Note

High detritus/phytoplankton content in net-plankton samples from coral reef water: source of over-estimation in zooplankton biomass by measuring seston weight

Ryota Nakajima^{1,}*, Teruaki Yoshida², Bin Haji Ross Othman² & Tatsuki Toda¹

¹ Department of Environmental Engineering for Symbiosis, Faculty of Engineering, Soka University, Hachioji, Tokyo 192–8577, Japan ² Marine Ecosystem Research Centre, Faculty of Science and Technology, Universiti Kebangsaan Malaysia, 43600 UKM, Bangi, Selangor, Malaysia

Received 16 November 2009; Accepted 5 February 2010

Abstract: We examined the bias in the estimation of zooplankton biomass in net-samples in coral reef waters by measuring seston weight, which contains non-living matter (or detritus) and net-phytoplankton in addition to zooplankton. Net-samples were collected at a coral reef at Tioman Island, Malaysia, and divided them into two aliquots to be used for both measurements of seston weight and zooplankton biomass. Seston weight was on average 2.2 times higher than net-zooplankton biomass, and non-zooplankton content (detritus/phytoplankton) contributed on average 49.2% to the seston weight. Consequently, measurement of net-plankton seston weight as zooplankton biomass in coral reef waters is inadequate due to the highly variable contribution of detritus/phytoplankton content and involves the possibility of over-estimation of zooplankton biomass.

Key words: bias, coral reef, detritus, net-zooplankton, phytoplankton

In studies of marine trophodynamics or plankton production ecology, it is always necessary to measure accurately the biomass of zooplankton. Some researchers measure biomass as accurately as possible, but others use conventional methods to approximate it. One of the conventional methods is to use seston weight of net-samples to approximate zooplankton biomass. Seston is a collective term describing the living and nonliving organic particles in the water column (Zeitzchel 1970). Every planktologist knows that the net-plankton samples contain non-living matter (or detritus) and net-phytoplankton in addition to zooplankton. If detritus and/or phytoplankton can be visually confirmed to represent an insignificant proportion of the seston, the use of seston weight may be adequate for approximation of zooplankton biomass (Yahel et al. 2005). However, if detritus/phytoplankton occupies a significant proportion of the seston in a net-sample, it can lead to a considerable over-estimation of zooplankton biomass. Such a problem may be more severe in coral reef waters, since these environments are more susceptible to the effect due to high detrital content. For example, in Tikehau atoll, French Polynesia, detrital carbon represents over 60% of the sestonic carbon in the net samples (Blanchot et al. 1989). Nevertheless, seston weight has often been used for biomass estimation of net-zooplankton in coral reef waters (Table 1), probably because of its simplicity and the omission of the laborious process of measuring the exact zooplankton biomass. Plankton sizes in the tropics are relatively smaller compared with temperate and boreal species and nets of smaller mesh size are often employed. However, unlike in open waters, coral reef waters contain a substantial amount of detrital material including fish feces, coral mucus aggregates, filtering structures and discarded houses of gelatinous zooplankton, dead organic matter (e.g. dead turf or epilithic algae, carrion and moults), as well as microalgae (e.g. filamentous cyanobacteria, dinoflagellates and diatoms) (reviewed by Crossman et al. 2001, Wilson et al. 2003) which easily gets caught in nets with smaller mesh sizes. This results in zooplankton getting entangled in the detrital aggregation and creates an arduous task if one were to isolate the individuals for identification and enumeration. At present, knowledge of how much zooplankton biomass is overestimated by measuring seston weight in net-samples from coral reef waters is scarce. In this study, we collected net-plankton at a coral reef, and divided them into two aliquots to be used for both measurements of seston weight and zooplankton biomass in order to quantitatively determine the bias in the estimation of zooplankton biomass by measuring seston weight in coral reef waters.

This study was conducted at a jetty in the Marine Park Centre of Tioman Island, Malaysia (2°50′00″N, 104°10′00″E). The reef at the Marine Park Centre is called Mango Reef. From the

^{*} Corresponding author: Ryota Nakajima; E-mail, rnakajim@soka.ac.jp

R. NAKAJIMA et al.

Study site	Biomass	Source
Seston		
Laccadives (India)	$99-189 \text{ mg W m}^{-3}$	Transter & George (1972)
Laurel Reef (Puerto Rico)	$\sim 8 \mathrm{ml}\mathrm{S}\mathrm{m}^{-3}$	Glynn (1973)
Eniwetok Atoll (Marshall Islands)	$2.0-239.4 \mathrm{mg}\mathrm{W}\mathrm{m}^{-3}$	Gerber & Marshall (1974)
Kingston Harbor (Jamaica)	$3.05 - 8.22 \text{ mg D m}^{-3}$	Moore & Sander (1979)
Eniwetok Atoll (Marshall Islands)	$2.18-5.56 \mathrm{mg}\mathrm{C}\mathrm{m}^{-3}$	Gerber & Marshall (1982)
Great Barrier Reef (Australia)	$\sim 1036 \mathrm{mg W m^{-3}}$	Ikeda et al. (1982)
Tikehau Atoll (French Polynesia)	$8.35 \mathrm{mg}\mathrm{C}\mathrm{m}^{-3}$	Le Borgne et al. (1989)
Laccadives (India)	$2-58 \text{ ml S} 100 \text{ m}^{-3}$	Goswami & Goswami (1990)
Uvea Atoll (New Caledonia)	$12.8 \mathrm{mg}\mathrm{AFD}\mathrm{m}^{-3}$	Le Borgne et al. (1997)
Florida Keys (US)	$0.5 - 8.5 \text{ ml S} 10 \text{ m}^{-3}$	Leichter et al. (1998)
Great Barrier Reef (Australia)	$57-1200 \text{ mg DW m}^{-3}$	McKinnon et al. (2005)
Eilat (Israel)	$1.8-2.9 \mathrm{mg}\mathrm{AFD}\mathrm{m}^{-3}$	Yahel et al. (2005)
Malakal (Palau)	$299.5 \text{ mg W m}^{-3}$	Hamner et al. (2007)
Redang Island (Malaysia)	$5.7 - 18.5 \mathrm{mg}\mathrm{C}\mathrm{m}^{-3}$	Nakajima et al. (2008)
True zooplankton		
Virgin Island (US)	$5.6 \mathrm{mg}\mathrm{C}\mathrm{m}^{-3}$	Hickel (1974)
Tikehau Atoll (French Polynesia)	$4 \mathrm{mg}\mathrm{C}\mathrm{m}^{-3}$	Blanchot et al. (1989)
Tikehau Atoll (French Polynesia)	$4 \mathrm{mg}\mathrm{C}\mathrm{m}^{-3}$	Charpy & Charpy-Roubaud (1990)
Great Barrier Reef (Australia)	$0.03 - 0.75 \text{mg} \text{C} \text{m}^{-3}$	Roman et al. (1990)
Koror and Malakal (Palau)	3.1–6.7 mg W m-3	Motoda (1994)
Takapoto Atoll (French Polynesia)	$8.76 \mathrm{mg}\mathrm{C}\mathrm{m}^{-3}$	Sakka et al. (2002)
Discovery Bay (Jamacia)	$1.0 - 15.6 \mathrm{mg}\mathrm{C}\mathrm{m}^{-3}$	Heidelberg et al. (2004)
Tioman Island (Malaysia)	$4.56 \mathrm{mg}\mathrm{C}\mathrm{m}^{-3}$	Nakajima et al. (2009)

 Table 1. Summary of quantitative studies on net-zooplankton biomass in the water column over coral reefs by measuring seston or true zooplankton.

S: settiled volume, W: wet weight, D: dry weight, AFD: ash free dry weight, C: carbon weight

shore towards the open water, the bottom was comprised of fine sand, followed by rocky bottom and then sandy bottom. The reef flat spreads beyond the sandy bottom region ending in a gradual sandy slope. There is no distinct reef crest separating the open sea and back reef zones, allowing water from the open sea to freely enter the nearshore area. There are neither seagrass beds nor mangroves near to the reef. The reef flat is 2-3 m deep and the coral communities have a live coverage of 35% (Toda et al. 2007). Sampling was carried out at the jetty some 100 m north of the reef, where the depth is deeper than Mango Reef at 7.5-10.0 m depending on the tide. The bottom of the jetty is covered with fine-to-medium grained carbonate sand with small patches of live corals of Acropora spp. and with a considerable influence of offshore water, being characterized by high turbidity and a high sedimentation rate (Maekawa 2003). Some anthropogenic effects may be present due to boats stopping at the jetty. A small stream is located approximately 500 m south of the jetty. Net-samples were collected every 3-h for 48-h during four study periods (22-24 August and 1-3 October in 2004 and 25-27 February and 2-4 June in 2005) by five gentle vertical tows of a plankton net (mesh size $100-\mu$ m, diameter 30 cm, length 100 cm) equipped with a flowmeter (Rigo Co., Ltd.) from the water column 1 m above the sea bottom to the surface. The net-collected samples were pooled and immediately brought back to the laboratory of the marine park within 5 min. A total of 64 net-plankton samples were collected. The sea condition at the sampling site was calm with no strong wind or rainfall during the study periods except at 0000 h and 0300 h on 3rd October where heavy rain and strong wind were observed, though we did not measure the amount of precipitation or wind velocity. The net-collected samples were divided into two aliquots with a Folsom plankton splitter (Omori & Ikeda 1984). One aliquot was used for weight determination of organic carbon and the other for microscopic analysis. The aliquot destined for organic carbon weight determination was immediately filtered onto a pre-combusted and pre-weighed GF/A filter (Whatman), and the filter was placed over fuming HCl to remove carbonates for 24-h (Strickland & Parsons 1972). The filter was then dried and organic carbon weight on the filter was measured following Nagao et al. (2001) using an elemental analyzer (Fisons EA 1108 CHNS/O). The measured organic carbon was of the seston weight. The aliquot for microscopic analysis was fixed with 5% buffered formalin seawater. Large zooplankton and rare species (e.g. mysids, larval decapods, fish larvae, etc.) were first counted and sorted out, then the remainder was split (1/1-1/32), and all zooplankton were identified and enumerated under a dissecting microscope. The lengths of the appropriate body portions of the zooplankton, e.g. prosome length for copepods, trunk length for larvaceans, were measured using an eyepiece micrometer following the methods of Uye (1982) and Hirota (1986). At least 300 zooplankton individu-



Fig. 1. Temporal variations of zooplankton biomass (filled circle) and seston weight (open circle) in net samples (>100 μ m) at a coral reef of Tioman Island.

als were measured for each sample. The length estimates were converted to carbon biomass using previously reported lengthweight regression equations (Hirota 1981, Uye 1982, Hirota 1986, Fisheries Agency 1987, Chisholm & Roff 1990, Uye & Ichino 1995, Webber & Roff 1995, Uye et al. 1996, Hopcroft et al. 1998, Satapoomin 1999) taking into account body shrinkage by formalin preservation (Szyper 1976, Wang et al. 1995, Scheinberg et al. 2005). 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 wherever possible. For regressions that estimate zooplankton dry weight from body length (i.e. Webber & Roff 1995, Hopcroft et al. 1998), the carbon content was assumed to be 47% of dry weight (Hirota 1981). The statistical difference between seston weight and zooplankton biomass was determined by a two-sided Mann-Whitney's U-test. Differences with p < 0.05 was considered significant.

Seston weight and net-zooplankton biomass was significantly different during the study period except in February (p < 0.0001 for August, October and June, and p=0.1016 for February, Fig. 1). The average carbon weight (mg C m⁻³) (±SD) of seston in August, October, February and June was 7.5 (±2.8), 7.7 (±4.1), 3.5 (±1.1), and 6.7 (±2.2) mg C m⁻³, respectively, and was 2.3, 2.3, 1.2, and 2.8 times higher than the actual zooplankton carbon biomass (overall mean: 2.2 ± 0.7 times high). There was an abrupt peak in seston weight at 0300 h on 3rd October and this was possibly caused by the addition of a large amount of detritus caused by re-suspension of bottom sediments due to the strong wind. The weight of non-zooplankton content (detritus/phytoplankton) in the net samples, which was obtained by subtracting the zooplankton biomass from the seston weight, contributed on average (\pm SD) 58.9 (\pm 18.5)% in August, 52.3 (±26.8)% in October, 20.4 (±27.1)% in February, and 65.2 (± 13.9)% in June to the seston weight (overall mean: $49.2 \pm 13.8\%$). Previous studies that compared the seston and zooplankton weight are rare. In coral reefs, Blanchot et al. (1989) examined the relative biomass of zooplankton in $200\,\mu\text{m}$ net-seston samples taken from Tikehau atoll, French Polynesia. They sampled for 11 days in April and reported that the relative biomass of zooplankton in the seston was 64%. This value is similar to those of June in our study (65%). In temperate waters, Morioka et al. (1990) and Nakashima et al. (1992) compared zooplankton and non-zooplankton weight in net samples in Goto-nada waters, west of Kyushu, Japan. They used 100 μ m mesh net and sorted the zooplankton from the other seston in formalin fixed samples to measure the dry weight. They found the proportion of non-zooplankton (detritus/phytoplankton) to be 43-65% in March and 13-17% in May, and reported that the percentage can vary considerably with season. Our non-zooplankton component in the net-seston also varied greatly with season in this study, suggesting that the proportion of detritus/phytoplankton in the seston is highly variable temporally for coastal waters in general, though the actual content would be different depending on the study site.

We observed the contents of the detritus/phytoplankton fraction in the net samples under a stereomicroscope and an inverted microscope, and found dead animal tissue (e.g. carrion and moults), feces, gel-like materials, colony-forming filamentous cyanobacteria (i.e. Trichodesmium) and diatoms as possible non-zooplankton contents. Although we do not know the source, the gel-like materials may be derived from products secreted or exuded from organisms such as coral mucus and larvacean houses (Hansen et al. 1992, Moore et al. 2004). The gel-like materials trapped a myriad of particles and formed large complex aggregations which were often visually dominant in the net samples. Coral mucus is known to trap various organic particles while suspended in the water column due to its mucoid structure and it also forms aggregations (Wild et al. 2004). Filamentous cyanobacteria also accumulated in the net and formed aggregations with many trapped particles and zooplankton. Due to the small size of tropical zooplankton species, plankton nets with finer mesh sizes are often employed, such as the 100 μ m mesh net we used in this study. Therefore, these gel-like materials and filamentous cyanobacteria are easily trapped in the plankton net. With regards to the diatoms in our net-samples, we observed relatively large diatoms including Rhizosolenia spp., Coscinodiscus spp, Chaetoceros spp, and Thalassionema spp. Occurrence of a considerable amount of phytoplankton in net-plankton samples has been reported by several authors (e.g. Hirota & Szyper 1976). Contamination by these large phytoplankton is also a potential cause of the high detritus/phytoplankton contents in net-plankton at the present study site. Coral reef waters are generally considered to be poor in inorganic nutrients and similarly, concentrations of phosphorous and nitrogen were particularly low at our study site (PO₄ \leq 0.1 μ M, NO₂ \leq 0.4 μ M, NO₃ $\leq 0.4 \,\mu$ M, Nakajima 2009). However, unlike other coral reefs, among the inorganic nutrients silicate concentration was high (SiOH₄ \leq 8 μ M, Nakajima 2009) at our study site as both Si : P (82) and Si: N (16) ratios were higher than the Redfield ratio of marine diatoms (atomic ratios of N:P:Si=16:1:16, Brzezinski 1985). This may be conductive for diatom growth if other nutrients are non-limiting. Although further examination was not conducted in this study, transport of sediments by wind, red tides of Trichodesmium, and/or detritus derived from dead turf or epilithic algae (Larkum 1983) are considered as other possible causes for fluctuation of non-zooplankton contents. A major part of the primary production (up to 80%) of benthic algae in coral reefs is known to enter the detrital pool (Hatcher 1983, Hansen et al. 1992).

In this study, we compared net-seston and net-zooplankton and found that the relative proportion was highly variable due to the non-zooplankton contents (detritus/phytoplankton). Thus, estimation of zooplankton biomass from seston weight using a conversion factor seems not feasible. In conclusion, the results of this study indicated that measurement of net-plankton seston weight as a proxy for zooplankton biomass in coral reef waters is inaccurate due to the highly variable contribution of detritus/phytoplankton content and the risk for over-estimation of zooplankton biomass. Information such as weight measurements of each individual zooplankter using lengthweight regression is necessary to determine the true net-zooplankton biomass in coral reef waters.

Acknowledgments

The authors thank Prof. S. Taguchi (Soka University) for his helpful comments on the manuscript; M.Y. Ng, F. L. Alice Ho and S. P. Kok for their field assistance; Y. Fuchinoue, A. Takamoto, A. Nishiuchi and K. Tsuchiya for their help in sample analysis; and the two anonymous reviewers for their comments that improved the manuscript. The work described in this report was partially funded by a grant from Japan Society for the Promotion of Science (JSPS) for the Multilateral Cooperative Research Program, Coastal Oceanography, awarded to Prof. S. Nishida (Ocean Research Institute, The University of Tokyo) and by a grant to B.H.R.O. from Universiti Kebangsaan Malaysia Research Grant UKM-GUP-ASPL-08-04-231.

References

- Blanchot J, Charpy L, Le Borgne R (1989) Size composition of particulate organic matter in the lagoon of Tikehau atoll (Tuamotu archipelago). Mar Biol 102: 329–339.
- Brzezinski MA (1985) The Si: C: N ratio of marine diatoms: interspecific variability and the effect of some environmental variables. J Phycol 21: 347–357.
- Charpy L, Charpy-Roubaud CJ (1990) Trophic structure and productivity

of the lagoonal communities of Tikehau atoll (Tuamotu Archipelago, French Polynesia). Hydrobiologia 207: 43–52.

- Chisholm LA, Roff JC (1990) Size-weight relationships and biomass of tropical neritic copepods off Kingston, Jamaica. Mar Biol 106: 71–77.
- Crossman DJ, Choat JH, Clements KD, Hardy T, McConochie J (2001) Detritus as food for grazing fishes on coral reefs. Limnol Oceanogr 46: 1596–1605.
- Fisheries Agency (1987) Zooplankton research manual. Fisheries Agency Research Division, Tokyo, 19 pp.
- Gerber RP, Marshall N (1974) Ingestion of detritus by the lagoon pelagic community at Eniwetok Atoll. Limnol Oceanogr 19: 815–824.
- Gerber RP, 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.
- Glynn PW (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.
- Goswami SC, Goswami U (1990) Diel variation in zooplankton in Minicoy lagoon and Kavaratti atoll (Lakshdweep Islands). Indian J Mar Sci 19: 120–124.
- Hamner WH, Colin PL, Hamner PP (2007) Export-import dynamics of zooplankton on a coral reef in Palau. Mar Ecol Prog Ser 334: 83–92.
- Hansen JA, Klumpp DW, Alongi DM, Dayton PK, Riddle MJ (1992) Detrital pathways in a coral reef lagoon II. Detritus deposition, benthic microbial biomass and production. Mar Biol 113: 363–372.
- Hatcher BG (1983) The role of detritus in the metabolism and secondary production of coral reef ecosystems. In: Proceedings of the Inaugural Great Barrier Reef Conference (ed Baker JT). Townsville, Australia, James Cook University, pp. 317–325.
- Heidelberg KB, Sebens KP, Purcell JE (2004) Composition and sources of near reef zooplankton on a Jamaican forereef along with implications for coral feeding. Coral Reefs 23: 263–276.
- Hickel W (1974) Seston composition of the bottom waters of Great Lameshur Bay, St. John, US Virgin Islands. Mar Biol 24: 125–130.
- Hirota J, Szyper JP (1976) Standing stocks of zooplankton size-classes and trophic levels in Kaneohe Bay, Oahu, Hawaiian Islands. Pac Sci 30: 341–361.
- Hirota R (1981) Dry weight and chemical composition of the important zooplankton in the Setonaikai (Inland Sea of Japan). Bull Plankton Soc Japan 28: 19–24. (in Japanese with English abstract)
- Hirota R (1986) Zooplankton. In: Coastal environmental research manual (ed The Oceanographic Society of Japan). Kouseishakouseikaku, Tokyo, pp. 177–191. (in Japanese)
- Hopcroft RR, Roff JC, Lombard D (1998) Production of tropical copepods in Kingston Harbour, Jamaica: the importance of small species. Mar Biol 130: 593–604.
- Ikeda T, Carleton JH, Mitchell AW, Dixon P (1982) Ammonia and phosphate excretion by zooplankton from the inshore waters of the Great Barrier Reef. II* Their in situ contributions to nutrient regeneration. Aust J Mar Freshw Res 23: 683–698.
- Larkum AWD (1983) The primary productivity of plant communities on coral reefs. In: Perspectives on coral reefs (ed Banes DJ). Townsville, Australia, Australian Institute of Marine Science, pp. 221–230.
- 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.
- Leichter JJ, Shellenbarger G, Genovese SJ, Wing SR (1998) Breaking internal waves on a Florida (USA) coral reef: a plankton pump at work? Mar Ecol Prog Ser 166: 83–97.
- Maekawa T (2003) Coral recruitment study in Tioman Island, Malaysia. Ms. D. Thesis, Soka University, 73 pp.

- McKinnon AD, Duggan S, De'ath G (2005) Mesozooplankton dynamics in nearshore waters of the Great Barrier Reef. Est Coast Shelf Sci 63: 497–511.
- Moore JC, Berlow EL, Coleman DC, de Ruiter PC, Dong Q, Hastings A, Johnson NC, McCann KS, Melville K, Morin PJ, Nadelhoffer K, Rosemond AD, Post DM, Sabo JL, Scow KM, Vanni MJ, Wall DH (2004) Detritus, trophic dynamics and biodiversity. Ecol Lett 7: 584–600.
- Moore E, Sander F (1979) A comparative study of zooplankton from oceanic, shelf, and harbor waters of Jamaica. Biotropica 11: 196–206.
- Morioka Y, Nakashima J, Kimoto K (1990) Zooplankton biomass share of the collection with plankton net in the waters to the west of Kyushu, March 1987. Bull Seikai Natl Fish Res Inst 68: 143–151.
- Motoda S (1994) An estimation of primary and secondary production of the coral reef areas in Palau, Western Caroline Islands. Midoriishi 5: 5–8. (in Japanese)
- 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 (2009) Abundance, biomass and estimated production rate of net-zooplankton community in the tropical coral-reef waters at Tioman Island, Peninsular Malaysia. Ph. D. Thesis, Soka University, 202 pp.
- Nakajima R, Yoshida T, Othman BHR, Toda T (2008) Diel variation in abundance, biomass and size composition of zooplankton community over a coral-reef in Redang Island, Malaysia. Plankton Benthos Res 3: 216–226.
- Nakajima R, Yoshida T, Othman BHR, Toda T (2009) Diel variation of zooplankton in the tropical coral-reef water of Tioman Island, Malaysia. Aquat Ecol 43: 965–975.
- Nakashima J, Morioka Y, Kimoto K (1992) Further investigation of zooplankton biomass share in the collections with plankton net in the waters to the west of Kyushu. Bull Seikai Natl Fish Res Inst 70: 47–52.
- Omori M, Ikeda T (1984) Methods in marine zooplankton ecology. John Wiley & Sons, New York, 332 pp.
- Roman MR, Furnas MJ, Mullin MM (1990) Zooplankton abundance and grazing at Davies Reef, Great Barrier Reef, Australia. Mar Biol 105: 73–82.
- 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.
- Satapoomin S (1999) Carbon content of some common tropical Andaman Sea copepods. J Plankton Res 11: 2117–2123.
- Scheinberg RD, Landry MR, Calbet A (2005) Grazing of two common ap-

pendicularians on the natural prey assemblage of a tropical coastal ecosystem. Mar Ecol Prog Ser 294: 201–212.

- Strickland JDH, Parsons TR (1972) A practical handbook of seawater analysis, 2nd ed. Bulletin of Fisheries Research Board of Canada, Ottawa, 310 pp.
- Szyper JP (1976) The role of *Sagitta enflata* in the sourthern Kaneohe Bay ecosystem. Ph. D. Thesis, University of Hawaii, 147 pp.
- Toda T, Okashita T, Maekawa T, Kee Alfian BAA, Kushairi MRM, Nakajima R, Chen W, Takahashi KT, Othman BHR, Terazaki M (2007) Community structures of coral reefs around Peninsular Malaysia. J Oceanogr 63: 113–123.
- Transter DJ, George J (1972) Zooplankton abundance at Kavaratti and Kalpeni atolls in the Laccadives. In: Proceedings of 1st International Symposium on Corals and Coral Reefs (eds Mukundan C, Pillai CSG). Mandapam, India, June 1969, Marine Biological Association of India, Cochin, pp. 239–256.
- Uye S (1982) Length-weight relationships of important zooplankton from the Inland Sea of Japan. J Oceanogr 38: 149–158.
- Uye S, Ichino S (1995) Seasonal variations in abundance, size composition, biomass and production rate of *Oikopleura dioica* (Fol) (Tunicate: Appendicularia) in a temperate eutrophic inlet. J Exp Mar Biol Ecol 189: 1–11.
- 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.
- Wang Z, Thiébaut E, Dauvin JC (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 MK, Roff JC (1995) Annual biomass and production of the oceanic copepod community off Discovery Bay, Jamaica. Mar Biol 123: 481–495.
- Wild C, Huettel M, Klueter A, Kremb SG, Rasheed M, Jørgenssen BB (2004) Coral mucus functions as an energy carrier and particle trap in the reef ecosystem. Nature 428: 66–70.
- Wilson SK, Bellwood DR, Choat JH, Furnas MJ (2003) Detritus in the epilithic algal matrix and its use by coral reef fishes. Oceanogr Mar Biol Annu Rev 41: 279–309.
- Yahel R, Yahel G, Genin A (2005) Near-bottom depletion of zooplankton over coral reefs: I: diurnal dynamics and size distribution. Coral Reefs 24: 75–85.
- Zeitzschel B (1970) The quantity, composition and distribution of suspended particulate matter in the Gulf of California. Mar Biol 7: 305–318.