Copepod Gut Contents, Ingestion Rates, and Feeding Impacts in Relation to Their Size Structure in the Southeastern Taiwan Strait

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Li-Chun Tseng, Ram Kumar, Hans-Uwe Dahms, Qing-Chao Chen, and Jiang-Shiou Hwang (2008)
Copepod gut contents, ingestion rates, and feeding impacts in relation to their size structure in the southeastern Taiwan Strait. *Zoological Studies* **47**(4): 402-416. Copepod gut contents, ingestion rates, and grazing impact on phytoplankton were estimated at 19 sampling stations off the Penghu Archipelago (the Pescadores), in the Taiwan Strait during the summer monsoon season. Copepods were collected on board the *Ocean Research Vessel* III of the National Science Council within the upper 5 m by horizontal tows using a NORPAC 4.5-m-long conical net with a 1 m opening diameter and a 333 μm mesh size. The gut fluorescence method was used to estimate in situ ingestion rates and clearance rates of copepods. The abundance and species composition of copepods varied among sampling stations. A size-fractionation approach was applied, and the gut pigment contents and ingestion rates were estimated in 3 size categories (small, < 1 mm; medium, 1-2 mm; and large, > 2 mm). Results showed that gut pigment contents were higher for larger copepods and lower for smaller ones. Estimates of the copepod grazing impact showed that < 1% of the total phytoplankton standing stock was grazed daily during the early summer monsoon period. Grazing impact for the 23 most abundant taxa, which accounted for up to 90% of all copepods counted at each station, demonstrated large spatial variability ranging 0.001%-0.210% of the chlorophyll *a* standing stock. The highest grazing impact was recorded at station 18, a coastal station situated in the Penghu Channel, southwest of Penghu I., whereas the lowest impact was recorded at station 11 near the center of the Strait, northeast of Penghu I. The smaller copepod fractions were responsible for most of the grazing impact, due to their numerical dominance in these coastal waters. Variables affecting copepod community grazing impact estimates are discussed.
http://zoolstud.sinica.edu.tw/Journals/47.4/402.pdf

Key words: Taiwan Strait, Copepod, Gut contents, Feeding, Trophic ecology.

Zooplankton are the primary processors of photosynthetically fixed carbon in the oceans, and play pivotal roles in transferring matter and energy to higher trophic levels (Ingrid et al. 1996, Turner et al. 2001). Zooplankton grazing transfers substantial amounts of organic matter from surface waters to deeper water layers. The magnitude of the downward flux of organic carbon is determined by the partitioning of carbon among various size classes of grazers. Meso- and macrozooplankton substantially contribute to the downward flux of carbon from the euphotic zone as they produce larger fecal pellets, which have relatively higher sinking rates and carbon values (Cadee et al. 1992, Fortier et al. 1994, Froneman et al 2000). In contrast, photosynthetically fixed carbon that enters the "microbial loop", including phytoplankton, bacteria, and other protists, does not significantly contribute to the downward transfer of carbon, since these organisms disperse particulate organic matter (POM) that then remains suspended for longer periods of time (Longhurst 1991, Froneman et al. 2000). A consideration of both the classical food web (dominated by meso-

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and macrozooplankton) and the microbial loop is therefore important for estimating the downward flux of carbon and the efficiency of a biological pump.

Copepods are likely the most abundant metazoans in the ocean (Raymont 1980, Humes 1994, Verity and Paffenhöfer 1996) and constitute > 90% of the total zooplankton abundance in the Taiwan Strait (Lo et al. 2004) and other parts of the world's oceans (Calbet et al. 2000, Froneman 2000). Hence, quantifying rates of phytoplankton utilization by copepods is a necessary step for understanding the mechanisms that regulate phytoplankton populations in marine ecosystems and the downward flux of organic matter. Relationships among primary production, grazing, and the export of organic material are strongly determined by the size structure of the trophic pathways (Morales et al. 1990, Landryu et al. 1994a b, Froneman et al. 1997, Sautour et al. 2000).

Temporal, spatial, and size effects of copepod feeding on phytoplankton have been of major concern in a number of recent studies (Hansen et al. 1997, Romam and Gauzens 1997, Gowen et al. 1999, Head et al. 1999). As for Taiwanese waters, a study in northern Taiwan showed that phytoplankton stocks grazed by copepods are highly variable, ranging between 0.05%-11% of daily consumption (Wong et al. 1998). Another study elucidated the spatial distribution, taxonomic composition, and abundance of copepods in this area (Lo et al. 2004). Copepods generally dominate, accounting for > 90% of the total mesozooplankton abundance (Lo et al. 2004). However, there are few data available on copepod feeding impacts on phytoplankton around Taiwan, where water temperatures are close to tropical conditions (Chu 1971) and circulation patterns are otherwise well studied (Jan and Chao 2003, Jan et al. 2002).

In the present study, we examined the grazing impacts of 3 copepod size groups and the feeding impacts of 23 dominant copepods on ambient photosynthesizing plankton in the southeastern Taiwan Strait during the summer monsoon season.

MATERIALS AND METHODS

In order to elucidate the feeding impacts of copepods in relation to their size structure, 3 copepod size categories were considered: small (< 1 mm), medium (1-2 mm), and large (> 2 mm). In each size category, the gut pigment contents, abundances, and grazing impacts

Table 1. Location, date, time, and depth of sampling at 19 stations in the southeastern Taiwan Strait

St.	Latitude (N)	Longitude (E)	Date (d of June/time)	Depth at station (m)
1	22°23.968'	120°00.168'	16/16:35	863
2	22°24.093'	119°36.072'	16/20:51	1047
3	22°36.104'	119°28.988'	16/23:03	157
4	22°47.153'	119°20.282'	17/06:57	86
5	22°36.017'	119°39.167'	17/00:34	318
6	22°47.978'	119°30.230'	17/04:46	91
7	23°00.296'	119°36.134'	17/13:00	82
8	23°27.096'	119°30.028'	17/22:06	64
9	23°27.028'	119°17.960'	17/23:39	46
10	23°27.189'	119°06.030'	18/01:16	44
11	24°06.040'	119°18.168'	18/11:38	61
12	24°00.219'	119°30.102'	18/13:21	66
13	23°54.256'	119°42.076'	18/15:03	73
14	23°48.100'	119°54.096'	18/17:10	68
15	23°36.158'	119°52.178'	18/19:15	133
16	23°24.085'	119°51.113'	18/20:52	111
17	23°12.037'	119°51.161'	19/22:34	145
18	23°01.872'	119°51.212'	19/00:05	172
19	22°36.050'	120°03.056'	19/07:48	367

on phytoplankton were estimated using the gut fluorescence method.

Sampling

Day and night samples were taken at 19 stations in the southeastern Taiwan Strait, particularly in the area around the Penghu Archipelago (the Pescadores) (Fig. 1). Samples for this study were collected on board the *Ocean Research Vessel* III during cruise 455. Table 1 gives a detailed account of each sampling station selected for the feeding study in the southeastern Taiwan Strait. Temperature and salinity of the upper 5 m layer were recorded with a Seabird CTD instrument before sampling, and water samples were taken for chlorophyll *a* (Chl *a*) analysis, using Niskin bottles. Two quantitative zooplankton samples were taken for a gut pigment content analysis and estimation of copepod abundances. Zooplankton samples were collected with a conical net (4.5 m long, with a 1 m mouth diameter and 333 μm mesh size) from the upper 5 m water layer by means of horizontal tows. After retrieval,

the content of the 1st tow was fixed in a 5% formalin/seawater solution for later identification and enumeration. The content of the 2nd tow was stored in a plastic bag and immediately frozen in liquid nitrogen. Thereafter, samples were stored in a -20°C freezer in the dark until the gut pigments were analyzed. Details of copepod identification and enumeration followed Lo et al. (2004).

Copepod size fraction and abundance estimates

Estimates of copepod abundances were made by dividing quantitative samples with a Folsom splitter and identifying and counting a defined portion under a dissecting microscope. Thereafter, subsamples were moved to a scaled glass dish to estimate body lengths, and individuals were separated into 3 size categories of small (< 1 mm), medium (1-2 mm), and large (> 2 mm). Only the dominant copepod species that are known from the literature to be "potentially herbivorous" were considered to be grazers, and their abundances were estimated in 2 replicate samples. Abundance
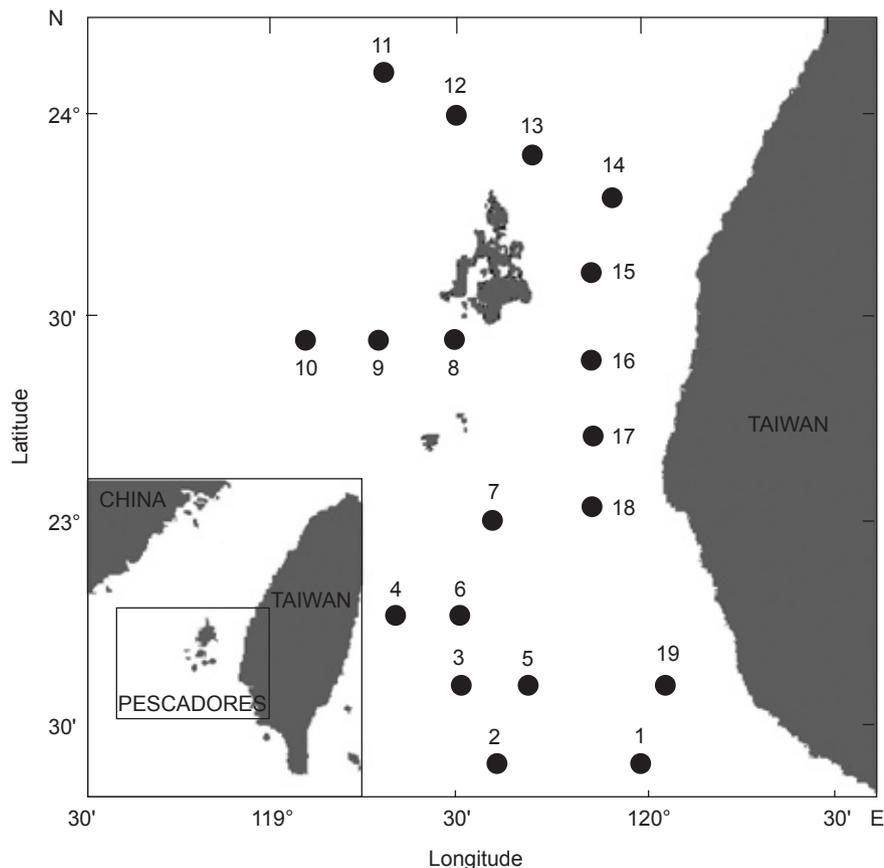

Fig. 1. Map of the Taiwan Strait showing locations of sampling stations around the Penghu Archipelago in the southeastern Taiwan Strait.

estimates of the 3 size groups were extrapolated to individuals/m^3.

Chl *a* extraction

Chl *a* levels in seawater were measured as described in Parsons et al. (1984). Duplicate seawater samples for the Chl *a* analysis were extracted overnight in 90% acetone at 4°C in the dark (Parsons et al. 1984). Chl *a* fluorescence in the acetone extract was measured before and after acidification with a Turner Designs Model 10 spectrofluorometer in our laboratory of National Taiwan Ocean University, Taiwan under dim light conditions.

Copepod gut pigment contents and ingestion rates

Gut pigment contents of copepods were analyzed fluorometrically, following the method of Mackas and Bohrer (1976) with modifications proposed by Morales et al. (1990). These mainly affected the non-homogenization of samples and non-correction for background fluorescence and pigment destruction in copepod guts. The frozen zooplankton samples were thawn and washed with filtered seawater to remove adhering algae and debris. The 23 dominant copepod species (comprising > 90% of the total mesozooplankton) were all potentially herbivorous according to the structure of their mouth parts and to existing knowledge of their feeding biology. For each species within the 3 size groups, 10-15 individual copepods were extracted in 5 ml of 90% aqueous acetone maintained at 4°C in the dark without homogenization in a refrigerator (Atkinson 1996, Hwang et al. 1998, Wong et al. 1998). After extraction overnight, the solution was centrifuged, and the upper clear layer was measured using a Turner Design Model 10 fluorometer in the laboratory illuminated with dim light. The extract was then acidified with 0.1 ml of 10% HCl and measured again. Due to pheopigment loss during the experiment, all pheopigment values were multiplied by a factor of 1.51 according to Dagg and Wyman (1983). Gut pigment content was expressed as ng chlorophyll *a* per individual copepod, obtained from the addition of Chl *a* and pheopigment (pheophorbide expressed as Chl *a* equivalent) concentrations in the gut.

Gut evacuation rates of each copepod size group were measured from samples collected in southwestern Taiwan (Lee 1998). The copepods used to measure the evacuation rates were sampled from surface waters, then transferred to a maintenance tank with 0.45 μm filtered seawater, after rinsing them with filtered seawater. Modest aeration was provided to keep copepods alive during the study of copepod gut evacuation rate. Copepod sub-samples were taken at 0, 1, 2, 3, 5, 8, 10, 15, 20, 25, 30, 40, 50, 60, 80 and 100 minutes of the experiments. Sub-samples were frozen in liquid nitrogen immediately and stored in a freezer at dark condition till analysis (For details in Hwang et al. 1998; Wong et al. 1998). In the laboratory, Chl *a* was measured in the copepod gut as described above. The evacuation rate was determined from decreased levels of Chl *a* in the gut content by the equation:

$$G_t = G_0 e^{-kt};$$

where G_t is the value of gut content at a given time, G_0 is the value of gut content of the 1st sample (0 min), and *k* is the constant value of the evacuation rate (1/min). The following evacuation values for each size group were 0.013, 0.015, and 0.017/min for large-, medium-, and small-sized copepods, respectively. The ingestion rate (I) was calculated by:

$$I = kG;$$

where I is the ingestion rate (ng Chl *a*/copepod/h), *k* is the gut evacuation rate (1/min) as provided above for 3 size groups, and G is the gut pigment content (ng Chl *a*/copepod). The clearance rate of Chl *a* per individual was calculated as follows:

$$F = I/C$$

where F is the clearance rate (ml/copepod/h), and C is the *in situ* Chl *a* concentration (ng Chl *a*/ml) in surface waters.

Copepod feeding impact

To estimate the feeding impact (FI, ml/m^3/d) of copepods on phytoplankton in surface seawaters, the total ingestion rate for each copepod size fraction was calculated and then related to the phytoplankton standing stock in the water column, as the total Chl *a* concentration. In order to determine this, individual ingestion rates of the dominant herbivorous copepods in each size fraction were multiplied by the herbivorous copepod abundances in that size fraction, assuming that copepods of similar body sizes have similar ingestion rates under the same environmental conditions (Morales et al. 1990):

$$FI = F \times A;$$

where A is the density of copepods per

volume seawater (copepods/m^3).

RESULTS

Hydrographic conditions

Figures 2A-B show isoline plots of surface water temperatures (Fig. 2A), salinities (Fig. 2B), and Chl *a* concentrations (Fig. 2C) recorded at 19 stations in the study area. Temperatures ranged between 24.8 and 30.6°C (average, 28.55 ± 1.79°C), while salinities ranged between 33.8 and 34.4 PSU (average, 33.9 ± 0.15 PSU). Early summer was characterized by the advent of the southwesterly monsoon resulting in the intrusion of South China Sea (SCS) surface waters with intermediate temperature, salinity, and nutrient levels which moved with the Kuroshio Branch Current (KBC), a North Pacific warm, highly saline, nutrient-poor water current, carrying zooplankton from the SCS. In this period, total mixing of the water column and an upward flux of nutrients to the photic zone occurred (authors' unpubl. data). The surface Chl *a* concentration for most stations was low, ranged between 0.10 and 4.03 ng/ml with an averaged of 0.88 ± 1.25 ng/ml (Fig. 2).
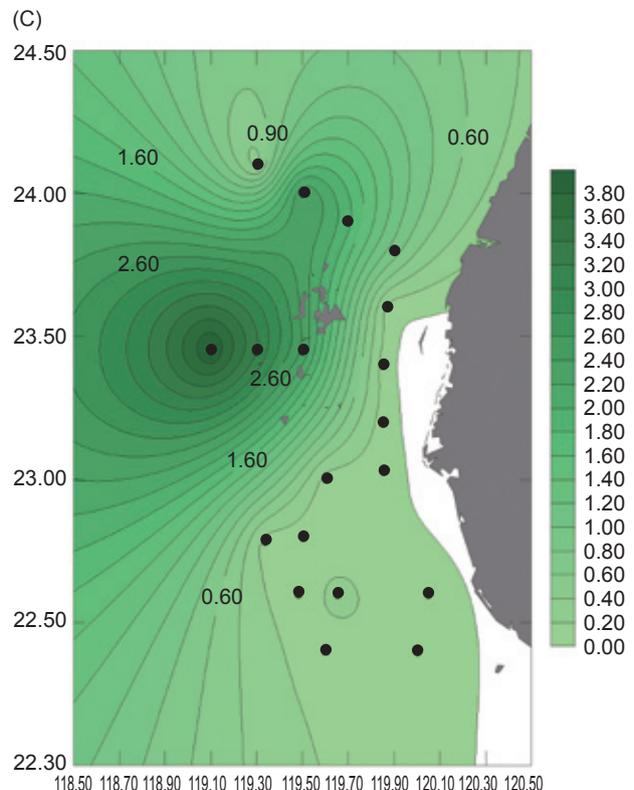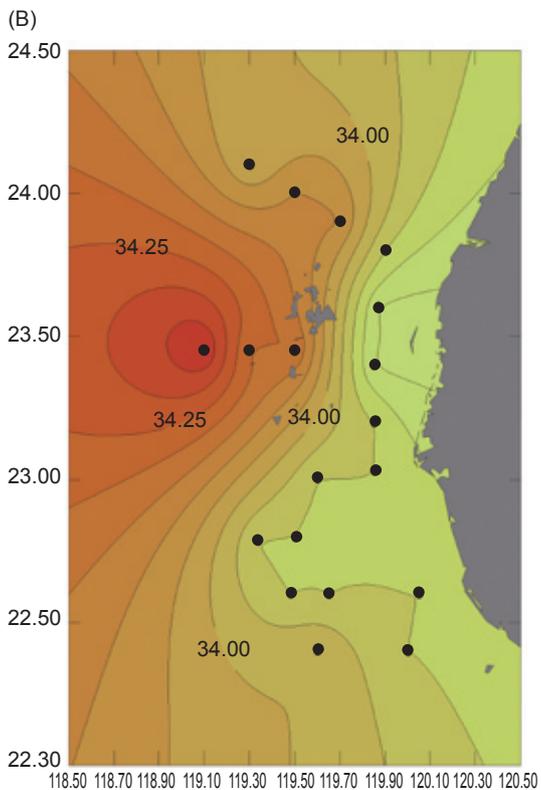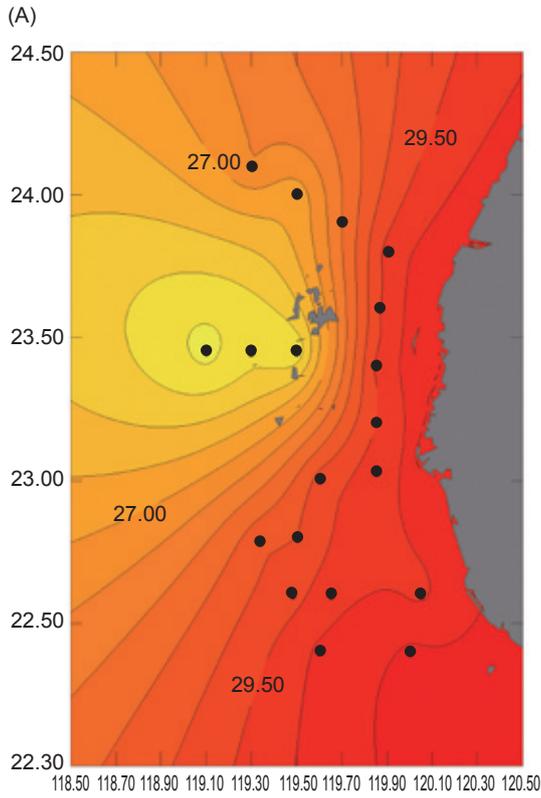
Fig. 2. Surface water temperature (°C) (A), salinity (PSU) (B), and chlorophyll *a* (ng/ml) (C) concentration at 19 sampling stations in the southeastern Taiwan Strait during the summer monsoon season.

Copepod species, size composition, and abundance

Copepods were the most abundant group of zooplankton in all samples. The dominant copepods included 18 genera and 23 species comprising > 90% of the total copepod abundance. Densities of the 23 most abundant copepod species which were used for the gut content analysis at each station are given in table 2. Among them, 22 species belonged to the Calanoida and 1 species belonged to the Poecilostomatoida (Table 2). The most frequent large-sized copepods were *Undinula vulgaris* (Dana, 1849), *Subeucalanus subcrassus* (Giesbrecht, 1888), *Labidocera detruncata* (Dana, 1849), and *Scolecithrix danae* (Lubbock, 1856). The most frequently encountered medium-sized copepods included *Cosmocalanus darwini* (Lubbock, 1860), *Centropages calaninus* (Dana, 1849), *Pleuromamma gracilis* (Claus, 1863),

Table 2. Taxonomic composition and density (individuals/m³) of 23 copepod species (used for the gut content analyses) at each of sampling stations 1-19. [a]Body length > 2 mm; [b]body length 1-2 mm; [c]body length < 1 mm

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Order Calanoida																			
Family Acartiidae																			
Acartia danae[c]								0.16	1.15	7.68									
Acartia negligens[c]								0.24							0.08				
Family Calanidae																			
Canthocalanus pauper[c]		0.33	0.05	1.95	2.44	0.77					0.03			0.24	0.08	5.08	0.87	3.22	
Cosmocalanus darwini[b]					0.16				0.39	4.87	0.01	8.07			3.61			0.87	
Undinula vulgaris[a]	5.77	0.85	1.67	0.72	1.47	1.25		2.22	0.13	92.1		1.35			1.18		0.50		0.17
Family Centropagidae																			
Centropages calaninus[b]	0.24	0.05	0.88	0.72	1.14	0.20	0.39	0.40			0.05	1.88	0.43	0.44	0.34	0.42	0.51	2.35	0.39
Family Clausocalanidae																			
Clausocalanus furcatus[c]																		0.79	
Family Eucalanidae																			
Paracalanus attenuatus[a]		0.21			0.25			0.32							0.25	1.15	0.69		
Subeucalanus subcrassus[a]									0.52										
Subeucalanus subtenuis[a]									5.32										
Family Lucicutiidae																			
Lucicutia flavicornis[c]		0.65																	
Family Metridiidae																			
Pleuromamma gracilis[b]								0.64											
Family Paracalanidae																			
Acrocalanus gracilis[c]	5.54	0.19	1.35	0.83		0.42	0.44		0.13	64.4	0.05	9.69	4.05	4.30	0.46	3.03	0.19	3.22	0.87
Acrocalanus monachus[c]	7.17	0.14	0.14	0.25		0.28			0.65						1.93		1.92	2.58	
Calocalanus pavo[c]	0.29	0.09	0.25	0.07					0.36	2.36		0.27			0.08		0.37	2.15	0.20
Calocalanus plumulosus[c]															0.04				
Family Pontellidae																			
Calanopia elliptica[b]						0.27			0.52	7.68		1.88			0.13				
Calanopia minor[c]															0.25				
Labidocera detruncata[a]		0.90	2.27	1.09	1.14	0.28	0.36			1.18		1.88	0.43	0.17	0.46	1.20	2.42	2.79	0.17
Family Scolecithrichidae																			
Scolecithrix danae[a]								1.13	1.69	1.77								0.86	
Family Temoridae																			
Temora discaudata[b]		0.28						1.27	0.13	5.31			0.07		0.42		0.31		
Temora turbinata[c]		0.05						1.43				2.10							
Order Poecilostomatoida																			
Family Corycaeidae																			
Corycaeus gibbula[c]		0.42	0.23	7.37		0.24									3.32		1.01		0.43

Calanopia elliptica (Dana, 1849), and *Temora discaudata* (Giesbrecht, 1889). Small-sized copepods included 11 dominant species of *Acartia*

danae (Giesbrecht, 1889), *Acartia negligens* (Dana, 1849), *Canthocalanus pauper* (Giesbrecht, 1888), *Clausocalanus furcatus* (Brady, 1883), *Lucicutia*
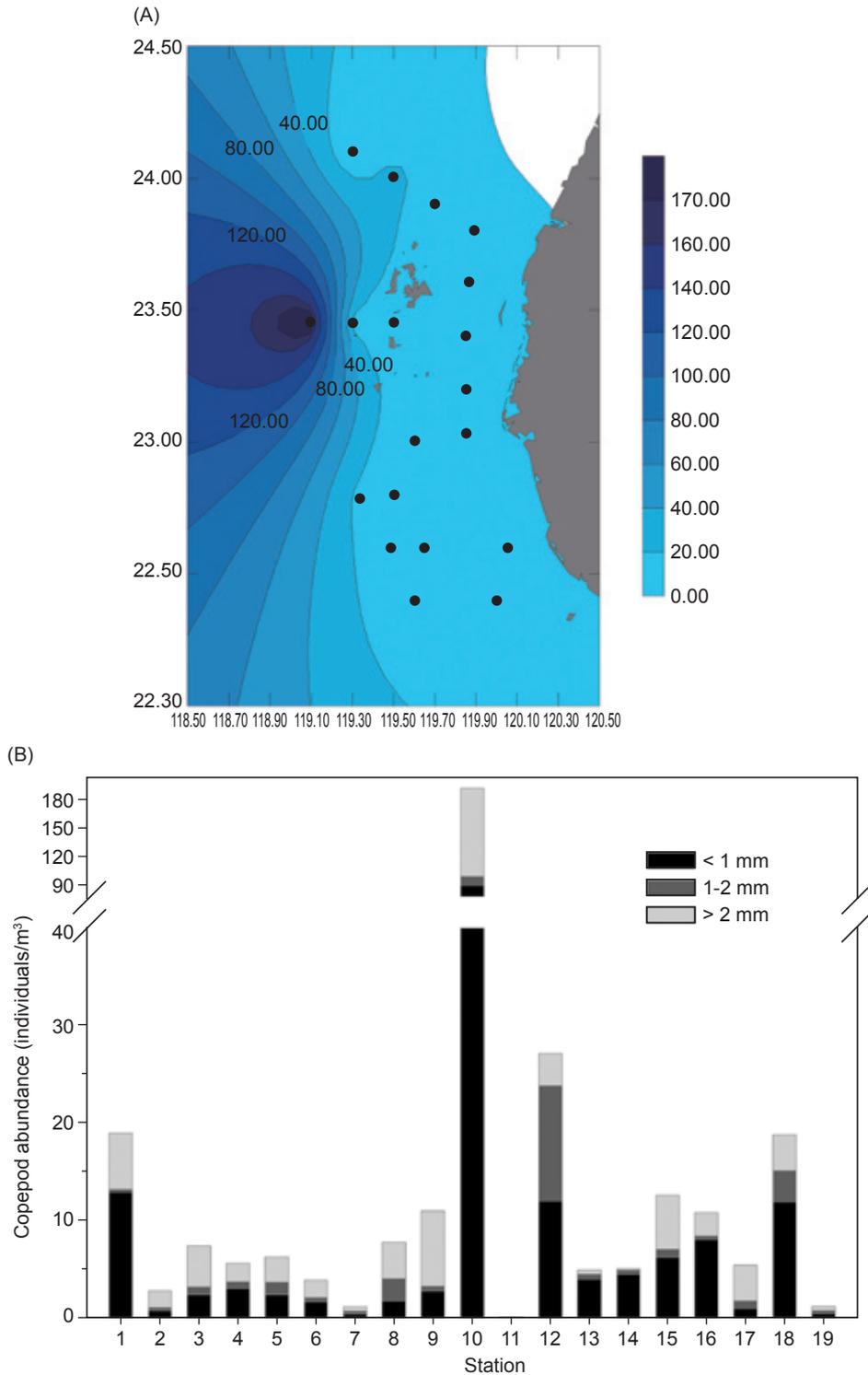

Fig. 3. Copepod abundance (individuals/m³) (A) and size composition (B) at 19 feeding stations in the southeastern Taiwan Strait during the summer monsoon season.

flavicornis (Claus, 1863), *Acrocalanus gracilis* (Giesbrecht, 1888), *Acrocalanus monachus* (Giesbrecht, 1888), *Calocalanus pavo* (Dana, 1849), *Calocalanus plumulosus* (Claus, 1863), *Calanopia minor* (A. Scott, 1902), and *Temora turbinata* (Dana, 1849).

The copepods *Undinula vulgaris*, *Centropages calaninus*, *Acrocalanus gracilis*, and *Labidocera detruncata* were found at most stations. Large numbers of *Undinula vulgaris* and *Acrocalanus gracilis* were collected at midnight on 17 June at station 10, with densities of 92.1 and
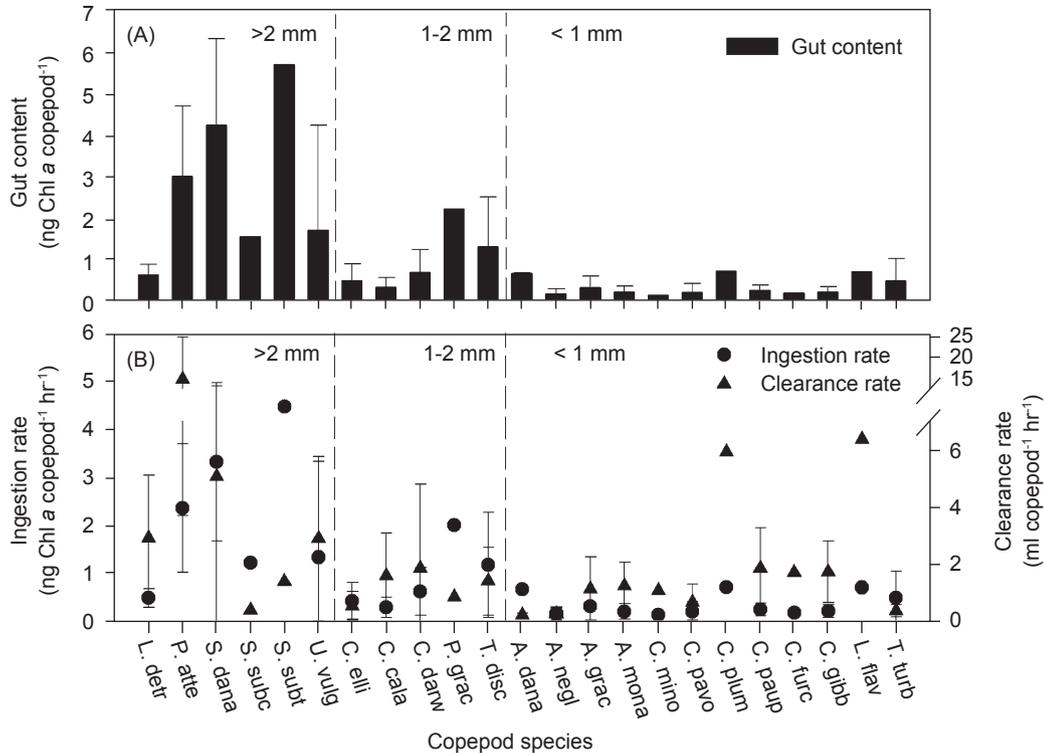
Fig. 4. Species-specific average value (± SD) of gut chlorophyll *a* contents (A), and ingestion and clearance rates (B) in the southeastern Taiwan Strait. L. detr, *Labidocera detruncata*; P. atte, *Paracalanus attenuatus*; S. dana, *Scolecithrix danae*; S. subc, *Subeucalanus subcrassus*; S. subt, *Subeucalanus subtenuis*; U. vulg, *Undinula vulgaris*; C. elli, *Calanopia elliptica*; C. cala, *Centropages calaninus*; C. darw, *Cosmocalanus darwini*; P. grac, *Pleuromamma gracilis*; T. disc, *Temora discaudata*; A. dana, *Acartia danae*; A. negl, *Acartia negligens*; A. grac, *Acrocalanus gracilis*; A. mona, *Acrocalanus monachus*; C. mino, *Calanopia minor*; C. pavo, *Calocalanus pavo*; C. plum, *Calocalanus plumulosus*; C. paup, *Canthocalanus pauper*; C. furc, *Clausocalanus furcatus*; C. gibb, *Corycaeus gibbulus*; L. flav, *Lucicutia flavicornis*; and T. turb, *Temora turbinata*.

Table 3. Comparisons of copepod abundances, feeding impacts, mesh size, and feeding primary production values at different study sites. [a]Included copepodids. [b]units: x 10^3 individuals/m^3. [c]Included only calanoid copepods

Study site	Abundance (individuals/m^3)	Feeding impact (%)	Feeding primary production (%)	Mesh size (μm)	Reference
Southern Benguela	3595-9241	1-5	-	200	Peterson et al. (1990)
Northeast Atlantic	336-2703	< 1	2	200	Morales et al. (1991)
South Georgia	6376[a]	< 3	< 4	200	Atkinson (1996)
Kerguelen Is.	23-742	0.1-0.3	2.4-4.6	200	Razouls et al. (1998)
Northern Taiwan	14.2-3286.5[c]	0.05-11	-	330	Wong et al. (1998)
Western Irish Sea	30.0-543.7[b]	0.7-8.6	4-76	280	Gowen (1999)
Southwest Taiwan	0.13-18.7	< 0.1-0.21	-	330	Present study

64.4 individuals/m^3, respectively. The isoline plot of copepod densities (Fig. 3A) and the proportions of different size groups were highly variable among the 19 stations (Fig. 3B). The average portions of small, medium, and large copepods were 48.0%, 16.5%, and 35.4%, respectively. Copepod abundances varied with sampling time and station. Samples collected at night showed higher abundances of larger-sized copepods than those during daytime. Integrating all samples, the density of copepods ranged between 0.14 and 187.4 individuals/m^3, with an average density of 18.50 ± 41.46 individuals/m^3.

Copepod gut contents, ingestion, and clearance rates

Gut pigment contents of copepods varied greatly among species and stations. The species-specific average gut pigment contents, ingestion rates, and clearance rates of large-, medium-, and small-sized fractions are shown in figure 4. Among the large-sized fraction, the calanoid copepod *Undinula vulgaris* showed maximum variability with a gut pigment content ranging between 0.12 and 8.17 ng Chl *a*/individual. *Scolecithrix danae* had gut pigment contents ranging 2.08-7.04 ng Chl *a*/individual (Fig. 4). The lowest value of gut contents among the large-sized group was found in *Labidocera detruncata* (0.22-1.08 ng Chl *a*/individual). Differences in gut pigment contents among specific copepod species in the medium-sized group were not significant. The minimum gut pigment content (Fig. 4) was recorded in *Cosmocalanus darwini* (0.04-1.6 ng Chl *a*/individual), and the maximum value was recorded in *Temora discaudata* (0.17-3.11 ng Chl *a*/individual). Gut pigments in the small-sized group ranged from the lowest value of 0.01 ng Chl *a*/individual in *Calocalanus pavo* to the highest value of 1.09 ng Chl *a*/individual in *Temora turbinata*. Differences in gut pigment contents

Fig. 5. Correlation between copepod gut content (chlorophyll (Chl) *a*) and ambient Chl *a* concentration for 3 size groups ((A) large size (> 2 mm), (B) medium (1-2 mm), and (C) small (< 1 mm) copepods) at 19 stations in the southeastern Taiwan Strait.

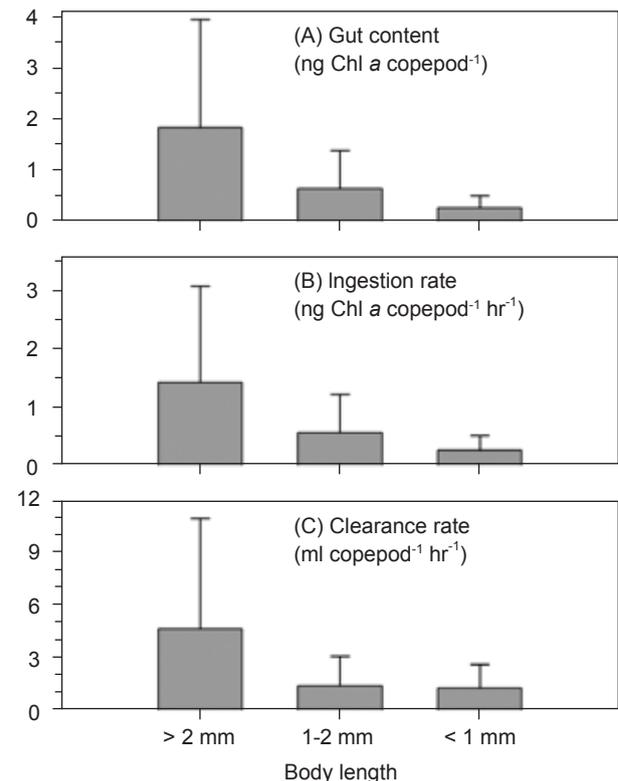

Fig. 6. Average values of (A) gut chlorophyll (Chl) *a* content, (B) ingestion rate, and (C) clearance rate for small- (< 1 mm), medium- (1-2 mm), and large-sized (> 2 mm) fractions of copepods in the southeastern Taiwan Strait during the summer monsoon season.

among copepods of the small-sized group were limited. A proportionately higher amount of gut pigment contents in the larger size fraction were recorded at stations 1, 10, 13, and 14. The gut pigment contents for medium-sized copepods ranged between 0.04 and 3.11 ng chlorophyll *a*/individual copepod, with the highest value for *Temora discaudata* at station 8 at midnight.

Daily ingestion rates were calculated from the gut pigment contents and evacuation rates. There was no consistent pattern for ingestion rates among copepods. Among the large-sized group, the maximum variability in ingestion rates was shown by *Undinula vulgaris* which ranged between 0.09 and 6.37 ng Chl *a*/individual/h (Fig. 4). The ingestion rates recorded for other species of the large-sized group fell within the range shown by *Undinula vulgaris*. Among the medium- and small-sized group of copepods, the minimum and maximum amount of Chl *a* ingested by *Calocalanus pavo* was 0.01 ng Chl *a*/individual/ h, and for *Temora discaudata* it was 2.8 ng Chl *a*/ individual/h (Fig. 4A).

Among the large-sized group of copepods, the maximum value of the clearance rate was recorded for *Paracalanus attenuatus* (30.25 ml/copepod/h) (Fig. 4B). Among medium-sized copepods, the highest clearance rate was shown

by *Cosmocalanus darwini* (8.3 ml/copepod/h) (Fig. 4B). Most of the small-sized copepods had < 1 ng Chl *a* as the gut content in the study area. Large-sized copepods had a higher clearance rate and were consuming more Chl *a* than small-sized copepods.

However, gut contents of copepods varied to a large extend with station and body size (Fig. 4). The uptake of phytoplankton by copepods was higher when the environmental Chl *a* increased at the sampling stations (Fig. 5). All 3 copepod size groups showed a significant correlation between the ambient Chl *a* concentration and the gut pigment content. This held for large-sized (Pearson correlation, $n = 40$, $r = 0.530$, $p = 0.0004$; Fig. 5a), medium-sized (Pearson correlation, $n = 37$, $r = 0.654$, $p < 0.0001$; Fig. 5B), and small-sized copepods (Pearson correlation, $n = 67$, $r = 0.661$, $p < 0.0001$; Fig. 5C). We found a significant correlation between the Chl *a* concentration in ambient waters and gut contents (Pearson correlation, $n = 144$, $r = 0.433$, $p < 0.0001$; Fig. 5D).

Large-sized copepods showed significantly higher gut pigment contents (1.84 ± 0.865 ng Chl *a*/individual) than did medium-sized (0.65 ± 0.26 ng Chl *a*/individual) (one-way ANOVA, $p < 0.01$) and small-sized species (0.28 ± 0.076 ng Chl *a*/
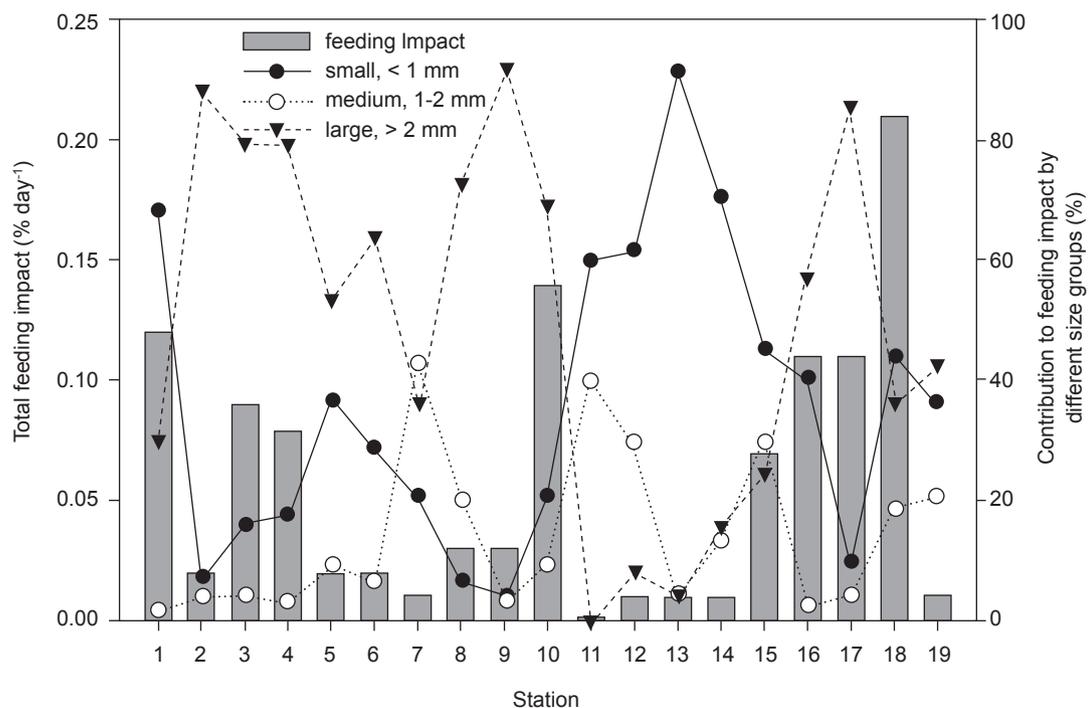

Fig. 7. Relative contributions of feeding by small-, medium-, and large-sized fractions of copepods to the total copepod feeding impact at 19 stations in the southeastern Taiwan Strait during the summer monsoon season.

individual) (one-way ANOVA, $p < 0.01$) (Fig. 6A). The amount of gut pigment in the medium- and small-sized fractions did not significantly differ ($p = 0.283$, one-way ANOVA) (Fig. 6A).

Grazing impact

The grazing impact of the copepod community on the total Chl *a* standing stock ranged between 0.001%-0.211% with a mean of 0.06% at 19 stations in waters around Penghu I. The lowest value was measured at station 11 on the 18th of June at noon, and the highest value was obtained at station 18 on the 19th of June at midnight. The small-sized group of copepods accounted for most of the community grazing impact on phytoplankton, as a result of their higher relative abundances. The relative contributions of the 3 size groups significantly differed on a spatial scale (Fig. 6). The feeding impact on the total Chl *a* standing stock imposed by the larger-sized group of copepods was higher at the southern stations (stns. 2, 3, 4, 8, and 9), whereas the northern stations (stns. 11, 12, 13, and 14) were more affected by small-sized copepods (one-way ANOVA, $p < 0.01$; Fig. 7). These results suggest that the amount of phytoplankton consumed by the copepod assemblages around Penghu I. was low.

DISCUSSION

The 7 most abundant species identified in our samples collected during the summer monsoon season in the southeastern Taiwan Strait were *Acartia negligens*, *Acrocalanus gracilis*, *Clausocalanus furcatus*, *Cosmocalanus darwini*, *Lucicutia flavicornis*, *Temora discaudata*, and *Undinula vulgaris*. These species were reported by Lo et al. (2004) who previously analyzed copepod distribution and abundances in this area. These species are also abundant in waters north of Taiwan (Hwang et al. 1998, Wong et al. 1998), where *Acrocalanus gracilis* and *Undinula vulgaris* were dominant (Hwang and Turner 1995, Hwang et al. 1998, Wong et al. 1998).

Ingestion and clearance rates recorded in this study were within the range of those reported from copepods collected from the northern coast of Taiwan (Hwang et al. 1998, Wong et al. 1998; Table 3) and in several other regions of the world's oceans (reviewed by Morales et al. 1990). As in the present study, gut pigment contents tended to increase with increasing copepod size in several

other studies as well as with phytoplankton concentration and cell size (> 10 μm) (Bautista and Harris 1992, Hansen et al. 1994, Froneman et al. 2000). However, grazing budgets estimated here and in previous studies did not include postembryonic stages (nauplii and copepodids) which may have resulted in an underestimation of overall grazing rates by copepod standing stocks.

Assumptions and methodological artifacts of the gut fluorescence method have been extensively reviewed (e.g., Dam and Petersen 1988, Morales and Harris 1990, Petersen et al. 1990). The gut fluorescence method has been criticized for not fulfilling some of its assumptions (Wang and Conover 1986, Lopez et al. 1988, Dam and Peterson 1991, Landry et al. 1994a). However, its application to copepod size fractions (Morales et al. 1990, 1991) shows the practical advantage of this approach. It allows straightforward large-scale oceanic data collection for estimating *in situ* grazing impacts of herbivorous copepods (Wong et al. 1998, Sautour et al. 2000).

It is noteworthy that the ambient Chl *a* concentration was low at the present study site (Chan et al. 2006, Tan et al. 2004). There were 5 stations with a Chl *a* concentration of > 1.0 μg/L and 13 stations with ≤ 0.3 μg/L. The Chl *a* concentration of surface seawater averaged 0.82 mg/m³. Atkinson (1996) suggested that in areas with low Chl *a* concentrations, copepods may be prompted to switch to feeding on ciliates and other food sources. Low Chl *a* concentrations and the dominance of smaller-sized phytoplankton (< 5 μm) might force copepods to utilize heterotrophic food sources, resulting in a low feeding impact on phytoplankton standing stocks.

In situ copepod feeding impacts are influenced by several factors, including body size (Morales et al. 1991), the relative abundances of different copepod species (Atkinson 1996), time of the day (Bollens and Stearn 1992, Saito and Taguchi 1996), season (Razouls et al. 1998), nutritional preferences, available food types (Atkinson 1996, Prince et al. 2006), food concentration (Tsuda and Nemoto 1987, Ellis and Small 1989, Landry et al. 2000), and seawater temperatures (Dagg and Wyman 1983, Dam and Peterson 1988). Marine zooplankton gathers more food from a particle size of 2 to 2000 μm with increasing body size, (reviewed in Hansen et al. 1994, 1997). Generally, large-sized copepods have more gut pigments than do smaller ones (Morales et al. 1990, present study). Larger copepods have a larger gut volume and higher

energy expenditures required for metabolism, and hence, the value of Chl *a* in the gut increases with increasing body size. Interestingly, both the highest and lowest levels of gut pigments were found in the large-sized *Undinula vulgaris* in this study. However, a higher abundance of small-sized copepods may impose higher impacts on phytoplankton standing stocks. Using a 333 μm mesh net may have underestimated the grazing impact of copepods that pass through a 333 μm net, since small-sized copepods are abundant in the tropical waters of Taiwan. However, the present study using a NORPAC net (333 μm mesh) matches most research in the western Pacific Ocean (Motoda 1957, Hwang et al. 2000a b, 2004a b, 2006, Hwang and Wong 2005, Dur et al. 2007, Hwang et al. 2007). Nevertheless, for overall copepod feeding impact comparisons, a small mesh size (e.g., ≤ 100 μm mesh) is recommended.

Some copepods select phytoplankton by size. Atkinson (1996) used a phytoplankton size of > 10 μm for his experiments and found that some algae cells were too small to be handled by copepods. Roman and Gauzens (1997) suggested that the minimal size limit of phytoplankton for copepod grazing is 2 μm. Therefore, the copepod feeding impact on phytoplankton should decrease with an increasing proportion of small-sized phytoplankton. In the present study, we did not measure the phytoplankton size composition, and there are no relevant data available for waters southwest of Taiwan. However, in our preliminary study, only a negligible amount of Chl *a* (< 0.001 μg/L) was recorded in seawater from the study area when filtered through a 10 μm mesh. Chang et al. (1996) found that the ultraplankton (< 5 μm) component was high and sometimes approximated 100% of the total phytoplankton density in the East China Sea, north of Taiwan during the summer of 1994. The low feeding impact of copepods on phytoplankton in the southeastern Taiwan Strait may therefore be due to the phytoplankton size approaching the lower size limit of the copepod's dietary niche breadth.

The feeding rhythm of copepods appears to be an important factor in their feeding impact on phytoplankton (Lee 1998, Dagg et al. 1989). Mackas and Bohrer (1976) found the maximum copepod feeding at night in surface waters as well as those present in deeper layers. Saito and Taguchi (1996) and Lee (1998) also found that high gut pigment contents occurred during nighttime and were minimal during daytime. We also obtained species-specific differences in day and night abundances and copepod gut contents. Samples collected during the night had higher abundances of large-sized copepods than those during day time. The larger copepod, *Undinula vulgaris*, and the most abundant copepod, *Acrocalanus gracilis*, had significantly higher gut content values in night samples than those collected during daytime. Therefore, the measurement of copepod feeding impacts on phytoplankton should consider sampling time and copepod diel vertical migrations (Haney 1988). Copepod feeding is dynamic and may exhibit wide variations (Hwang et al. 1998, Lee 1998, Calbet et al. 1999, Buffan-Dubau and Carman 2000). This may explain why some small-sized copepods had relatively higher Chl *a* values in their gut contents than large-sized copepods in the present study.

Peterson et al. (1990) found that nearshore copepods consumed about 1% and midshelf copepods about 5% of the overall phytoplankton per day. Morales et al. (1991) suggested that copepods consumed, on average, < 1% of the phytoplankton standing stocks, and the grazing impact was provided mainly by small-sized copepods (with a length of 200-500 μm). Atkinson (1996) found that < 4% of primary production of phytoplankton per day off South Georgia in the Southern Ocean was removed by copepods. In northern Taiwan, Wong et al. (1998) reported that feeding impacts of calanoid copepods on phytoplankton ranged 0.05%-11% in coastal waters near a nuclear power plant. Razouls et al. (1998) reported that copepods off the Kerguelen Islands ingested 0.12% of the mean phytoplankton standing stocks. In the present study, the highest feeding impact of copepods on phytoplankton was 0.21%. These results indicate that copepods must consume a large amount of non-phytoplankton food sources to sustain their nutritional requirements. Romam and Gauzens (1997) suggested that in the equatorial Pacific, the major carbon sources of copepods are heterotrophic protists. Razouls et al. (1998) indicated that the main energy source of mesozooplankton copepods in Kerguelen I. waters was not phytoplankton. Merrell and Stoecker (1998) found that both, copepod adults and nauplii cleared heterotrophic protists at a considerably higher rate than they cleared phytoplankton. Previous studies also described several copepods as being opportunistic feeders or omnivores, which do not exclusively feed on phytoplankton, although this may be their primary choice (Turner 1991, Roff et al. 1995, Atkinson 1996, Peterson and Dam

1996, Verity and Paffenhöfer 1996, Merrell and Stoecker 1998, Kang and Poulet 2000). Verity and Paffenhöfer (1996) suggested that the feeding impact of copepods would be underestimated if heterotrophic food organisms were not quantified. In a recent study on copepod grazing in the Antarctic Circumpolar Current, all grazers also preyed on microzooplankton, most steadily on ciliates (Schultes et al. 2006). Accordingly, our results might have underestimated copepod feeding impacts, since previous studies indicated that copepods in the waters off southwestern Taiwan also feed on heterotrophic organisms (Wu et al. 2004).

Several authors have reported enhanced copepod feeding, growth, and fecundity at spatiotemporal discontinuities in horizontal and vertical hydrographic structures, in parallel with local Chl *a* maxima and the dominance of large phytoplankton cells. Such phenomena occur in tidal fronts, upwellings, spring blooms, and during storm events (Hanson and Leggett 1986, Peterson and Bellantoni 1987, Kiørboe et al. 1988 1990, Nielsen and Kiørboe 1991, Peterson et al. 1991, Schnetzer et al. 2007). We recorded significant spatial discontinuities in gut contents and feeding impacts of copepods in the waters around Penghu I. However, a significant correlation was recorded between Chl *a* concentrations in ambient waters and gut contents. Variabilities in grazing impacts during the present study period were mainly due to differences in both, copepod abundances and copepod feeding rates. Although large copepods showed the highest ingestion rates on an individual basis, most of the phytoplankton was consumed by small- and medium-sized copepods, due to their numerical dominance. Our results further support the notion that in coastal food webs, phytoplankton production is generally underexploited by copepod grazing, and most phytoplankton production ends up in pathways (microbial loop) or sinks to the sea bottom (Jimenez et al. 1989).

Obligatory herbivorous copepods appear to be an exception rather than the rule in copepod feeding; however, species-specific propensities for herbivory differ widely. An unsolved problem yet is, to what extent copepods additionally utilize heterotrophic organisms in their diets.

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