whatman) and some bacterial biomass has been known to pass through it, the contribution of bacterial carbon to POC may be overestimated (Lee et al., 1995). We therefore calculated the bacterial proportion in the POC fraction assuming that 30% of bacterial biomass passed through the GF/F filter (Lee et al., 1995). However, the biomass of the attached bacteria to the detritus was not distinguished in this study, thus the estimated amount of detritus may be overestimated to some degree.

2.7. Trophic structure

In order to estimate the relative contribution of grazing and microbial food webs to mesozooplankton food requirements, production from either the grazing food web (phytoplankton) or microbial food web (microzooplankton + HNF) were compared to the food requirement of particle-feeding mesozooplankton. To determine the potential carbon flow from prey organisms to consumers, the amount of carbon required (= food requirement, $\text{mg C m}^{-3}\ \text{day}^{-1}$) for metazoan and protozoan zooplankton was estimated using a gross growth efficiency of 0.3 (Ikeda and Motoda, 1978) and 0.4 (Fenchel, 1982), respectively. We performed a sensitivity analysis for the calculation of food requirement of metazoan and protozoan zooplankton, using a lower (0.25 for metazoan; 0.3 for protozoan) and upper (0.35 for metazoan; 0.5 for protozoan) gross growth efficiency (Kobari et al., 2008; Steinberg et al., 2008).

HNF and microzooplankton can efficiently graze on relatively smaller phytoplankton (such as pico- and nanophytoplankton), while mesozooplankton mainly capture larger phytoplankton (such as microphytoplankton) (Sheldon, 1977; Vargas and González, 2004). We therefore assumed that mesozooplankton can feed and utilize “residual” phytoplankton that was not consumed by HNF and microzooplankton. In order to estimate the available (=residual) phytoplankton production for mesozooplankton, we subtracted half of the food requirements by HNF and microzooplankton from the production of phytoplankton based on the assumption that they feed both autotrophic and heterotrophic preys equally to simplify the feeding habits. Similarly, the production of HNF that can be utilized by mesozooplankton was estimated by subtracting half of the food requirement by microzooplankton from the production of HNF (=residual HNF production), based on the assumption that microzooplankton can efficiently graze on HNF rather than mesozooplankton (Nakano et al., 2001).

3. Results

3.1. Seasonal changes in autotrophic plankton

Chl-*a* concentrations in the water column were low throughout the study periods, ranging from $0.249 \pm 0.021\ \text{mg chl-}a\ \text{m}^{-3}$ in spring to $0.263 \pm 0.048\ \text{mg chl-}a\ \text{m}^{-3}$ in fall and did not vary significantly among seasons (ANOVA, $P = 0.45$). Phytoplankton C biomass estimated from chl-*a* ranged from $12.4 \pm 1.0\ \text{mg C m}^{-3}$ to $13.2 \pm 2.4\ \text{mg C m}^{-3}$ (Fig. 3a). In contrast to the stable phytoplankton biomass, primary production varied significantly (ANOVA, $P = 0.006 \times 10^{-5}$) from $2.1 \pm 0.3\ \text{mg C m}^{-3}\ \text{d}^{-1}$ in winter to $29.5 \pm 1.4\ \text{mg C m}^{-3}\ \text{d}^{-1}$ in summer (Fig. 3a).

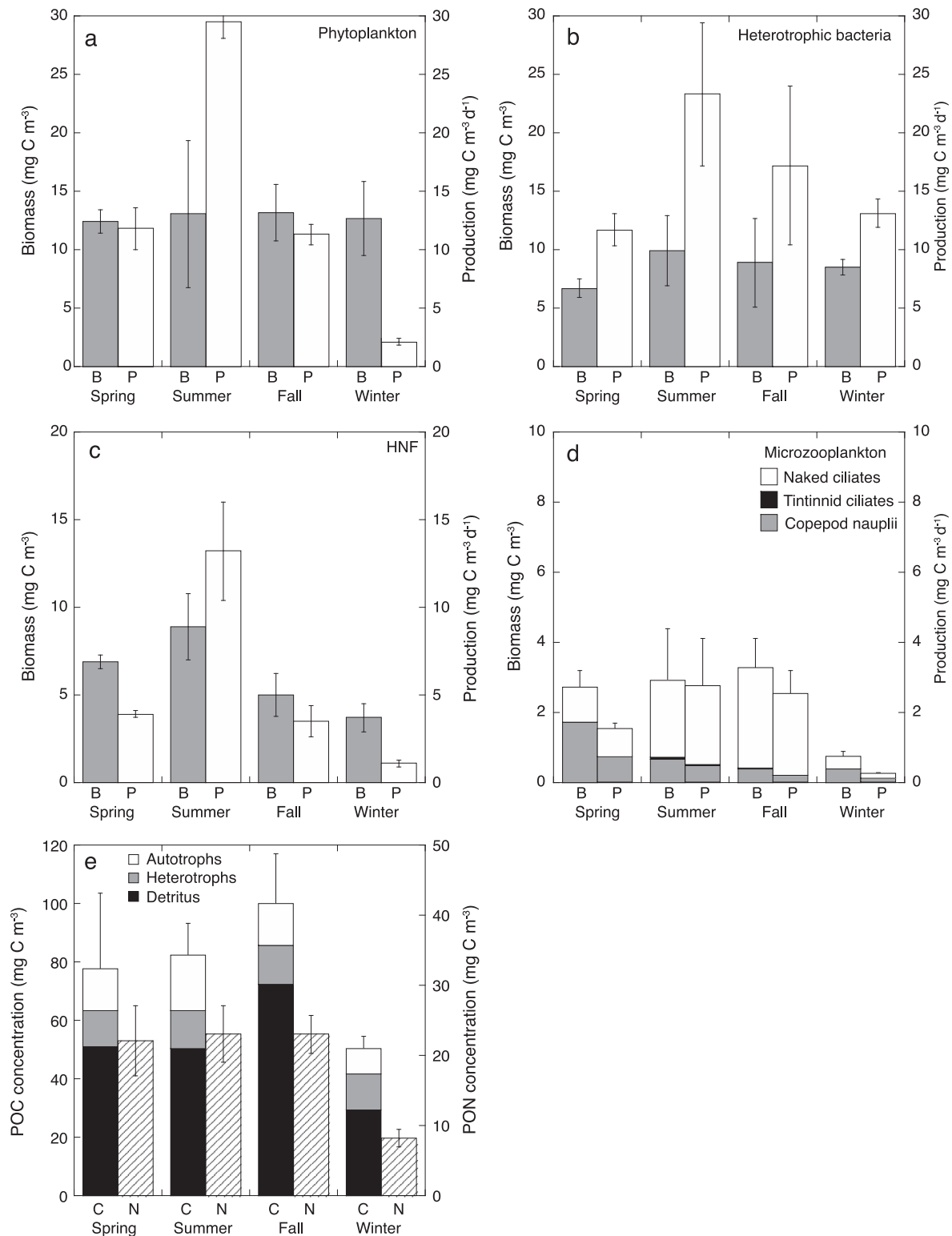


Fig. 3. Seasonal changes in biomass (B) and production (P) of (a) phytoplankton, (b) heterotrophic bacteria, (c) heterotrophic nanoflagellates (HNF) and (d) microzooplankton, and (e) concentrations of particulate organic carbon (POC) and nitrogen (PON) with composition of POC at Sesoko Island, Okinawa. Error bars indicate standard deviation.

3.2. Seasonal changes in heterotrophic plankton

The biomass of the heterotrophic microorganisms (i.e., bacteria, HNF and microzooplankton) was generally higher in summer when temperatures were highest, though naked ciliates showed higher biomass in fall (Fig. 3b–d). Mean bacterial biomass ranged from 6.7 ± 0.8 mg C m⁻³ in spring to 9.9 ± 3.0 mg C m⁻³ in summer.

Bacterial specific growth rate (d⁻¹) ranged from 1.56 ± 0.17 d⁻¹ in winter to 2.08 ± 0.15 d⁻¹ in summer, which resulted in the bacterial production rate ranging from 11.7 ± 1.4 mg C m⁻³ day⁻¹ in spring to 23.3 ± 6.1 mg C m⁻³ day⁻¹ in summer (Fig. 3b).

Mean biomass of nanozooplankton (HNF) varied between 3.7 ± 0.8 mg C m⁻³ in winter and 8.9 ± 1.9 mg C m⁻³ in summer (Fig. 3c). HNF growth rate (d⁻¹) ranged from 0.29 ± 0.08 d⁻¹ in

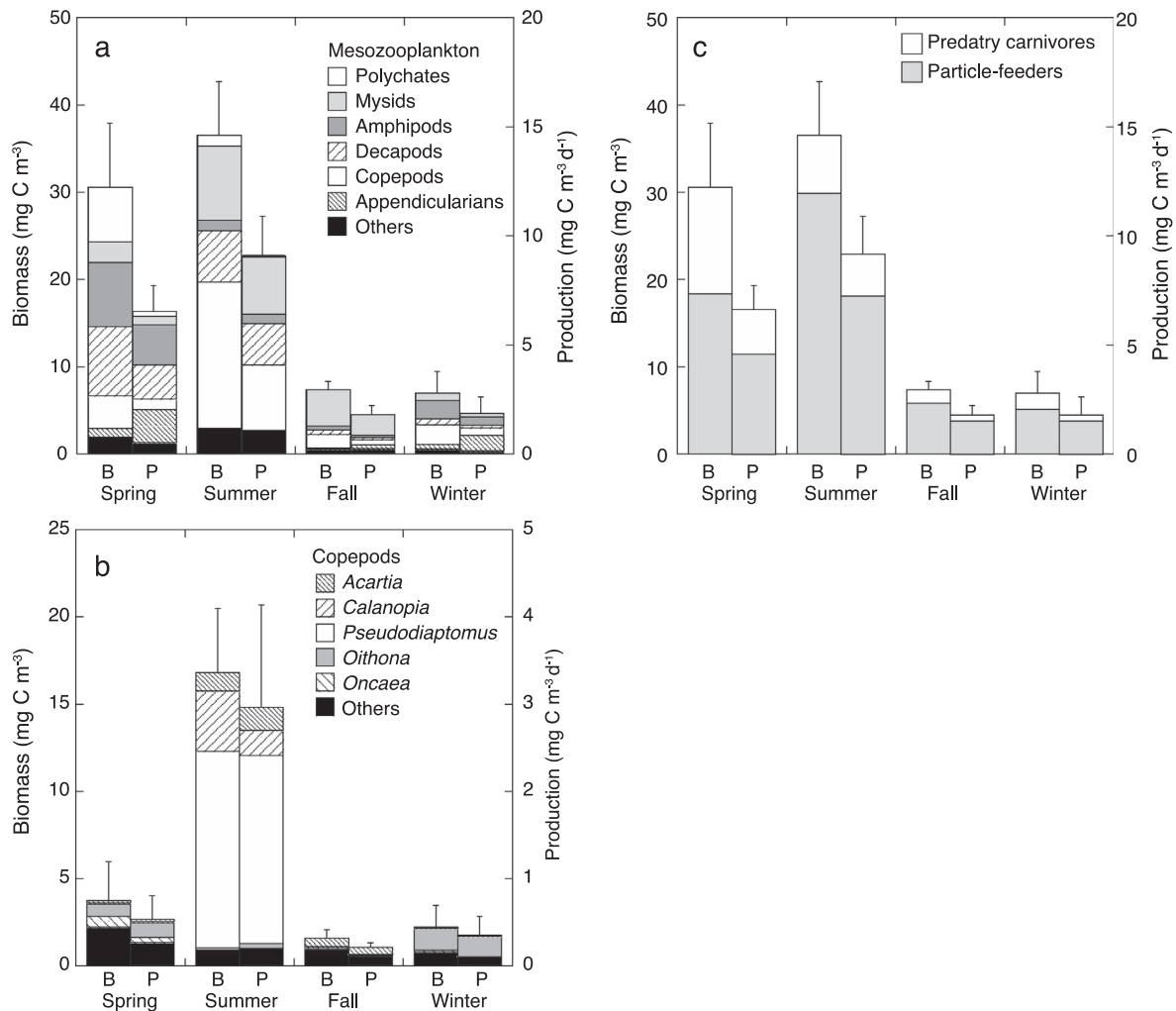


Fig. 4. Seasonal changes in composition, biomass (B) and production (P) of (a) mesozooplankton and (b) copepods, and (c) the contribution of carnivores and particle-feeders to mean biomass or production of mesozooplankton at Sesoko Island, Okinawa. Error bars indicate standard deviation.

spring to $1.48 \pm 0.39 \text{ d}^{-1}$ in summer, which resulted in the production rate ranging from $1.1 \pm 0.2 \text{ mg C m}^{-3} \text{ day}^{-1}$ in winter to $13.2 \pm 2.8 \text{ mg C m}^{-3} \text{ day}^{-1}$ in summer (Fig. 3c).

Microzooplankton (tintinnids, naked ciliates and copepod nauplii) biomass ranged from 0.7 ± 0.2 to $3.3 \pm 0.8 \text{ mg C m}^{-3}$ (Fig. 3d). Of these microzooplankton assemblages, naked ciliates and copepod nauplii constituted 36.8–87.5% and 12.1–63.2% of the total biomass of microzooplankton, respectively, and tintinnids were poorly represented ($\sim 1\%$). The estimated production rate of microzooplankton ranged from $0.3 \pm 0.03 \text{ mg C m}^{-3} \text{ day}^{-1}$ in winter to $2.7 \pm 1.4 \text{ mg C m}^{-3} \text{ day}^{-1}$ in summer (Fig. 3d).

3.3. POC composition

Mean (\pm SD) POC concentration ranged from $50.4 \pm 4.0 \text{ mg C m}^{-3}$ in winter to $100.1 \pm 16.5 \text{ mg C m}^{-3}$ in fall, while PON varied from $8.2 \pm 1.2 \text{ mg C m}^{-3}$ to $23.1 \pm 4.0 \text{ mg C m}^{-3}$ (Fig. 3e). C/N ratio of POM was 3.5 ± 0.6 in spring, 3.6 ± 0.3 in summer, 4.3 ± 0.4 in fall and 6.2 ± 1.0 in winter. Autotrophic plankton (phytoplankton) C biomass contributed 13.2–25.1%; heterotrophic plankton (i.e., bacteria, HNF and microzooplankton) contributed 14.5–22.8%, and the remainder indicated that detritus contributed 57.9–72.4% to total POC (Fig. 3e).

3.4. Mesozooplankton biomass and production

Mesozooplankton showed higher biomass in spring and summer compared to fall and winter (Fig. 4a). Mean (\pm SD) biomass of mesozooplankton ranged from $7.0 \pm 2.4 \text{ mg C m}^{-3}$ in winter to $36.5 \pm 6.1 \text{ mg C m}^{-3}$ in summer, while the abundance ranged from $1243 \pm 106 \text{ inds. m}^{-3}$ in fall to $6689 \pm 2079 \text{ inds. m}^{-3}$ in summer (Table S1). Copepods were one of the most dominant groups, constituting 12.3–46.1% of the mesozooplankton biomass. Mysids (mostly *Anisomysis* sp.), amphipods (dominated by Synopiidae sp.) and decapods each constituted 7.8–54.9%, 3.5–28.3% and 7.8–25.9% of the total mesozooplankton biomass, respectively. The estimated production rate (mean \pm SD) of the mesozooplankton community varied from $1.8 \pm 0.4 \text{ mg C m}^{-3} \text{ d}^{-1}$ in fall to $9.1 \pm 1.8 \text{ mg C m}^{-3} \text{ d}^{-1}$ in summer. Similar to the biomass, copepods, mysids, amphipods and decapods were important groups to the mesozooplankton production, contributing 8.1–32.6%, 6.3–51.1%, 4.8–27.7%, and 5.1–23.7%, respectively. In addition, appendicularians predominantly contributed to the total production (8.6–38.8%, except summer) due to their fast growth rate.

The copepod biomass varied between $1.6 \pm 0.5 \text{ mg C m}^{-3}$ in fall and $16.8 \pm 3.6 \text{ mg C m}^{-3}$ in summer (Fig. 4b). The copepod

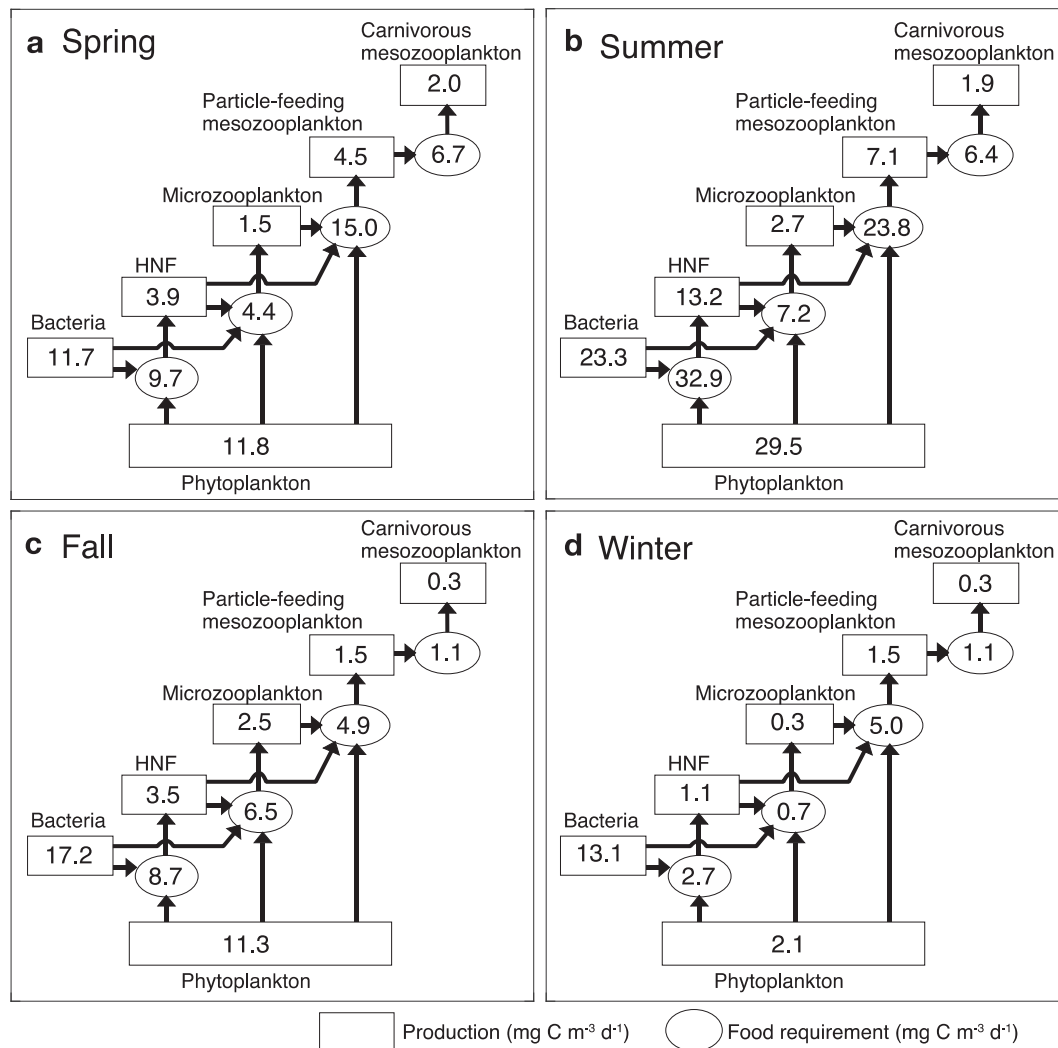


Fig. 5. Schematic carbon-flow diagrams in the coral reef water during four seasons of the year at Sesoko Island, Okinawa. Values in boxes denote production rate ($\text{mg C m}^{-3} \text{ d}^{-1}$) and values in circles are food requirements ($\text{mg C m}^{-3} \text{ d}^{-1}$) of the components above them. Black arrows indicate carbon flows from prey to predators. HNF, heterotrophic nanoflagellates. The food requirement was calculated assuming a gross growth efficiency of 0.3 (Ikeda and Motoda, 1978) for metazoan and 0.4 (Fenchel, 1982) for protozoan zooplankton (see the methods section). In this study, we assume that mesozooplankton can feed and utilize “residual” phytoplankton that is not consumed by HNF and microzooplankton. The available (=residual) phytoplankton production for mesozooplankton is obtained by subtracting half of the food requirements by HNF and microzooplankton from the production of phytoplankton based on the assumption that they feed on both autotrophic and heterotrophic prey equally, to simplify the feeding habits.

community was dominated by *Acartia* (dominated by *A. fossae* and *A. negligens*, 1.8–29.5%), *Clausocalanus* (0.1–15.7%), *Calanopia* (mostly *C. thompsoni*, 0.0–20.5%), *Pseudodiaptomus* (mostly *P. nihonkaiensis*, 0.0–66.9%), *Tortanus* (dominated by *T. digitalis*, *T. erabuensis*, and *T. ryukyuensis*, 1.0–35.7%), *Oithona* (mostly *O. simplex* and *O. tenuis*, 0.8–55.4%), and *Oncaea* (mostly *O. venusta*, 0.0–16.8%). The copepod production rate varied from $0.21 \pm 0.06 \text{ mg C m}^{-3} \text{ d}^{-1}$ in fall to $2.95 \pm 1.19 \text{ mg C m}^{-3} \text{ d}^{-1}$ in summer.

Among the mesozooplankton biomass, those of particle-feeders such as appendicularians, *Paracalanus* and *Oithona* copepods ranged from $5.2 \pm 2.0 \text{ mg C m}^{-3}$ in winter to $29.9 \pm 3.2 \text{ mg C m}^{-3}$ in summer, while predatory carnivores such as *Tortanus* copepods and chaetognaths varied from $1.6 \pm 0.4 \text{ mg C m}^{-3}$ in fall to $12.2 \pm 3.4 \text{ mg C m}^{-3}$ in spring (Fig. 4c). The production of particle-feeding mesozooplankton ranged from $1.5 \pm 0.5 \text{ mg C m}^{-3} \text{ d}^{-1}$ in fall to $7.1 \pm 0.9 \text{ mg C m}^{-3} \text{ d}^{-1}$ in summer, while the predatory mesozooplankton production varied from 0.3 ± 0.1 in fall to $2.0 \pm 0.6 \text{ mg C m}^{-3} \text{ d}^{-1}$ in spring.

3.5. Trophic structure

The productions of assemblages from grazing and microbial food webs and mesozooplankton and their trophic relationship are shown in Fig. 5a–d. The daily food (carbon) requirements of nanozooplankton (HNF) ranged from $2.7 \pm 0.6 \text{ mg C m}^{-3} \text{ d}^{-1}$ in winter to $32.9 \pm 6.9 \text{ mg C m}^{-3} \text{ d}^{-1}$ in summer (overall: $13.5 \pm 13.3 \text{ mg C m}^{-3} \text{ d}^{-1}$), while those of microzooplankton varied from $0.8 \pm 0.2 \text{ mg C m}^{-3} \text{ d}^{-1}$ in winter to $7.6 \pm 3.7 \text{ mg C m}^{-3} \text{ d}^{-1}$ in summer (overall: $5.0 \pm 3.0 \text{ mg C m}^{-3} \text{ d}^{-1}$). The combined food requirement of HNF and microzooplankton ranged from 3.4–40.2 $\text{mg C m}^{-3} \text{ d}^{-1}$, which corresponded to 59.7–82.1% of the production of phytoplankton and 22.3–76.2% of the combined production of phytoplankton and bacteria. Assuming that half of each food requirement by HNF and microzooplankton relies on phytoplankton, the combined food requirement by HNF and microzooplankton ranged from 1.7–20.1 $\text{mg C m}^{-3} \text{ d}^{-1}$, which was equivalent to 59.7–82.1% of phytoplankton production. Assuming the other half of the food requirements by HNF and microzooplankton are

Table 5

Mean food requirements of particle-feeding mesozooplankton and the relative (%) contribution of available production from grazing, microbial and combined (grazing + microbial) food webs to the food requirements. The productions of grazing and microbial food webs were obtained after subtracting of the food requirements by nano- and microzooplankton. The ranges in parenthesis are the lower and upper ends of sensitivity analysis for gross growth efficiency.

Parameter	Spring (May 2011)	Summer (August 2011)	Fall (November 2011)	Winter (January 2012)
Food requirement ($\text{mg C m}^{-3} \text{ d}^{-1}$)	15.0 (12.8–17.9)	23.8 (20.4–28.6)	4.9 (4.2–5.8)	5.0 (4.3–6.0)
% contribution of grazing food web	31.8 (14.3–47.5)	39.4 (9.8–65.5)	76.4 (21.1–125.0)	7.3 (–2.8–16.1)
% contribution of microbial food web	21.3 (14.6–27.8)	51.7 (39.2–63.6)	56.8 (29.6–81.3)	18.9 (14.1–23.5)
% contribution of combined food web (grazing + microbial food webs)	53.1 (28.9–75.4)	91.1 (49.0–129.1)	133.1 (50.7–206.3)	26.2 (11.3–39.6)

satisfied by heterotrophic organisms (bacteria and HNF, respectively), the other half of the food requirement of HNF corresponded to 10.1–70.8% of bacterial production, while those of microzooplankton were equivalent to 27.4–93.1% of HNF production.

The food requirement by predatory mesozooplankton ranged from $1.1 \pm 0.5 \text{ mg C m}^{-3} \text{ d}^{-1}$ in winter to $6.7 \pm 2.1 \text{ mg C m}^{-3} \text{ d}^{-1}$ in spring, which corresponded to 69.9%–150.5% of the production of their particle-feeding mesozooplankton prey. The transfer efficiency (%) from particle-feeding mesozooplankton to predatory carnivorous mesozooplankton was 45.1% (spring), 26.9% (summer), 21.8% (fall) and 21.0% (winter). The food requirement of the particle-feeding mesozooplankton ranged from $4.9 \pm 1.5 \text{ mg C m}^{-3} \text{ d}^{-1}$ in fall to $23.8 \pm 3.1 \text{ mg C m}^{-3} \text{ d}^{-1}$ in summer (Table 5, Fig. 6). The contribution of the grazing food web (=residual phytoplankton production after removal of the requirement by HNF and microzooplankton) to the food requirement of particle-feeding mesozooplankton was on average $38.7 \pm 28.6\%$ (7.3% in winter to 76.4% in fall) (Fig. 6). Similarly, the contribution of the microbial food web, i.e., the productions of microzooplankton + residual nanozooplankton (HNF production after removal of the requirement by microzooplankton) was on average $37.2 \pm 19.8\%$ (18.9% in winter to 56.8% in fall). The microbial food web production corresponded to 67.1–257.7% (average: $132.6 \pm 88.2\%$) of the grazing food web production. When considering the combined production from both the grazing and microbial food webs, the combined production was $7.9 \text{ mg C m}^{-3} \text{ d}^{-1}$ in spring, $21.7 \text{ mg C m}^{-3} \text{ d}^{-1}$ in summer, $6.5 \text{ mg C m}^{-3} \text{ d}^{-1}$ in fall, and $1.3 \text{ mg C m}^{-3} \text{ d}^{-1}$ in winter,

which corresponded to 53.1%, 91.1%, 133.1%, and 26.2% of the food requirement of particle-feeding mesozooplankton, respectively (Table 5, Fig. 6). The transfer efficiency (%) from the component organisms from both the food webs to particle-feeding mesozooplankton was 56.5% (spring), 32.9% (summer), 22.5% (fall) and 114.6% (winter).

4. Discussion

4.1. Mesozooplankton production

This study describes the biomass and production of coral reef mesozooplankton and their prey to elucidate the planktonic trophic structure not previously well-described quantitatively. We estimated mesozooplankton production rates using the multiple regression models based on temperature and body mass for various zooplankton species (Brown and Sibly, 2012; Hirst et al., 2003; Hirst and Lampitt, 1998). Although the production rates estimated by our empirically-derived regression models may differ from actual *in situ* measurements of species-specific growth rates, which are time-consuming and not practical in application, our models allowed for more general and rapid estimation and comparison of the relative production of each component of the entire zooplankton community (Huo et al., 2012).

The production rates of mesozooplankton from various coral reefs are summarized in Table 1. It is difficult to directly compare the results from different studies because of the differences in sampling methods (e.g., net mesh size, net mouth diameter) and timing (e.g., day, morning, night) and differences in the estimation of specific growth rates (e.g., egg production rates based on culture experiments, models based on temperature-body mass, and use of reported turnover time). Yet, the overall mean production rate of the mesozooplankton community in this study ($4.8 \text{ mg C m}^{-3} \text{ d}^{-1}$) was comparable to those from atolls in French Polynesia, New Caledonia and Lakshadweep (Table 1). Our mesozooplankton community production in summer ($9.1 \text{ mg C m}^{-3} \text{ d}^{-1}$) was ca. 7-fold higher than that in the tropical coral reef of Malaysia.

4.2. Planktonic food web structure

The significant seasonal variation of phytoplankton primary production, in contrast to the stable phytoplankton biomass, indicates very high grazing mortality for phytoplankton in this system. Although we did not conduct the size-fractionation of phytoplankton in this study, a previous study reported that the annual average proportions of pico-, nano- and microphytoplankton to total phytoplankton biomass at the same sampling site were 52%, 34% and 11% (Tada et al., 2001). Assuming that size-fractionated primary production is directly proportional to size-fractionated biomass (Shinada et al., 2001), the major contributor to the primary production would be pico- and nanophytoplankton (ca. 80%), which would likely be intensely grazed by nanozooplankton (HNF) and microzooplankton (Ferrier-Pagès and Gattuso, 1998; González et al., 1998; Sakka et al., 2000). In fact, half of the food requirement

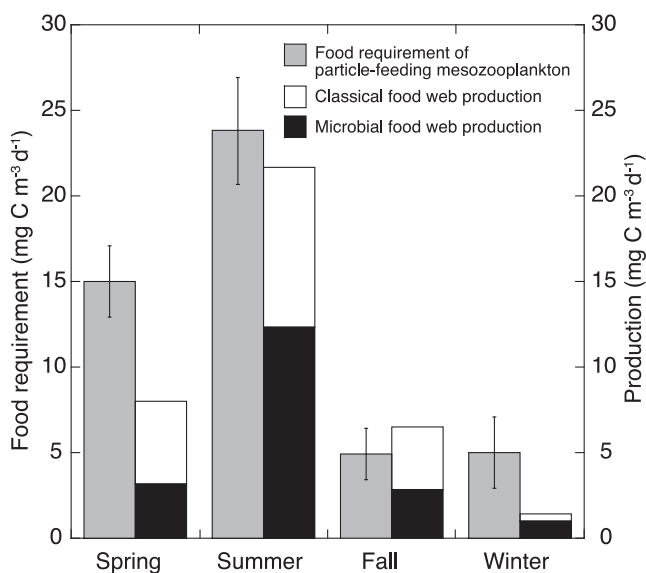


Fig. 6. Seasonal changes in food requirement of particle-feeding mesozooplankton (mean \pm SD) and the available production from grazing and microbial food webs after subtracting the food requirements by HNF and/or microzooplankton. The food requirement was calculated assuming a gross growth efficiency of 0.3 (Ikeda and Motoda, 1978) for metazoan and 0.4 (Fenchel, 1982) for protozoan zooplankton (see the methods section).

by HNF and microzooplankton in this study even corresponded to 60–82% of phytoplankton production. This suggests that the majority of phytoplankton production would be consumed by HNF and microzooplankton throughout the year. Moreover, the carbon requirements of mesozooplankton were even higher than the available (=residual) phytoplankton production after removal of the fraction by HNF and microzooplankton. This high grazing on phytoplankton entirely by heterotrophic plankton is most likely the reason for the stable phytoplankton biomass relative to the variable primary production.

The food requirements of particle-feeding mesozooplankton ($4.9\text{--}23.8\text{ mg C m}^{-3}\text{ d}^{-1}$) were close or even higher than the primary production of phytoplankton ($2.1\text{--}29.5\text{ mg C m}^{-3}\text{ d}^{-1}$). Considering that the major portion of the phytoplankton community is dominated by picophytoplankton in this location (ca. 50%, Tada et al., 2001), which is too small to be consumed by most mesozooplankton (Landry and Lehner-Fournier, 1988; Ohtsuka and Kubo, 1991), it is not likely that in this case phytoplankton production meets the mesozooplankton requirement. In fact, the available (or residual) phytoplankton production could only satisfy 7%–76% (average: 39%) of the mesozooplankton requirements (Fig. 6). As demonstrated by sensitivity analyses (Table 5), the particle-feeding mesozooplankton carbon demand in fall (November 2011) can be lower than residual phytoplankton production if upper gross growth efficiencies are applied for both the metazoan and protozoans. However, considering higher variability of the relative contribution of the grazing food web to mesozooplankton carbon demand (16.1–125.0%) for the pairs of upper gross growth efficiency, the moderate gross growth efficiency values we used (or ever lower values) are reasonable for the estimation of the contribution of grazing food webs. These results indicate that phytoplankton alone do not meet their metabolic demands. Similar results were reported from other coral reefs in the GBR (Roman et al., 1990) and Malaysia (Nakajima et al., 2014), where they

reported that low phytoplankton stocks failed to meet the metabolic demands of the zooplankton community. Therefore phytoplankton production does not satisfy the metabolic demands of mesozooplankton in coral reefs.

If low phytoplankton production fails to meet mesozooplankton nutritional demands, food requirements can be subsidized by production from the microbial food web such as nanozooplankton (HNF) and microzooplankton (Ara and Hiromi, 2009; Bouvy et al., 2016; David et al., 2006). Some particle-feeding mesozooplankton (e.g., *Acartia* copepods) selectively feed on microzooplankton (e.g., ciliates) rather than phytoplankton (Robertson, 1983; Stoecker and Sanders, 1985). Although the ingestion by particle-feeding mesozooplankton is lower than that of microzooplankton, previous studies also showed that smaller mesozooplankton, such as *Oithona* and *Paracalanus* copepods, feed on HNF (Gifford et al., 2007; Vargas and González, 2004). Since the ingestion rate on HNF by microzooplankton is higher than that by mesozooplankton (Vargas and González, 2004), only the residual HNF production after subtracting the food requirements of microzooplankton was considered available to the mesozooplankton community in this study. The microbial food web production, the production of microzooplankton + residual HNF, corresponded to 67–258% (average: 133%) of the grazing food web production (=residual primary production), suggesting the importance of the component organisms from microbial food web as diet for mesozooplankton. Similar results were reported from the low phytoplankton concentration of Gironde estuary where copepods fed significantly on microzooplankton (protozoans) to meet their metabolic demand in phytoplankton scarce environment (David et al., 2006). Yet, the mesozooplankton food requirements were not satisfied by the components from the microbial food web alone, even considering lower and upper gross growth efficiencies as indicated in the sensitivity analysis (Table 5), explaining 14–81% (19–57% with moderate gross growth efficiency) of the consumer's requirements (Fig. 6).

Table 6
Summary of detritus concentration (mg C m^{-3}) and its contribution (%) to particulate organic carbon (POC) from several coral reefs. Values in parenthesis indicate the average. FR, French Polynesia; GBR, Great Barrier Reef.

Site	Specific sampling site	POC size (μm)	POC (mg C m^{-3})	Detritus (mg C m^{-3})	Detritus (%)	Reference
Enewetak Atoll (Marshall Islands)	Lagoon	>0.45	24–54 (40)	24	77–93 (85)	Gerber and Marshall (1982)
Tikehau Atoll (Tuamotu, FR)	Lagoon	>0.7	203	177	88	Charpy and Charpy-Roubaud (1990)
Takapoto atoll (FR)	Lagoon	>0.7	198	116 ^a	59	Sakka et al. (2002)
Davies Reef (GBR, Australia)	Lagoon	>0.7	115.7	89	>75	Roman et al. (1990))
Tioman Island (Malaysia)	Reef-flat	>0.7	167–276 (189)	169	86–92 (89)	Nakajima et al. (2011)
Miyako Island (Okinawa, Japan)	Lagoon	>0.3	76–125 (97)	51	35–73 (52)	Casareto et al. (2000)
Sesoko Island (Okinawa, Japan)	Reef-flat	>0.7	50–100 (78)	51	58–72 (64)	This study

^a Value includes CaCO_3 (sample not acidified).

Table 7
Summary of C:N ratio of some possible detritus sources.

	Study site	Water type	C:N ratio	Reference
Vascular plants	Delaware Bay (USA)	Tidal marshes	34	Wainright et al. (2000)
Macroalgae	Southern coast of Korea	Inter/subtidal coast	9.8–43.8	Kang et al. (2003)
Seagrasses	Southern coast of Korea	Inter/subtidal coast	11.1–69.4	Kang et al. (2003)
Mangrove detritus	Guayas (Ecuador)	Tropical estuary	12.1	Cifuentes et al. (1996)
Phytoplankton			6.6–8.7	Holligan et al. (1984), Redfield. (1963)
Filamentous algae	Lizard Is. (Australia)	Coral reef	6.8–20.0	Wilson et al. (2003)
Algal detritus	Lizard Is. (Australia)	Coral reef	6.3–17.2	Wilson et al. (2003)
Fish feces (Parrotfish)	Palmyra Atoll	Coral reef	10.1	Smriga et al. (2010)
Fish feces (Red snapper)	Palmyra Atoll	Coral reef	3.4	Smriga et al. (2010)
Fish feces (Surgeonfish)	Palmyra Atoll	Coral reef	5.7	Smriga et al. (2010)
Coral mucus (<i>Acropora nobilis</i>)	Bidong Is. (Malaysia)	Coral reef	5	Nakajima et al. (2009a)
Coral mucus (<i>Acropora formosa</i>)	Tioman Is. (Malaysia)	Coral reef	4.5	Nakajima et al. (2009a)

The relative contributions of grazing versus microbial food webs to particle-feeding mesozooplankton dietary requirements were 7–76% (average 39%) and 19–57% (average 37%), respectively. The combined production of the components from the two food webs almost satisfied or completed the mesozooplankton food demands in summer and fall, meeting 91% and 133% of the mesozooplankton requirements, respectively. A previous study showed that the gross growth efficiency of particle-feeding mesozooplankton in laboratory experiments was ca. 30% (Ikeda and Motoda, 1978). This implies that, if prey populations were grazed completely by predator populations, their transfer efficiency would be close to 30% (Uye and Shimazu, 1997). The transfer efficiency found in summer and fall (32.9% and 22.5% from the combined food web production to mesozooplankton production) is close to this potential value, suggesting that the prey-predator process at Sesoko reef in summer and fall is very efficient. Yet the combined production from the two food webs apparently did not completely satisfy the food demand in spring and winter, explaining 26–53% of the particle-feeding mesozooplankton food requirements. The transfer efficiency (%) in these seasons (57–115%) exceeds that of the potential maximum (30%, (Ikeda and Motoda, 1978)). These results indicate that the mesozooplankton community utilized other organic matter sources (such as detritus) to supplement their diets and meet demands. In the present study, we used a plankton net of 180 μm mesh, in which a significant amount of small copepods such as *Paracalanus*, *Oithona* and many copepodite stages may have been missed (Hopcroft et al., 1998b). The estimated mesozooplankton production may be even higher if a finer-mesh net (e.g., 100 μm) was employed together with our 180 μm net. This would suggest an even higher food requirement by mesozooplankton, resulting in even greater estimates of the importance of other sources of organic matter to mesozooplankton. These results also show that the heterotrophic components of the microbial food web (HNF and microzooplankton) and mesozooplankton consume the equivalent of the entire phytoplankton production (particulate net production) each day, while the microzooplankton were almost entirely eaten by higher trophic levels (mesozooplankton) each day.

The importance of other organic matter (detritus) in mesozooplankton diets has been discussed in various studies (Meyer and Bell, 1989). The major portion of POC consisted of detritus in this study (58–72%), which was similar in other coral reefs (52–89%, Table 6). Generally the assimilation efficiency of detritivores is lower than that of carnivores and herbivores (Lalli and Parsons, 1997). Still, detritivory is considered important during periods of scarce food availability for many mesozooplankton species (Zagursky and Feller, 1985). For example, the harpacticoid copepod *Microsetella norvegica* is a typical herbivore in phytoplankton-rich eutrophic waters but this species switches its diet to detritivory in oligotrophic environments (Ohtsuka et al., 1993; Ohtsuka and Nishida, 1997). The calanoid copepod *Bestiolina similis* also consumes detritus to meet a deficit between its carbon demand and primary production (McKinnon and Klumpp, 1998). Similarly, our mesozooplankton in spring, summer and winter were likely supported, in part, by detritus in our food-limited system.

Although this study is not designed to examine the origin of detritus, the C/N ratio of POM may give some hints for its origin. Since the major portion (ca. >60%) of POM was occupied by detritus, the C/N ratio of POM might be mainly reflecting the C/N ratio of detritus. The C/N ratios of some potential sources of POM have been reported (Table 7). The C/N ratio of POM varied from 3.5–6.2 in our study site, suggesting a minor contribution of plant or algal input to the reef water POM, and the detritus likely originated from animal origins such as fish feces and coral mucus (Table 7). This is also consistent with the fact that there are no seagrass beds

or mangroves in the Sesoko Island. Interestingly the C/N ratio of POM was very low (3.5–3.6) in spring and summer compared to the other seasons (4.3–6.2), suggesting that the quality of detritus may have been different among the seasons. Further investigations on the origin and production of detritus as well as ingestion of these detritus are proposed in order to obtain a better understanding of pelagic trophic dynamics in coral reef ecosystems.

5. Conclusion

Here, we demonstrated that the phytoplankton-based grazing food web alone does not satisfy the food requirements of the mesozooplankton community on a coral reef in Okinawa and that a significant part of their demand could be fulfilled by production from the microbial food web. The relative contributions of grazing and microbial food webs were on average 38.7% (7.3–76.4%) and 37.2% (18.9–56.8%), respectively, of the food requirements of particle-feeding mesozooplankton, emphasizing the importance of the multivorous food web to coral reef mesozooplankton. These results also show that the heterotrophic components of the microbial food web (HNF and microzooplankton) and mesozooplankton consume the equivalent of the entire phytoplankton production (particulate net production) each day, while the microzooplankton were almost entirely eaten by higher trophic levels (mesozooplankton) each day. In some seasons, however, even the combined productions from both of the two food webs were not enough to satisfy the food requirement of mesozooplankton, emphasizing the importance of other organic carbon sources such as detritus. Detailed investigation on the origin and production of detritus is necessary for a better understanding of pelagic trophodynamics in coral reef ecosystems.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.pocean.2017.06.007>.

References

- Allredge, A.L., King, J.M., 2009. Near-surface enrichment of zooplankton over a shallow back reef: implications for coral reef food webs. *Coral Reefs* 28, 895–908.
- Allredge, A.L., King, J.M., 1977. Distribution, abundance, and substrate preferences of demersal reef zooplankton at Lizard Island Lagoon, Great Barrier Reef. *Mar. Biol.* 41, 317–333. <http://dx.doi.org/10.1007/BF00389098>.
- Alvaro Morales, R., Murillo, M.M., 1996. Distribution, abundance and composition of coral reef Zooplankton, Cahuita National Park, Limon, Costa Rica. *Rev. Biol. Trop.* 44, 619–630.
- Anderson, A., Rudeh  ll,   ., 1993. Proportion of plankton biomass in particulate organic-carbon in the Northern Baltic Sea. *Mar. Ecol. Prog. Ser.* 95, 133–139. <http://dx.doi.org/10.3354/meps095133>.
- Ara, K., Hiromi, J., 2009. Seasonal variability in plankton food web structure and trophodynamics in the neritic area of Sagami Bay, Japan. *J. Oceanogr.* 65, 757–779.
- Azam, F., Fenchel, T., Field, J.G., Gray, J.C., Meyer-Reil, L.A., Thingstad, F., 1983. The ecological role of water-column microbes in the sea. *Mar. Ecol. Prog. Ser.* 10, 257–264. <http://dx.doi.org/10.3354/meps010257>.

- Båmstedt, U., 1986. Chemical Composition and Energy Content, The Biological Chemistry of Marine Copepods. Clarendon Press, Oxford.
- Bartram, W.C., 1981. Experimental development of a model for the feeding of neritic copepods on phytoplankton. *J. Plankton Res.* 3, 25–51.
- Berggreen, U., Hansen, B., Kjørboe, T., 1988. Food size spectra, ingestion and growth of the copepod *Acartia tonsa* during development: Implications for determination of copepod production. *Mar. Biol.* 99, 341–352.
- Berglund, J., Müren, U., Båmstedt, U., Andersson, A., 2007. Efficiency of a phytoplankton-based and a bacterial-based food web in a pelagic marine system. *Limnol. Oceanogr.* 52, 121–131.
- Bouvy, M., Got, P., Domaizon, I., Pagano, M., Leboulanger, C., Bouvier, C., Carré, C., Roques, C., Dupuy, C., 2016. Plankton communities in the five Iles Eparses (Western Indian Ocean) considered to be pristine ecosystems. *Acta Oecologica* 72, 9–20.
- Brown, J.H., Sibly, R.M., 2012. The Metabolic Theory of Ecology and Its Central Equation. In: *Metabolic Ecology: A Scaling Approach*. John Wiley and Sons, pp. 21–33.
- Calbet, A., Saiz, E., 2005. The ciliate-copepod link in marine ecosystems. *Aquat. Microb. Ecol.* 38, 157–167.
- Carleton, J.H., Doherty, P.J., 1998. Tropical zooplankton in the highly-enclosed lagoon of Taiao Atoll (Tuamotu Archipelago, French Polynesia). *Coral Reefs* 17, 29–35.
- Caron, D.A., Dam, H.G., Kremer, P., Lessard, E.J., Madin, L.P., Malone, T.C., Napp, J.M., Peele, E.R., Roman, M.R., Youngbluth, M.J., 1995. The contribution of microorganisms to particulate carbon and nitrogen in surface waters of the Sargasso Sea near Bermuda. *Deep. Res. Part I* 42, 943–972.
- Carrillo-Baltodano, A., Morales-Ramírez, A., 2016. Changes in abundance and composition of a Caribbean coral reef zooplankton community after 25 years. *Rev. Biol. Trop.* 64, 1029–1040.
- Casareto, B.E., Suzuki, Y., Fukami, K., Yoshida, K., 2000. Particulate organic carbon budget and flux in a fringing coral reef off Miyako Island, Okinawa, Japan in July 1996. In: *Proceedings of the 9th International Coral Reef Symposium*. pp. 95–100.
- Charpy-Roubaud, C.J., Charpy, L., Lemasson, L., 1989. Benthic and planktonic primary production of an open atoll lagoon (Tikehau, French Polynesia). In: *Proceedings 6th International Coral Reef Symposium*. pp. 551–556.
- Charpy, L., Blanchot, J., 1999. Picophytoplankton biomass, community structure and productivity in the Great Astrolabe lagoon, Fiji. *Coral Reefs* 18, 255–262.
- Charpy, L., Charpy-Roubaud, C.J., 1990. Trophic structure and productivity of the lagoonal communities of Tikehau atoll (Tuamotu Archipelago, French Polynesia). *Hydrobiologia* 207, 43–52.
- Chisholm, L.A., Roff, J.C., 1990. Size-weight relationships and biomass of tropical neritic copepods off Kingston, Jamaica. *Mar. Biol.* 106, 71–77. <http://dx.doi.org/10.1007/BF02114676>.
- Chisholm, S.W., 1992. Phytoplankton Size. In: Falkowski, P.G., Woodhead, A.D. (Eds.), *Primary Productivity and Biogeochemical Cycles in the Sea*. Springer, pp. 213–237. http://dx.doi.org/10.1007/978-1-4899-0762-2_12.
- Cifuentes, L.A., Coffin, R.B., Solorzano, L., Cardenas, W., Espinoza, J., Twilley, R.R., 1996. Isotopic and elemental variations of carbon and nitrogen in a mangrove estuary. *Estuar. Coast. Shelf Sci.* 43, 781–800.
- Coma, R., Ribes, M., Orejas, C., Gili, J., 1999. Prey capture by a benthic coral reef hydrozoan. *Coral Reefs* 18, 141–145.
- David, V., Sautour, B., Galois, R., Chardy, P., 2006. The paradox high zooplankton biomass-low vegetal particulate organic matter in high turbidity zones: what way for energy transfer? *J. Exp. Mar. Biol. Ecol.* 333, 202–218. <http://dx.doi.org/10.1016/j.jembe.2005.12.045>.
- Dufour, P., Charpy, L., Bonnet, S., Garcia, N., 1999. Phytoplankton nutrient control in the oligotrophic South Pacific subtropical gyre (Tuamotu Archipelago). *Mar. Ecol. Prog. Ser.* 179, 285–290.
- Dupuy, C., Pagano, M., Got, P., Domaizon, I., Chappuis, A., Marchessaux, G., Bouvy, M., 2016. Trophic relationships between metazooplankton communities and their plankton food sources in the Iles Eparses (Western Indian Ocean). *Mar. Environ. Res.* 116, 18–31.
- Fenchel, T., 1982. Ecology of Protozoa The Biology of Free-Living Phagotrophic Protists. Springer-Verlag, Berlin.
- Ferrier-Pagès, C., Furla, P., 2001. Pico- and nanoplankton biomass and production in the two largest atoll lagoons of French Polynesia. *Mar. Ecol. Prog. Ser.* 211, 63–76. <http://dx.doi.org/10.3354/meps211063>.
- Ferrier-Pagès, C., Gattuso, J.P., 1998. Biomass, production and grazing rates of pico- and nanoplankton in coral reef waters (Miyako Island, Japan). *Microb. Ecol.* 35, 46–57. <http://dx.doi.org/10.1007/s002489900059>.
- Fukuoka, K., Shimoda, T., Abe, K., 2015. Community structure and abundance of copepods in summer on a fringing coral reef off Ishigaki Island, Ryukyu Islands, Japan. *Plankt. Benthos Res.* 10, 225–232. <http://dx.doi.org/10.3800/pbr.10.225>.
- Furnas, M.J., Mitchell, A.W., Gilmartin, M., Revelante, N., 1990. Phytoplankton biomass and primary production in semi-enclosed reef lagoons of the central Great Barrier Reef Australia. *Coral Reefs* 9, 1–10. <http://dx.doi.org/10.1111/j.1461-0248.2011.01607.x>.
- Gerber, R.P., Marshall, N., 1982. Characterization of the suspended particulate organic matter and feeding by the lagoon zooplankton at Eniwetok atoll. *Bull. Mar. Sci.* 32, 290–300.
- Gerber, R.P., Marshall, N., 1974. Ingestion of detritus by the lagoon pelagic community at Eniwetok Atoll. *Limnol. Oceanogr.* 19, 815–824.
- Giering, S.L.C., Sanders, R., Lampitt, R.S., Anderson, T.R., Tamburini, C., Boutrif, M., Zubkov, M.V., Marsay, C.M., Henson, S.A., Saw, K., 2014. Reconciliation of the carbon budget in the ocean's twilight zone. *Nature* 507, 480–483.
- Gifford, S.M., Rollwagen-Bollens, G., Bollens, S.M., 2007. Mesozooplankton omnivory in the upper San Francisco Estuary. *Mar. Ecol. Prog. Ser.* 348, 33–46. <http://dx.doi.org/10.3354/meps07003>.
- Glynn, P., 1973. Ecology of a Caribbean coral reef. The Porites reef-flat biotope: Part II. Plankton community with evidence for depletion. *Mar. Biol.* 22, 1–21.
- Go, Y., Nakamura, S., Nakano, Y., 1997. Preliminary study of zooplankton around coral reefs of Sesoko Island, Okinawa. *Galaxea* 13, 145–156.
- González, J.M., Torrón, J.P., Dufour, P., Charpy, L., 1998. Temporal and spatial dynamics of the pelagic microbial food web in an atoll lagoon. *Aquat. Microb. Ecol.* 16, 53–64. <http://dx.doi.org/10.3354/ame016053>.
- Goswami, S.C., Goswami, U., 1990. Diel variation in zooplankton in Minicoy lagoon and Kavaratti atoll (Lakshadweep islands). *Indian J. Mar. Sci.* 19, 120–124.
- Goswami, S.G., 1983. Production and zooplankton community structure in the lagoon and surrounding sea at Kavaratti Atoll (Lakshadweep). *Indian J. Mar. Sci.* 12, 31–35.
- Grindley, J., Wooldridge, T., 1974. The plankton of Richards Bay. *Hydrobiol. Bull.* 8, 201–212.
- Hama, T., Miyazaki, T., Ogawa, Y., Iwakuma, T., Takahashi, M., Otsuki, A., Ichimura, S., 1983. Measurement of photosynthetic production of a marine phytoplankton population using a stable ^{13}C isotope. *Mar. Biol.* 73, 31–36.
- Hamner, W.M., Colin, P.L., Hamner, P.P., 2007. Export–import dynamics of zooplankton on a coral reef in Palau. *Mar. Ecol. Prog. Ser.* 334, 83–92.
- Hamner, W.M., Jones, M.S., Carleton, J.H., Hauri, I.R., Williams, D.M., 1988. Zooplankton, planktivorous fish, and water currents on a windward reef face: Great Barrier Reef, Australia. *Bull. Mar. Sci.* 42, 459–479.
- Hardy, S.A.C., 1924. The Herring in Relation to its Animate Environment. I. The food and Feeding Habits of the Herring with Special Reference to the East Coast of England. Fisheries Investigation, London.
- Hayashi, M., Uye, S.I., 2008. Geographical and seasonal variations in biomass and estimated production rates of net zooplankton in Yatsushiro Bay, Japan. *J. Oceanogr.* 64, 877–889.
- Hearn, C., Atkinson, M., Falter, J., 2001. A physical derivation of nutrient-uptake rates in coral reefs: Effects of roughness and waves. *Coral Reefs* 20, 347–356.
- Heidelberg, K., Sebens, K., Purcell, J., 2004. Composition and sources of near reef zooplankton on a Jamaican forereef along with implications for coral feeding. *Coral Reefs* 23, 263–276.
- Heidelberg, K.B., O'Neil, K.L., Bythell, J.C., Sebens, K.P., 2010. Vertical distribution and diel patterns of zooplankton abundance and biomass at Conch Reef, Florida Keys (USA). *J. Plankton Res.* 32, 75–91. <http://dx.doi.org/10.1093/plankt/fbp101>.
- Herndl, G.J., Velimirov, B., 1986. Microheterotrophic utilization of mucus released by the Mediterranean coral *Cladocora cespitosa*. *Mar. Biol.* 90, 363–369.
- Hirota, R., 1986. Zooplankton. In: *The Oceanographic Society of Japan (Ed.), Coastal Environmental Research Manual*. Kouseishakouseiaku, Tokyo, pp. 177–191.
- Hirota, R., 1981. Dry weight and chemical composition of the important zooplankton in the Setonakaiki. *Bull. Plankt. Soc. Jpn.* 28, 19–24.
- Hirst, G.A., Lampitt, S.R., 1998. Towards a global model of in situ weight-specific growth in marine planktonic copepods. *Mar. Biol.* 132, 247–257. <http://dx.doi.org/10.1007/s002270050390>.
- Hirst, G.A., Roff, J.C., Lampitt, S.R., 2003. A synthesis of growth rates in marine epipelagic invertebrate zooplankton. *Adv. Mar. Biol.* 44, 1–142.
- Hohenegger, J., Yordanova, E., Nakano, Y., Tatzreiter, F., 1999. Habitats of larger foraminifera on the upper reef slope of Sesoko Island, Okinawa, Japan. *Mar. Micropaleontol.* 36, 109–168.
- Holligan, P.M., Balch, W.M., Yentsch, C.M., 1984. The significance of subsurface chlorophyll, nitrite and ammonium maxima in relation to nitrogen for phytoplankton growth in stratified waters of the Gulf of Maine. *J. Mar. Res.* 42, 1051–1073.
- Hopcroft, R.R., Roff, J.C., Bouman, H.A., 1998a. Zooplankton growth rates: the larvaceans Appendicularia, *Fritillaria* and *Oikopleura* in tropical waters. *J. Plankton Res.* 20, 539–555.
- Hopcroft, R.R., Roff, J.C., Lombard, D., 1998b. Production of tropical copepods in Kingston Harbour, Jamaica: the importance of small species. *Mar. Biol.* 130, 593–604. <http://dx.doi.org/10.1007/s002270050281>.
- Houlbrèque, F., Tambutté, E., Richard, C., Ferrier-Pagès, C., 2004. Importance of a micro-diet for scleractinian corals. *Mar. Ecol. Prog. Ser.* 282, 151–160.
- Huo, Y., Sun, S., Zhang, F., Wang, M., Li, C., Yang, B., 2012. Biomass and estimated production properties of size-fractionated zooplankton in the Yellow Sea, China. *J. Mar. Syst.* 94, 1–8. <http://dx.doi.org/10.1016/j.jmarsys.2011.09.013>.
- Ikedo, T., Motoda, S., 1978. Estimated zooplankton production and their ammonia excretion in the Kuroshio and adjacent seas. *Fish. Bull.* 76, 357–366.
- Japan Fisheries Agency, 1987. Zooplankton Research Manual. Fisheries Agency Research Division of Japan, Tokyo.
- Kang, C.-K., Kim, J.B., Lee, K.-S., Kim, J.B., Lee, P.-Y., Hong, J.-S., 2003. Trophic importance of benthic microalgae to macrozoobenthos in coastal bay systems in Korea: dual stable C and N isotope analyses. *Mar. Ecol. Prog. Ser.* 259, 79–92.
- Kankaala, P., Arvola, L., Tulonen, T., Ojala, A., 1996. Carbon budget for the pelagic food web of the euphotic zone in a boreal lake (Lake Pääjärvi). *Can. J. Fish. Aquat. Sci.* 53, 1663–1674.
- Kobari, T., Nakamura, R., Unno, K., Kitamura, M., Tanabe, K., Nagafuku, H., Niibo, A., Kawakami, H., Matsumoto, K., Honda, M.C., 2016. Seasonal variability in carbon demand and flux by mesozooplankton communities at subarctic and subtropical sites in the western North Pacific Ocean. *J. Oceanogr.* 72, 403–418.
- Kobari, T., Steinberg, D.K., Ueda, A., Tsuda, A., Silver, M.W., Kitamura, M., 2008. Impacts of ontogenetically migrating copepods on downward carbon flux in the western subarctic Pacific Ocean. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 55, 1648–1660.

- Koshikawa, H., Harada, S., Watanabe, M., Sato, K., Akehata, K., 1996. Relative contribution of bacterial and photosynthetic production to metazooplankton as carbon sources. *J. Plankton Res.* 18, 2269–2281.
- Lalli, C.M., Parsons, T.R., 1997. *Biological Oceanography*. Elsevier Butterworth-Heinemann.
- Landry, M.R., Lehner-Fournier, J.M., 1988. Grazing rates and behaviors of *Neocalanus plumchus*: implications for phytoplankton control in the subarctic Pacific. *Hydrobiologia* 167–168, 9–19.
- Le Borgne, R., Blanchot, J., Charpy, L., 1989. Zooplankton of Tikehau atoll (Tuamotu archipelago) and its relationship to particulate matter. *Mar. Biol.* 102, 341–353.
- Le Borgne, R., Rodier, M., Le Bouteiller, A., Kulbicki, M., 1997. Plankton biomass and production in an open atoll lagoon: Uvea, New Caledonia. *J. Exp. Mar. Biol. Ecol.* 212, 187–210. [http://dx.doi.org/10.1016/S0022-0981\(96\)02749-9](http://dx.doi.org/10.1016/S0022-0981(96)02749-9).
- Lee, S., Fuhrman, J.A., 1987. Relationships between biovolume and biomass of naturally derived marine bacterioplankton. *Appl. Environ. Microbiol.* 53, 1298–1303.
- Lee, S., Kang, Y.C., Fuhrman, J.A., 1995. Imperfect retention of natural bacterioplankton cells by glass fiber filters. *Mar. Ecol. Prog. Ser.* 119, 285–290.
- Lefevre, M., 1985. Spatial variability of zooplanktonic populations in the lagoons of a high island (Moorea, French Polynesia). In: *Fifth International Coral Reef Congress*. Museum-EPHE, pp. 39–45.
- Legendre, L., Rassoulzadegan, F., 1995. Plankton and nutrient dynamics in marine waters. *Ophelia* 41, 153–172. <http://dx.doi.org/10.1080/00785236.1995.10422042>.
- Leichter, J.J., Shellenbarger, G., Genovese, S.J., Wing, S.R., 1998. Breaking internal waves on a Florida (USA) coral reef: a plankton pump at work? *Mar. Ecol. Prog. Ser.* 166, 83–97.
- Lignell, R., 1993. Fate of a phytoplankton spring bloom: sedimentation and carbon flow in the planktonic food web in the northern Baltic. *Mar. Ecol. Prog. Ser.* 94, 239–252.
- Lopes, R.M., Marcolin, C.R., Brandini, F.P., 2016. Influence of oceanic fronts on mesozooplankton abundance and grazing during spring in the south-western Atlantic. *Mar. Freshw. Res.* 67, 626–635.
- McFarland, W., Wahl, C., Suchanek, T., McAlary, F., 1999. The behavior of animals around twilight with emphasis on coral reef communities. In: Archer, S.N. (Ed.), *Adaptive Mechanisms in the Ecology of Vision*. pp. 583–628.
- McKinnon, A., Duggan, S., De'ath, G., 2005. Mesozooplankton dynamics in nearshore waters of the Great Barrier Reef. *Estuar. Coast. Shelf Sci.* 63, 497–511.
- McKinnon, A.D., Duggan, S., 2003. Summer copepod production in subtropical waters adjacent to Australia's North West Cape. *Mar. Biol.* 143, 897–907.
- McKinnon, A.D., Klumpp, D.W., 1998. Mangrove zooplankton of North Queensland, Australia. *Hydrobiologia* 362, 127–143. <http://dx.doi.org/10.1023/A:1003186601878>.
- Meyer, H.A., Bell, S.S., 1989. Response of harpacticoid copepods to detrital accumulation on seagrass blades: a field experiment with *Metis holothuriae* (Edwards). *J. Exp. Mar. Biol. Ecol.* 132, 141–149.
- Minutoli, R., Guglielmo, L., 2012. Mesozooplankton carbon requirement in the Tyrrhenian Sea: its vertical distribution, diel variability and relation to particle flux. *Mar. Ecol. Prog. Ser.* 446, 91–105.
- Moore, E., Sander, F., 1979. A Comparative Study of Zooplankton from Oceanic, Shelf, and Harbor Waters of Jamaica. *Biotropica* 11, 196–206. <http://dx.doi.org/10.2307/2388039>.
- Moore, E., Sander, F., 1976. Quantitative and qualitative aspects of the zooplankton and breeding patterns of copepods at two Caribbean coral reef stations. *Estuar. Coast. Mar. Sci.* 4, 589–607. [http://dx.doi.org/10.1016/0302-3524\(76\)90068-2](http://dx.doi.org/10.1016/0302-3524(76)90068-2).
- Motoda, S., 1994. An estimation of primary and secondary production of the coral reef areas in Palau, Western Caroline Islands. *Midoriishi* 5, 5–8.
- Motoda, S., 1940. Comparison of the conditions of water in the bay, lagoon and open sea in Palau. *Palau Trop. Biol. Sta. Stud.* 2, 41–48.
- Nagao, N., Toda, T., Takahashi, K., Hamasaki, K., Kikuchi, T., Taguchi, S., 2001. High ash content in net-plankton samples from shallow coastal water: possible source of error in dry weight measurement of zooplankton biomass. *J. Oceanogr.* 57, 105–107.
- Nakajima, R., Nakatomi, N., Kurihara, H., Fox, M.D., Smith, J.E., Okaji, K., 2016. Crown-of-thorns starfish larvae can feed on organic matter released from corals. *Diversity* 8, 18.
- Nakajima, R., Yoshida, T., Azman, B.A.R., Zaleha, K., Othman, B.H.R., Toda, T., 2009a. In situ release of coral mucus by *Acropora* and its influence on the heterotrophic bacteria. *Aquat. Ecol.* 43, 815–823.
- Nakajima, R., Yoshida, T., Othman, B., Toda, T., 2014. Biomass and estimated production rates of metazoan zooplankton community in a tropical coral reef of Malaysia. *Mar. Ecol. Prog. Ser.* 35, 112–131.
- Nakajima, R., Yoshida, T., Othman, B.H.R., Toda, T., 2011. Quality and quantity of particulate organic carbon in a coral reef at Tioman Island, Malaysia. *Sains Malaysiana* 40, 1375–1382.
- Nakajima, R., Yoshida, T., Othman, B.H.R., Toda, T., 2009b. Diel variation of zooplankton in the tropical coral-reef water of Tioman Island, Malaysia. *Aquat. Ecol.* 43, 965–975.
- Nakajima, R., Yoshida, T., Othman, B.H.R., Toda, T., 2008. Diel variation in abundance, biomass and size composition of zooplankton community over a coral-reef in Redang Island, Malaysia. *Plankt. Benthos Res.* 3, 216–226.
- Nakamura, Y., Turner, J.T., 1997. Predation and respiration by the small cyclopoid copepod *Oithona similis*: how important is feeding on ciliates and heterotrophic flagellates? *J. Plankton Res.* 19, 1275–1288.
- Nakano, S.I., Manage, P.M., Nishibe, Y., Kawabata, Z., 2001. Trophic linkage among heterotrophic nanoflagellates, ciliates and metazoan zooplankton in a hypereutrophic pond. *Aquat. Microb. Ecol.* 25, 259–270.
- Odate, T., Maita, Y., 1988. Seasonal changes in the biomass of zooplankton and their food requirement in Funka Bay. *J. Oceanogr. Soc. Jpn.* 44, 228–234.
- Ohtsuka, S., Kubo, N., 1991. Larvaceans and their houses as important food for some pelagic copepods. *Bull. Plankt. Soc. Jpn.* 1, 535–551.
- Ohtsuka, S., Kubo, N., Okada, M., Gushima, K., 1993. Attachment and feeding of pelagic copepods on larvacean houses. *J. Oceanogr.* 49, 115–120.
- Ohtsuka, S., Nishida, S., 1997. Reconsideration on feeding habits of marine pelagic copepods (Crustacea). *Oceanogr. Jpn.* 6, 299–320.
- Omori, M., Cha, S.-J., Isokawa, H., 2015. Species composition, abundance and seasonal variation of planktonic copepods at coral reefs of Akajima Island, Okinawa, Japan. *Bull. Plankt. Soc. Jpn.* 62, 98–109.
- Pagano, M., Champalbert, G., Aka, M., Kouassi, E., Arfi, R., Got, P., Troussellier, M., N'Dour, E.H., Corbin, D., Bouvy, M., 2006. Herbivorous and microbial grazing pathways of metazooplankton in the Senegal River Estuary (West Africa). *Estuar. Coast. Shelf Sci.* 67, 369–381.
- Pagano, M., Sagarra, P.-B., Champalbert, G., Bouvy, M., Dupuy, C., Thomas, Y., Charpy, L., 2012. Metazooplankton communities in the Ahe atoll lagoon (Tuamotu Archipelago, French Polynesia): spatiotemporal variations and trophic relationships. *Mar. Pollut. Bull.* 65, 538–548.
- Pomeroy, L.R., 1974. The Ocean's food web, a changing paradigm. *Bioscience* 24, 499–504.
- Porter, J.W., 1974. Zooplankton feeding by the caribbean reef-building coral *Montastrea cavernosa*. In: *Proceedings of the Second International Coral Reef Symposium*. pp. 111–125.
- Putt, M., Stoeker, D.K., 1989. An experimentally determined carbon: volume ratio for marine “oligotrichous” ciliates from estuarine and coastal waters. *Limnol. Ocean.* 34, 1097–1103.
- Redfield, A.C., 1963. The influence of organisms on the composition of sea-water. *Sea*, 26–77.
- Robertson, J.R., 1983. Predation by estuarine zooplankton on tintinnid ciliates. *Estuar. Coast. Shelf Sci.* 16, 27–36. [http://dx.doi.org/10.1016/0272-7714\(83\)90092-6](http://dx.doi.org/10.1016/0272-7714(83)90092-6).
- Roman, M., Furnas, M., Mullin, M., 1990. Zooplankton abundance and grazing at Davies Reef, Great Barrier Reef, Australia. *Mar. Biol.* 105, 73–82.
- Roman, M.R., 1984. Utilization of detritus by the copepod, *Acartia tonsa*. *Limnol. Oceanogr.* 29, 949–959.
- Roman, M.R., 1977. Feeding of the copepod *Acartia tonsa* on the diatom *Nitzschia closterium* and brown algae (*Fucus vesiculosus*) detritus. *Mar. Biol.* 42, 149–155.
- Sakka, A., Legendre, L., Gosselin, M., Delesalle, B., 2000. Structure of the oligotrophic planktonic food web under low grazing of heterotrophic bacteria: Takapoto Atoll, French Polynesia. *Mar. Ecol. Prog. Ser.* 197, 1–17.
- Sakka, A., Legendre, L., Gosselin, M., Niquil, N., Delesalle, B., 2002. Carbon budget of the planktonic food web in an atoll lagoon (Takapoto, French Polynesia). *J. Plankton Res.* 24, 301–320.
- Sale, P.F., McWilliam, P.S., Anderson, D.T., 1976. Composition of the near-ref zooplankton at Heron Reef, Great Barrier Reef. *Mar. Biol.* 34, 59–66. <http://dx.doi.org/10.1007/BF00390788>.
- Salvat, B., 1992. Coral reefs – a challenging ecosystem for human societies. *Glob. Environ. Change* 2, 12–18.
- Sampey, A., McKinnon, A.D., Meekan, M.G., McCormick, M.I., 2007. Glimpse into guts: overview of the feeding of larvae of tropical shorefishes. *Mar. Ecol. Prog. Ser.* 339, 243–257.
- Sebens, K., Vandersall, K., Savina, L., Graham, K., 1996. Zooplankton capture by two scleractinian corals, *Madracis mirabilis* and *Montastrea cavernosa*, in a field enclosure. *Mar. Biol.* 127, 303–317.
- Sheldon, R., 1977. Structure of pelagic food chain and relationship between plankton and fish production. *J. Fish. Res. Board Canada* 34, 2344–2353.
- Sherr, E.B., Caron, D.A., Sherr, B.F., 1993. Staining of heterotrophic protists for visualization via epifluorescence microscopy. In: Kemp, P.F., Sherr, B.F., Sherr, E. B., Cole, J.J. (Eds.), *Handbook of Methods in Aquatic Microbial Ecology*. CRC Press, New York, pp. 213–227.
- Sherr, E.B., Sherr, B.F., 1987. High rates of consumption of bacteria by pelagic ciliates. *Nature* 325, 710–711.
- Shibata, A., Imai, A.K.I., Hara, S., Kikuchi, T., Toda, T., Taguchi, S., 2007. Quantitative difference in bacterial abundance determined with each protocol for SYBR Green I and 4',6'-diamidino-2-phenylindole (DAPI) methods. *Plankt. Benthos Res.* 2, 63–66.
- Shinada, A., Ikeda, T., Ban, S., Tsuda, A., 2001. Seasonal dynamics of planktonic food chain in the Oyashio region, western subarctic Pacific. *J. Plankton Res.* 23, 1237–1247.
- Smriga, S., Sandin, S.A., Azam, F., 2010. Abundance, diversity, and activity of microbial assemblages associated with coral reef fish guts and feces. *FEMS Microbiol. Ecol.* 73, 31–42.
- Sorokin, Y.I., 1995. *Coral Reef Ecology*. Springer, Berlin Heidelberg.
- Sorokin, Y.I., Sorokin, P.Y., 2010. Plankton of the central Great Barrier Reef: abundance, production and trophodynamic roles. *J. Mar. Biol. Assoc. United Kingdom* 90, 1173–1187. <http://dx.doi.org/10.1017/S0025315410000597>.
- Sorokin, Y.I., Sorokin, P.Y., 2009. Analysis of plankton in the southern Great Barrier Reef: abundance and roles in trophodynamics. *J. Mar. Biol. Assoc. United Kingdom* 89, 235. <http://dx.doi.org/10.1017/S0025315409003063>.

- Steinberg, D.K., Van Mooy, B.A.S., Buesseler, K.O., Boyd, P.W., Kobari, T., Karl, D.M., 2008. Bacterial vs. zooplankton control of sinking particle flux in the ocean's twilight zone. *Limnol. Oceanogr.* 53, 1327.
- Stoecker, D.K., Capuzzo, J.M., 1990. Predation on Protozoa: Its importance to zooplankton. *J. Plankton Res.* 12, 891–908.
- Stoecker, D.K., Sanders, N.K., 1985. Differential grazing by *Acartia tonsa* on a dinoflagellate and a tintinnid*. *J. Plankton Res.* 7, 85–100. <http://dx.doi.org/10.1093/plankt/7.1.85>.
- Suárez-Morales, E., Gasca, R., 2000. The planktonic copepod community at Mahahual reef, Western Caribbean. *Bull. Mar. Sci.* 66, 255–267.
- Suresh, V.R., Mathew, K.J., 1997. Zooplankton ecology in Kavaratti atoll, Lakshadweep, India. *Indian J. Fish.* 44, 271–277.
- Suzuki, R., Ishimaru, T., 1990. An improved method for determination of phytoplankton chlorophyll using *N,N*-dimethylformamide. *J. Oceanogr.* 46, 190–194.
- Szyper, J.P., 1976. The Role of Sagitta Enflota in the Southern Kaneohe Bay Ecosystem. University of Hawaii.
- Tada, K., Sakai, K., Nakano, Y., Takemura, A., Montani, S., 2001. Size-fractionated phytoplankton biomass in coral reef waters off Sesoko Island, Okinawa, Japan. *J. Plankton Res.* 25, 991–997.
- Taylor, A.H., Geider, R.J., Gilbert, F.J.H., 1997. Seasonal and latitudinal dependencies of phytoplankton carbon-to-chlorophyll *a* ratios: results of a modelling study. *Mar. Ecol. Prog. Ser.* 152, 51–66.
- Tranter, D.J., George, J., 1972. Coral reefs as biotopes: invertebrates. In: *Proceedings of the Symposium on Corals and Coral Reefs*. The Association, p. 239.
- Uye, S., 1982. Length-weight relationships of important zooplankton from the Inland Sea of Japan. *J. Oceanogr. Soc. Jpn.* 38, 149–158.
- Uye, S., Nagano, N., Tamaki, H., 1996. Geographical and seasonal variations in abundance, biomass and estimated production rates of microzooplankton in the Inland Sea of Japan. *J. Oceanogr.* 52, 689–703.
- Uye, S.I., Shimazu, T., 1997. Geographical and seasonal variations in abundance, biomass and estimated production rates of meso-and macrozooplankton in the Inland Sea of Japan. *J. Oceanogr.* 53, 529–538.
- Van Woessik, R., Sakai, K., Ganase, A., Loya, Y., 2011. Revisiting the winners and the losers a decade after coral bleaching. *Mar. Ecol. Prog. Ser.* 434, 67–76. <http://dx.doi.org/10.3354/meps09203>.
- Vargas, C.A., González, H.E., 2004. Plankton community structure and carbon cycling in a coastal upwelling system. II. Microheterotrophic pathway. *Aquat. Microb. Ecol.* 34, 165–180. <http://dx.doi.org/10.3354/ame034165>.
- Verity, P.G., Lagdon, C., 1984. Relationships between lorica volume, carbon, nitrogen, and ATP content of tintinnids in Narragansett Bay. *J. Plankton Res.* 6, 859–868.
- Wainright, S.C., Weinstein, M.P., Able, K.W., Currin, C.A., 2000. Relative importance of benthic microalgae, phytoplankton and the detritus of smooth cordgrass *Spartina alterniflora* and the common reed *Phragmites australis* to brackish-marsh food webs. *Mar. Ecol. Prog. Ser.* 200, 77–91.
- Wang, Z., Thiébaud, E., Dauvin, J.C., 1995. Spring abundance and distribution of the ctenophore *Pleurobrachia pileus* in the Seine estuary: advective transport and diel vertical migration. *Mar. Biol.* 124, 313–324.
- Webber, M., Roff, J., 1995. Annual biomass and production of the oceanic copepod community off Discovery Bay, Jamaica. *Mar. Biol.* 123, 481–495.
- Welschmeyer, N.A., 1994. Fluorometric of chlorophyll *a* in the presence of chlorophyll *b* and pheopigments. *Limnol. Oceanogr.* 39, 1985–1992.
- White, J.R., Roman, M.R., 1992. Seasonal study of grazing by metazoan zooplankton in the mesohaline Chesapeake Bay. *Mar. Ecol. Prog. Ser.* 86, 251–261.
- Wilson, S.K., Bellwood, D.R., Choat, J.H., Furnas, M.J., 2003. Detritus in the epilithic algal matrix and its use by coral reef fishes. *Ocean. Mar. Biol. Annu. Rev.* 41, 279–310.
- Wylie, J.L., Currie, D.J., 1991. The relative importance of bacteria and algae as food sources for crustacean zooplankton. *Limnol. Oceanogr.* 36, 708–728.
- Yahel, R., Yahel, G., Berman, T., Jaffe, J.S., Genin, A., 2005a. Diel pattern with abrupt crepuscular changes of zooplankton over a coral reef. *Limnol. Oceanogr.* 50, 930–944. <http://dx.doi.org/10.4319/lo.2005.50.3.0930>.
- Yahel, R., Yahel, G., Genin, A., 2005b. Near- bottom depletion of zooplankton over coral reefs: I: Diurnal dynamics and size distribution. *Coral Reefs* 24, 75–85.
- Yahel, R., Yahel, G., Genin, A., 2002. Daily cycles of suspended sand at coral reefs: a biological control. *Limnol. Oceanogr.* 47, 1071–1083. <http://dx.doi.org/10.4319/lo.2002.47.4.1071>.
- Zagursky, G., Feller, R.J., 1985. Macrophyte detritus in the winter diet of the estuarine mysid, *Neomysis americana*. *Estuaries* 8, 355–362. <http://dx.doi.org/10.1007/BF02803962>.
- Zhou, L., Tan, Y., Huang, L., Li, G., 2015. Does microzooplankton grazing contribute to the pico-phytoplankton dominance in subtropical and tropical oligotrophic waters? *Acta Ecol. Sin.* 35, 29–38. <http://dx.doi.org/10.1016/j.chnaes.2014.12.007>.