

Flexible feeding patterns of copepod *Centropages tenuiremis* in fluctuating conditions: a possible survival strategy to cope with disturbance

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Abstract

Centropages tenuiremis is a species with a wide distribution range in disturbed coastal waters. However, due to a lack of dietary information, it remains unclear as to how they maintain such dominance in fluctuating conditions. In this study, *C. tenuiremis* was collected from the Daya Bay Nuclear Power Plant both in inlet and outfall regions at 06:00, 12:00 and 18:00 on April 27, 2011 and their *in situ* diet was analyzed using a PCR protocol targeting 18S ribosomal genes. Thirty-four species of prey organisms were identified totally, including Dinophyta, Bacillariophyta, Viridiplantae, Rhizaria, Apicomplexa, Chordata, Mollusca, Arthropoda and Fungi, indicating an obvious omnivorous feeding habit of *C. tenuiremis*. *Centropages tenuiremis* obviously exhibited spatial and temporal variations in diet composition. More plant prey (land plants and phytoplankton) were consumed in the morning (~50%), while more animal prey (metazoans and protozoans) were ingested at midday and night (60%–70%). Furthermore, a more diverse diet was detected in the outfall region (10–11 taxa), where the temperatures were relatively higher and more fluctuating, than in the control region (5–10 taxa). This finding indicated that *C. tenuiremis* could potentially expand its food spectrum under stressful condition. Specifically, *C. tenuiremis* exhibited phytoplankton preference (58.62%–67.64%) in the outfall region with a lower omnivory index (0.27–0.35) than in the control region (0.51–0.95). However, phytoplankton density was lower than that in the control region, suggesting a possible herbivorous tendency of *C. tenuiremis* under elevated temperatures to balance the energy acquirement and feeding effort. The flexible food choices of *C. tenuiremis* observed here could effectively buffer environmental fluctuations and might be an important survival strategy in coastal ecosystems.

Key words: *Centropages*, feeding response, feeding strategy, coastal ecosystem, Daya Bay

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1 Introduction

Coastal ecosystems are among the most frequently used and threatened natural ecosystems (Barbier et al., 2011). Anthropogenic disturbances have driven transformation of natural habitats in coastal waters, which in turn has made them even more turbulent due to their own complex physical and biological processes (Li et al., 2011; Taylor et al., 2014; Carstensen et al., 2015). Success of any species living in such a variable environment depends on its capacity to finding food and mates, as well as escaping predators (Kjørboe, 2011). Thus, feeding was an important guarantee for organisms to maintain population dominance, as well as an important process to drive the matter and energy flow

in coastal habitats. Studying feeding response of habitat organisms, especially wide-distributed species in coastal waters, under different disturbance factors is helpful for us to understand the adaptation for survival of the native organisms, and then it is necessary and instructive for health and stability of coastal ecosystems.

Thermal effluents from coastal power plant are one of the major threats to the surrounding waters of the coastal ecosystems. The average water temperature in outfall regions could be 9.5–10°C higher than waters in inlet areas in summer (Madden et al., 2013). The elevated temperature could dramatically affect the phytoplankton community structure (Li et al., 2011), and then af-

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fect food availability of zooplankton indirectly (Calbet, 2001). For another, rising temperature will directly influence physiological processes of zooplankton (Richardson, 2008), for instance, higher metabolic rate under rising temperature will change nutritional demands of zooplankton which then exert feed-back effects on their food intake (Boersma et al., 2016). Thus, the thermal effluents might affect pathways of matter and energy flow in aquatic ecosystems by alerting the food acquisition of zooplankton. Copepods could regulate feeding according to the food environment (Calbet et al., 2007; Gaudy and Thibault-Botha, 2007; Boersma et al., 2016), especially for some sensitive species, whereas few studies concerning the feeding response of these habitat copepods.

Centropages is an important and common copepod in the mesozooplankton assemblage of the fluctuating neritic coastal marine with very wide temporal and spatial distribution (Carlotti and Harris, 2007; Calbet et al., 2007). They fed on a wide spectrum of prey, including phytoplankton (diatoms and dinoflagellates) and animal prey (ciliates, appendicularia, and even fish eggs and larvae) due to their flexible swimming capacity (Calbet et al., 2007; Gaudy and Thibault-Botha, 2007; Benedetti et al., 2016). As these species cannot withstand food deficiency for a long time (~10 d) due to their low lipid reserves (Dagg, 1977), they seem to prefer prey with high nutrition or a low escape capacity, which cost less in feeding effort (Kjørboe, 2011). For example, *C. hamatus* showed an obvious feeding shift from mixed prey to an almost pure ciliate diet, when ciliates contributed to more than 5% carbon concentration of the available food (Saage et al., 2009). In addition, *Centropages* species would feed mostly on larger prey when supplied with low concentrations of food, which might decrease energy loss during feeding (Garrido et al., 2013). Thus, understanding their feeding response to their habitat environments threatened by anthropogenic disturbances helped to understand why they were widespread or always the dominant species in coastal waters. However, studies of *in situ* feeding response of *Centropages* to disturbance, especially for the important threat of thermal effluents in coastal waters, were limited.

The Daya Bay is a subtropical semi-enclosed bay with diverse natural habitats and rich biological resources (Li et al., 2011; Liu et al., 2013; Li et al., 2014). Due to increasing human activities in recent years, especially the operation of two nuclear power plants (Daya Bay Nuclear Power Plant (DNPP) and Ling'ao Nuclear Power Plant (LNPP)), the deterioration of natural habitats and transformations among native organism communities has been reported in the Daya Bay (Li et al., 2011; Liu et al., 2013; Li et al., 2014). The total thermal effluents of these two nuclear power stations were approximately 315 m³/s, resulting in apparent temperature elevation in the receiving regions (Zhang and Zhou, 2004). The exchange rate of sea water in the Daya Bay is relatively slow (approximately 15 d for each time) (Han and Ma, 1991), enhancing the influence of thermal effluents on habitat organisms. Phytoplankton community structure has been reported to shift from diatom-dominated to dinoflagellate-dominated in summer (Li et al., 2011). However, it remains unclear how this shift will affect their primary consumers (largely copepod).

Centropages tenuiremis is a dominant species with a wide distribution in the Daya Bay including the outfall regions, particularly in winter-spring (Liu et al., 2013; Li et al., 2014). According to previous reports, the suitable temperature range of *C. tenuiremis* was generally 18°C to 24°C (Huang and Zheng, 1986; Li and Gao, 2012; Liu and Li, 1998), and a lower temperature (4–26°C) resulted in a higher survival rate (Huang and Zheng, 1986). While in the outfall region, the temperatures were significantly

higher than the reported suitable temperature (Huang and Zheng, 1986; Li et al., 2011; Li and Gao, 2012). Thus, it remains unclear how the natural *C. tenuiremis* to cope with disturbance near nuclear power plants due to the lack of *in situ* dietary information. In this study, *in situ* diets of *C. tenuiremis* from both the thermal effluent area and unaffected area were analyzed by a previously described copepod/symbiotic ciliate-excluding eukaryote-inclusive PCR protocol, and the diet information was compared in order to reveal their feeding strategy in such conditions. The objective of this study was to uncover the food choices of *C. tenuiremis* in the disturbed waters of the Daya Bay and thus assess the adaptive and survival mechanisms of coastal copepods in fluctuating coastal ecosystems.

2 Materials and methods

2.1 Sample collection

All samples were collected in the inlet (R1, 22.592°–22.597°N, 114.547°–114.553°E) and outlet (R2, 22.609°–22.614°N, 114.572°–114.581°E) regions of the nuclear power plants at 06:00, 12:00 and 18:00 on April 27, 2011 (Fig. 1). The surface water environmental parameters (temperature, pH and salinity) were measured using a YSI-6600 Multi-Parameter Water Quality Sonde.

Copepod samples were collected by towing a plankton net (505 µm mesh) horizontally, 1–2 m below the surface for 5 min, repeated several times to ensure sufficient biomass collection. The ambient water samples (500 mL) were collected with Niskin bottles from the surface layer. All samples were immediately fixed on site in final 2% Utermöhl's solution to avoid DNA degradation or copepod gut content clearance and were then stored at 4°C in the laboratory (Guo et al., 2012).

2.2 Microscopic analysis of phytoplankton samples

Water samples were mixed gently, and then 50 mL subsamples were poured into a 50 mL centrifuge tube to allow phytoplankton cells to settle for 24 h in the dark. The samples were then concentrated to 1 mL using the Utermöhl settling method. Phytoplankton were identified and counted in a Sedgwick-Rafter counting chamber using an Olympus BX51 microscope.

2.3 Diet analysis of copepod samples

In the laboratory, copepods were identified and sorted under a stereomicroscope Leica S8APO. The identified dominant copepod species, *C. tenuiremis*, was picked out and rinsed with autoclaved 0.45 µm filtered seawater and then with sterilized water several times; then, they were observed under the stereomicroscope to confirm the absence of any attachments on their body surfaces. More than 30 female adults *C. tenuiremis* were combined and homogenized using an autoclaved disposable micropestle in a 1.5 mL microfuge tube; and then, the homogenate was incubated in 500 µL DNA buffer (1% SDS, 100 mmol/L EDTA and 200 µg/mL proteinase K) at 55°C for 48 h. DNA was extracted, and PCR was performed using a CEEC (copepod/symbiotic ciliate-excluding eukaryote-common) primer set, which can amplify most eukaryote 18S rDNAs while depressing amplification of symbiotic ciliate and copepods sequences (Hu et al., 2014, 2015). The PCR products were purified and cloned, and then, a certain number of clones for each sample were picked randomly and sequenced. The sequences obtained were manually trimmed of primer sequences at the 5' and 3' ends and then submitted to NCBI to blast against the nucleotide database. In this study, the

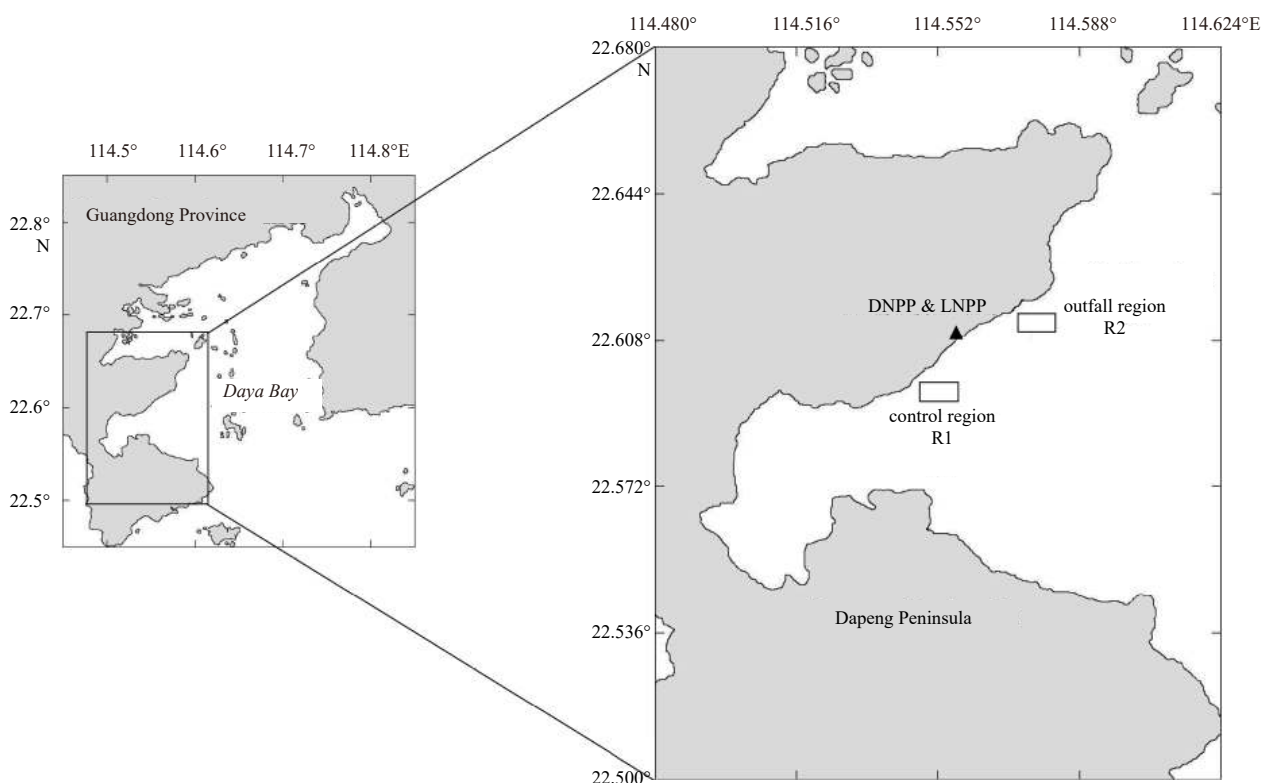


Fig. 1. Sampling locations (R1, R2) in the Daya Bay.

identified sequences were represented by the highest homologous sequences. The information obtained was tabulated, and our sequences were then clustered with the highest homologous sequences from the GenBank database using CLUSTAL W (1.8). The aligned results were then imported into MEGA 6.0, and a maximum-likelihood tree was inferred using bootstrap analysis with 1 000 replicates. We did not collect enough individuals of *C. tenuiremis* for molecular detection in the control region at night, and only five samples were constructed for the diet analyses of *C. tenuiremis* in all.

2.4 Data analysis

2.4.1 Diversity indices

The diversity index of “Simpson_1-D” (Simpson's diversity index) was employed for the description of species diversity of the community (Simpson, 1949). The diversity index of “Shannon_H”, also named the “Shannon-Wiener index”, is well to estimate a combined diversity of population richness and evenness (Shannon and Weaver, 1949). Chao1 is a good index to evaluate population richness (Chao, 1984). The three diversity indices values here were calculated using software of PAST 3.11.

2.4.2 Omnivory index

The concept of an omnivory index (OI) was introduced in the Ecopath software to describe the feeding behavior of different consumer groups (Christensen and Pauly, 1992). The OI was calculated as follows:

$$OI_i = \sum_{j=1}^n (TL_j - (TL_i - 1))^2 \cdot DC_{ij},$$

where n is the group number in the system; TL_j is the trophic level of prey j ; TL_i is the trophic level of predator i ; and DC_{ij} is the fraction of prey j in the diet of predator i , which in this paper is calculated as the percentage of sequence numbers of each prey in the total 18S rDNA library from each copepod sample. When the OI is equal to zero, it means the consumers feed on one single trophic level. A higher OI indicates that the prey is from more trophic levels and that more carnivorous feeding is occurring. A lower OI indicates a higher tendency of herbivorous feeding.

3 Results

3.1 Environmental parameters and phytoplankton community

The temperature was relatively stable during the day in the control region, with an average of $(24.3 \pm 0.47)^\circ\text{C}$. In contrast, in the outfall region, the average temperature was higher $(29.3 \pm 1)^\circ\text{C}$, with clear fluctuations and a 6°C difference between morning and night time (Table 1).

A consistently lower species number and cell abundance was identified in the outfall region compared with that of the control region. In the control region, the average cell abundance was 7×10^5 cell/L, with 22 species of diatoms, 18 species of dinoflagellates, 2 species of chrysophytes, and 1 species of cyanobacteria. The most dominant species were from the diatom genus *Chaetoceros*, accounting for almost 36.67% of the total abundance. In the outfall region, the average cell abundance was 64.29% lower than that in the control region. Although the number of species detected were composed of diatoms (19 species), dinoflagellates (11 species) and chrysophytes (2 species), the most dominant group was replaced by the dinoflagellate genus *Prorocentrum*, with a contribution of 38.66% of the total abundance (Table A1).

Table 1. The characterization of investigated regions

Sample ID	Sampling region	Sampling time	Environmental parameters				Phytoplankton communities in the water						
			H/m	S	pH	T/°C	Abundance/ 10 ⁵ cell·L ⁻¹	Species number	Proportion/%			Dominant genus	Diversity index
								Diatom	Dinoflagellate	Other			
M-R1	control region	morning	12.5	32	8.07	24	6.4	27	75.00	21.88	3.12	<i>Chaetoceros</i>	3.09
MD-R1		midday	12.5	32	8.07	25	2.9	14	17.24	75.86	6.90	<i>Prorocentrum</i>	2.27
N-R1		night	12.5	32	8.07	24	11.7	18	80.34	17.95	1.71	<i>Chaetoceros</i>	1.85
M-R2	outfall region	morning	14	32	8.02	30	4.5	23	62.22	33.33	4.44	<i>Chaetoceros</i> , <i>Prorocentrum</i>	3.03
MD-R2		midday	14	32	8.02	32	1	7	40.00	60.00	0.00	<i>Prorocentrum</i>	1.75
N-R2		night	14	32	8.02	26	2	9	10.00	85.00	5.00	<i>Prorocentrum</i>	1.82

Note: H indicates depth, S salinity, and T temperature.

3.2 Diet composition of *C. tenuiremis*

A total of 34 taxa of prey in *C. tenuiremis* were identified in this study. The species accumulation curve for each sample showed a decelerating trend of taxon increase and a total of 14 and 24 taxa of prey in *C. tenuiremis* in the control and outfall regions, respectively (Fig. 2). This finding was confirmed by Chao1 estimates that the taxa numbers obtained were likely to reach the actual numbers (Table 2).

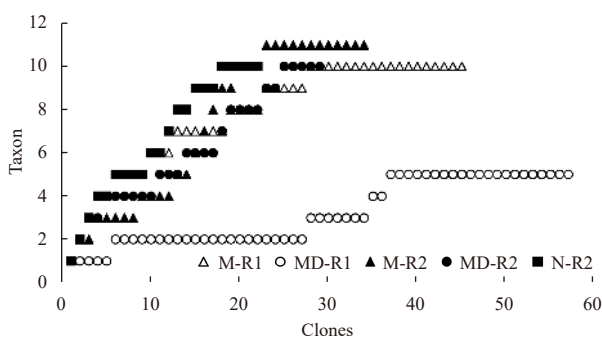


Fig. 2. Rarefaction curves of *C. tenuiremis* diet 18S rDNA clonelibraries.

Table 2. Prey diversity indices of *C. tenuiremis*

Sample ID	Taxa	Individuals/ clones	Simpson_1-D	Shannon_H	Chao1
M-R1	10	45	0.709 1	1.649	15
MD-R1	5	57	0.165 6	0.414 1	6
M-R2	11	34	0.764 7	1.893	14
MD-R2	10	29	0.863 3	2.13	10
N-R2	10	22	0.834 7	2.046	13

Diverse preys, including phytoplankton, metazoans, protozoans, land plants, and fungi were detected (Fig. 3a). In general, metazoans and land plants were the most common prey among all copepod samples, and the tunicate *Oikopleura dioica* (96%–99% identity to AB013014.1) and plant *Broussonetia papyrifera* (97%–99% identity to JF317359.1) were the most representative food respectively. Phytoplankton and protozoans with diverse species were mostly found in the outfall region. Phytoplankton consisted mainly of diatoms (e.g., *Hemiaulus sinensis* (92%–94% identity to HQ912624.1), *Rhizosolenia fallax* (99% identity to AY485480.1) and *Pseudo-nitzschia* sp. (97%–99% identity to AY485490.1)) and dinoflagellates (e.g., *Karenia-like* (93% identity to HM067005.1), *Peridinium-like* (93% identity to GU001637.1) and *Apicoporus-like* (93% identity to EU293238.1)). Rhizaria with species *Cercozoa-like* (94% identity to FJ824127.1) and *Protaspis-*

like (94%–98% identity to FJ824124.1) were the main protozoan species identified. Fungi made a relatively small contribution to the diet composition; however, the species were diverse (9 species), including *Davidiellaceae* sp. (99% identity to GU250935.1), *Cladosporium cladosporioides* (97%–99% identity to KP968529.1) and so on.

3.3 Diet variation of *C. tenuiremis*

The diet composition of *C. tenuiremis* exhibited distinct spatial and temporal variations. In the morning, fungi, metazoans and land plants were detected in the control region (Fig. 3b). Fungi and land plant sequences were most represented in the clone library. A land plant species *B. papyrifera* accounted for 48.89% of total clones. In the outfall region, a wider spectrum of prey including phytoplankton, fungi, metazoans, protozoans and land plants was detected. Phytoplankton, mostly dinoflagellates (e.g., *Karenia* and *Peridinium*), was the most abundant component (67.64%), although the cell abundance of phytoplankton in the ambient water was much lower than that in the control region. At noon, only 5 prey species from fungi, metazoans and land plants were detected in the control region, and *O. dioica* was the dominant food (91.23%). While copepod fed on a broader range of prey in outfall region, with 10 species from protozoa to phytoplankton, land plants, and metazoans. Phytoplankton accounted for 58.62% of the total diet, primarily of diatoms (e.g., *Hemiaulus*, *Rhizosolenia* and *Pseudo-nitzschia*) (Fig. 3b). At night, a highly diverse diet was detected in copepods from the outfall region. Metazoans were the dominant prey items, followed by protozoans. Among these, *Oikopleura* sp. held the highest percentage (45.46%) of the diet (Fig. 3b).

Moreover, *C. tenuiremis* consumed more plant-derived prey (phytoplankton or land plants) in the morning and more animal-derived prey (metazoan or protozoan) at midday and night, indicating a switch from herbivory to carnivory during the daytime. This trend was confirmed by the OI of *C. tenuiremis* from different samples. In the control region, the OI was 0.51 in the morning but 0.95 at midday. While in the outfall region, the OI increased from 0.27 in the morning to 0.35 at midday, and then to 0.72 at night. Overall, *C. tenuiremis* seemed to prefer phytoplankton prey in the outfall region, and correspondingly the OI of *C. tenuiremis* in the outfall region was lower than that of the control region. Thus, *C. tenuiremis* displayed flexible food choices spatially and temporally.

4 Discussion

As one of the potential disturbances for coastal ecosystems, thermal discharge could not only affect the survival and maintain of zooplankton but also the upward transformation of materials through their feeding process. Previous studies tried to exam-

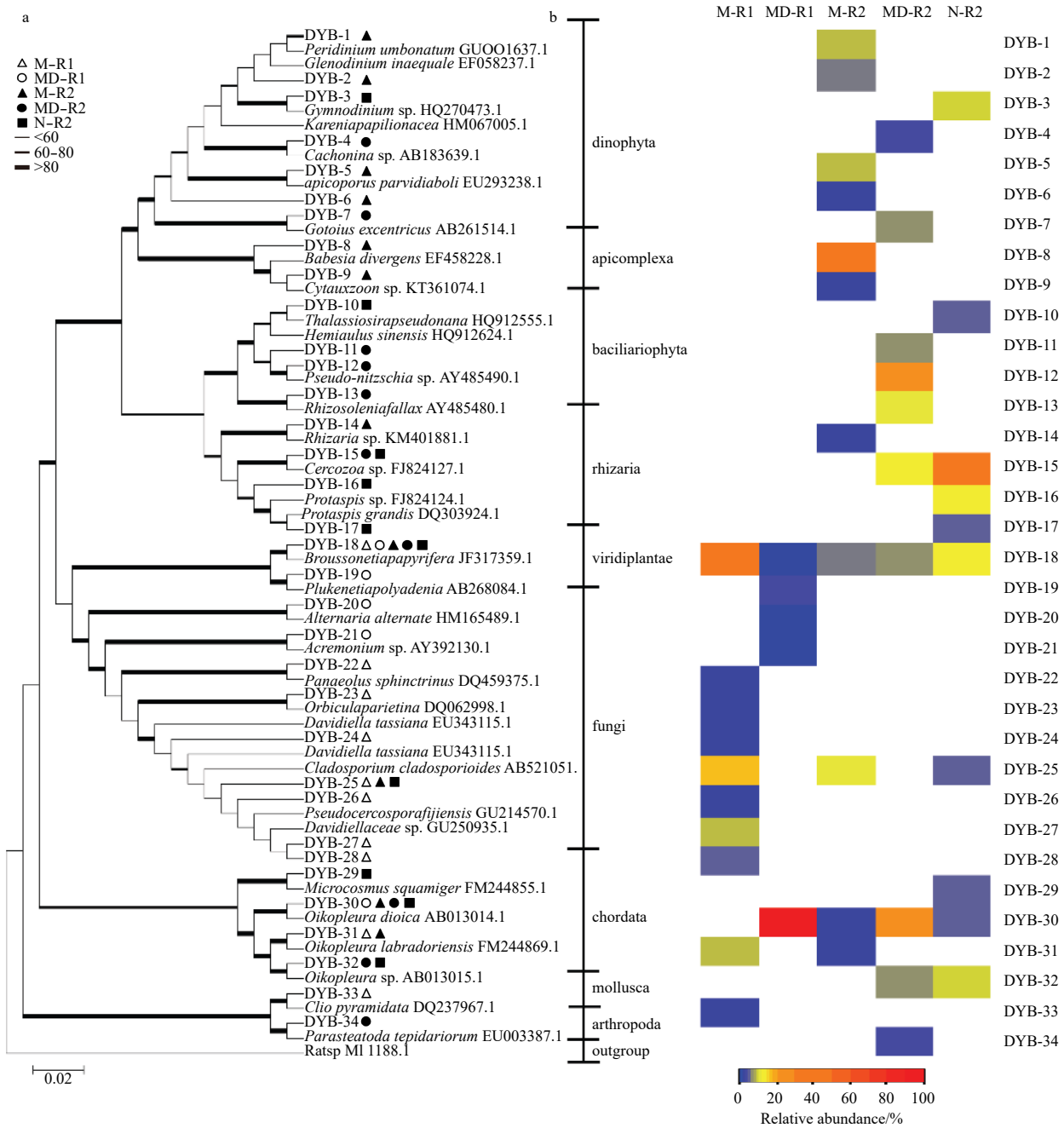


Fig. 3. Dietary composition and variation of *C. tenuiremis* from different samples. a. A maximum-likelihood tree of the 18S rDNA sequence for different samples of *C. tenuiremis* diet organisms. Representative sequences detected in the present study (DYB-XX) and the closely related organisms in blast analysis were included in the tree. The different symbols denoted the copepods from different samples. The thickness of branches denotes the strength of corresponding bootstrap support. b. Prey distribution for different samples of *C. tenuiremis*. The depth of color in each grid represents the relative abundances value of corresponding diet organisms.

the effects of thermal effluents especially the elevated temperature on the feeding response of copepod, were all obtained by laboratory experiments (Gao and Li, 1990; Yu et al., 2012). Feeding response of copepod under thermal stress in natural seas remains unclear due to insufficient on-site diet information. DNA-based molecular methods provide a useful tool to reveal the *in situ* feeding information of copepods (Hu et al., 2014, 2015). However, the copepods and prevalent ciliates DNA made compromises of the detection efficacy of diet species as they usually dominant of whole copepod samples (Guo et al., 2012; Hu et al.,

2014). The CEEC primer used in this study which was designed to specifically amplify 18S rDNA from eukaryotes and block the amplification of copepods and parasitic/symbiotic ciliates can effectively overcome the above shortcomings (Hu et al., 2014, 2015). Although it would still miss some kind of prey species, such as *Acartia pacifica* and nauplii due to cannibalism in some copepods (Lee, 1964; Daan et al., 1988), and other prokaryotes, it is still a better tool to study the diet of copepods. In this study, diurnal changes in the natural diet composition of *C. tenuiremis* collected at the Daya Bay were analyzed by molecular method in

the regions affected by thermal discharge. Thirty-four species of prey organisms were detected from 9 groups, including the reported prey items (such as phytoplankton) and unreported prey items (such as land plants) in *Centropages* copepods, indicating high resolution of molecular method in uncovering *in situ* food choices of copepod. *Centropages tenuiremis* was found to have more diverse range of prey and more phytoplankton diet in the outfall region than that in the control region, indicating a flexible food choice in disturbed coastal ecosystems.

4.1 Prey diversity of *C. tenuiremis*

A total of 34 taxa of prey belonging to phytoplankton, metazoans, protozoans, land plants, and fungi were detected in the diet of *C. tenuiremis*, in which diet diversity confirmed the omnivorous feeding of *C. tenuiremis*, in accordance with other species (e.g., *C. typicus*) of the *Centropages* genus (Calbet et al., 2007; Carlotti and Harris, 2007; Benedetti et al., 2016). In diet studies, for the most part, the detected prey of *C. tenuiremis* was with low resolution (Gao and Li, 1990; Liu and Li, 1998; Jagadeesan et al., 2017), making it unclear as to the actual diet of *C. tenuiremis*. Our study complemented the dietary information of natural copepod *C. tenuiremis* and expanded the knowledge of its *in situ* prey source in detail.

Some of prey organisms detected in our findings, such as phytoplankton, protozoans and metazoans, have already been observed in natural *C. tenuiremis* and other *Centropages* species before (Gao and Li, 1990; Liu and Li, 1998; Jagadeesan et al., 2017), indicating the importance and universality of these prey for natural *Centropages* in different environments. Early diet studies also demonstrated that many species of phytoplankton and protozoans, including *Coscinodiscus*, *Nitzschia*, *Thalassionema*, *Peridinium*, tintinnids and so on, were fed by natural *C. tenuiremis* (Lee, 1964; Yang, 2001). In this study, we also found that diatoms (e.g., *Hemiaulus*, *Rhizosolenia* and *Pseudo-nitzschia*) and dinoflagellates (e.g., *Karenia*, *Peridinium*) were commonly present in copepod diets with specific species or genera. It was consistent with the cognition of phytoplankton intake of *C. tenuiremis* before (Gao and Li, 1990; Liu and Li, 1998; Jagadeesan et al., 2017), and information on the detail phytoplankton species that fed by natural *C. tenuiremis* were also supplemented and improved. In the present study, dinoflagellates and diatoms were dominant in ambient waters, both in species number (88.89%–100%) and cell abundance (93.10%–100%), and their superiority in nutritional quality and prevalence in the food environment might explain their high ingestion by the copepod *C. tenuiremis*. Protozoans from the supergroup Rhizaria and unclassified Apicomplexa were also present in our study; these might be ingested by *C. tenuiremis*, considering their size (<50 μm) and distribution in the study area (Hoppenrath and Leander, 2006; Yabuki and Ishida, 2011). Metazoans were mainly of the appendicularian genera, *Oikopleura*. Previous studies reported that *C. typicus* prey on appendicularian juveniles and eggs (Calbet et al., 2007). The appendicularian *Oikopleura* sp. was an important component of the zooplankton community in the study area, reaching a density as high as 157.50–164.50 ind./L (Yang et al., 2002), which increases the likelihood of being captured by copepods. In addition, animal prey, such as *Oikopleura*, may have been carrying/assimilating nutrients from its diet of phytoplankton and microzooplankton (Troedsson et al., 2005). Therefore, direct feeding of copepod *C. tenuiremis* on animal prey *Oikopleura* might obtain additional materials and energy brought by the packing effects, as well as obtain targeted nutrients needed by animals more directly.

Moreover, other substantial prey represented in our results, such as land plants, have not been found to be prey for natural *C. tenuiremis*. Land plants, mainly *B. papyrifera*, were the most common prey group for all samples of *C. tenuiremis*. Land plants were reported as important supplementary food resources for coastal copepods (Hu et al., 2015). Previous study found that terrestrial materials can contribute to approximately 50.1% of the total suspended substance in the Daya Bay (Lin, 2016), raising the possibility of detritus consumption by copepods. For another, land plants in the form of pollen contain a high content of polyunsaturated fatty acids and phosphorus (Masclaux et al., 2011; Perez-Moreno and Read, 2001) and hence could be good quality prey items for zooplankton (such as *Daphnia longispina* and *Simocephalus vetulus*) especially with abundant microorganisms (i.e., heterotrophic bacteria, flagellates and fungi) (Masclaux et al., 2011, 2013). In our study, we found a high prevalence of fungi (40.00%) in copepod diets where the land plant *B. papyrifera* (48.89%) was the predominant food, raising the possibility that fungi act as an intermediate to upgrade the land plant quality. Therefore, diets with high diversity and typical supplementary material of coastal copepods may be one explanation for the wide distribution of *C. tenuiremis* in coastal ecosystems.

4.2 Prey choices of *C. tenuiremis*

Previous incubation studies revealed that food availability of zooplankton is one of the major factors shaping their feeding rates in the field (Saiz and Calbet, 2011). In our study, *C. tenuiremis* generally consumed more plant prey (land plants and phytoplankton) in the morning, while more animal prey (metazoans and protozoans) was consumed at midday and at night, corresponding to the variation of phytoplankton abundance from morning to night. The switched diets of *C. tenuiremis* with fluctuations in diurnal phytoplankton composition in a fluctuating food environment could help them to obtain comprehensive nutrition probably (Masclaux et al., 2011; Perez-Moreno and Read, 2001; Kiørboe et al., 2018). This switch is of great significance for coastal copepods with modest lipid storage, such as *C. tenuiremis*, in response to short time-scale changes in food availability (Dagg, 1977).

Except for the diurnal variation in diets of *C. tenuiremis*, the differences in diet composition between the control and the outfall region were even more apparent. A wider food spectrum with a much higher diversity of prey was detected in the outfall area than that in the control area. This result is consistent with a study suggesting that organisms could expand their food spectrum for survival when they were away from suitable environments (Quéméré et al., 2013; Lin et al., 2018). In this study, the temperatures in outfall region were obviously higher than the suitable temperature range of *C. tenuiremis* reported previously (Huang and Zheng, 1986; Li and Gao, 2012). More specifically, *C. tenuiremis* consumed diverse phytoplankton prey in the outfall region; however, minimal phytoplankton food was detected in the control site, even though the phytoplankton density was lower in the outfall region. The results from both laboratory and natural conditions conducted on other congeneric species (e.g., *C. typicus* and *C. hamatus*) found that the genus *Centropages* was more omnivorous-carnivorous and consistently displayed selection for large motile prey (Calbet et al., 2007; Saage et al., 2009). Moreover, *Centropages* species will decrease active feeding behavior to avoid predators, even under low food conditions (Calbet et al., 2007; Saage et al., 2009). Besides, feeding on pigmented phytoplankton would increase predation risk during daytime (Ma et al., 2007), and this observation may be the reason why *C.*

tenuiremis consumed land plants and metazoans as its main food in the control region in the morning and midday. Furthermore, land plant detritus and appendicularian larvae or eggs were relatively good prey, providing comprehensive nutrition for *C. tenuiremis*. Fluctuating phytoplankton communities and relatively stressful temperatures in the outfall region may prompt *C. tenuiremis* to expand its food sources for survival under such unfavorable conditions (Quéméré et al., 2013). The diversified food items in the outfall region may have enhanced the probability of obtaining a nutritionally complete ration of copepods when a phytoplankton diet was nutrient-deficient. Thus, *Centropages* copepods are capable of detecting changes in their surrounding environment and adjusting their feeding to maintain a trade-off between food requirements and predation risk (Kjørboe, 2011). This shift in consumer food choices in fluctuating regions in the short term has been considered to be important for ecosystems to buffer against environmental fluctuations (Kondoh, 2003).

Based on previous studies on the ecological effects of thermal discharge in the outfall region, the temperature rose dramatically in summer (Li et al., 2011). In our study, an almost 6°C increase in the temperature in the morning and at midday was found in the outfall region compared to that in the control region. In addition, compared to the control region, phytoplankton prey accounted for a significantly higher proportion (58.62%–67.64%) of the diet for *C. tenuiremis* in the outfall region. Boersma et al. (2016) demonstrated that *T. longicornis* exhibited an obvious prey shift from “meat” to “plant” as the temperature increased (Boersma et al., 2016). This herbivorous feeding tendency was also found in this study, confirmed by the OI of *C. tenuiremis* from different samples with different temperatures. In addition, when the temperature in the outfall region at night decreased close to the control region, *C. tenuiremis* rapidly changed its prey type to metazoan prey (50.01%), inferring a recovery feeding strategy of preference on metazoan prey (particularly for *Oikopleura*), similar to that in the control region at midday. High temperatures may limit the capacity of *C. tenuiremis* to feed on singular preferred food sources (Larsen et al., 2008), prompting it to exploit more diverse materials, especially phytoplankton. Moreover, feeding on higher digestible phytoplankton materials at high temperatures may be a feeding strategy to attain energetic gains at low feeding cost in order to meet increased demand for metabolic consumption under stressful temperatures (Floeter et al., 2005; Boersma et al., 2016).

The flexible food choices of *C. tenuiremis* under different conditions shown here implies that *C. tenuiremis* could survive optimally in fluctuating coastal ecosystems and this might be one of the reasons why *C. tenuiremis* could be widely distributed along the coastal waters. A flexible and responsive food choice under different food conditions can help them coexist more effectively with other competitors, such as *Acartia*. Such flexible feeding response of coastal copepods may be an important adaptive strategy to maintain their population stability in a fluctuating coastal environment, from both climate change and human disturbances. Further, this feeding response could effectively buffer potential future effects of short time-scale environmental changes on the food web structure of coastal ecosystems.

Prey 18S rDNA sequence data have been deposited to GenBank under accession numbers (KX913715–KX913748). The results of microscopic analysis of phytoplankton sample were shown in Appendix Table A1.

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Appendix:

Table A1. Phytoplankton cell abundance and species number from different samples

Species	M-R1	MD-R1	N-R1	M-R2	MD-R2	N-R2
Abundance/10 ⁵ cell·L ⁻¹	6.4	2.9	11.7	4.5	1	2
Number	27	14	18	23	7	9
Diatom						
<i>Cerataulina</i> sp.	3.13%					
<i>Chaetocero</i> sp.	3.13%		3.42%	6.67%		
<i>Chaetoceros affinis</i>	4.69%			4.44%		
<i>Chaetoceros compressus</i>	3.13%			4.44%		
<i>Chaetoceros densus</i>			45.30%			
<i>Chaetoceros lorenzianus</i>	10.94%		5.13%	4.44%		
<i>Coscinodiscus</i> sp.		3.45%	0.85%			
<i>Diploneis crabro</i>	1.56%			2.22%		
<i>Diploneis</i> sp.					10.00%	
<i>Guinardia</i> sp.		6.90%				
<i>Hemiaulus</i> sp.					10.00%	
<i>Leptocylindrus danicus</i>	9.38%			4.44%		
<i>Licmophora flabellata</i>				2.22%		
<i>Licmophora</i> sp.	1.56%			2.22%		
<i>Nitzschia</i> sp.	4.69%		1.71%	2.22%		5.00%
<i>Pleurosigma affine</i>	1.56%			2.22%		
<i>Pseudonitzschia pungens</i>	6.25%			6.67%		
<i>Pseudonitzschia</i> sp.			22.22%		10.00%	
<i>Rhizosolenia alata</i>	1.56%					
<i>Rhizosolenia setigela</i>			0.85%			
<i>Rhizosolenia</i> sp.					10.00%	
<i>Rhizosolenia styliformis</i>	6.25%		0.85%	4.44%		
<i>Streptotheca thamesis</i>	1.56%					
<i>Thalassionema nitzschioides</i>	4.69%	3.45%		4.44%		
<i>Thalassionema</i> sp.	7.81%	3.45%		6.67%		5.00%
<i>Thalassiosira rotula</i>	3.13%			4.44%		
Sum	75.00%	17.24%	80.34%	62.22%	40.00%	10.00%
Count	17	4	8	15	4	2
Dinoflagellate						
<i>Alexandrium</i> sp.	1.56%	6.90%				
<i>Ceratium furca</i>	1.56%					
<i>Ceratium fusus</i>			0.85%			
<i>Ceratium</i> sp.			1.71%			
<i>Ceratium trichoceros</i>			0.85%			
<i>Cochlodinium</i> sp.		3.45%				
<i>Gymnodinium</i> sp.						5.00%
<i>Gyrodinium dominans</i>				2.22%		
<i>Gyrodinium spirale</i>			0.85%			
<i>Heteroconium</i> sp.	3.13%					
<i>Karenia</i> sp.	1.56%			4.44%		
<i>Peridinium</i> sp.				2.22%		
<i>Prorocentrum compressum</i>		34.48%	0.85%			
<i>Prorocentrum dentatum</i>		3.45%				
<i>Prorocentrum micans</i>	6.25%	10.34%	7.69%	11.11%	40.00%	50.00%
<i>Prorocentrum minimum</i>			1.71%	6.67%		15.00%
<i>Prorocentrum sigmoides</i>		6.90%				5.00%
<i>Prorocentrum</i> sp.		3.45%	0.85%	2.22%		
<i>Prorocentrum triestinum</i>	3.13%			4.44%		
<i>Protoperidinium depressum</i>	3.13%	3.45%				

to be continued

Continued from Table A1

Species	M-R1	MD-R1	N-R1	M-R2	MD-R2	N-R2
<i>Protoperdinium</i> sp.					10.00%	5.00%
<i>Scrippsiella trochoidea</i>	1.56%	3.45%	2.56%		10.00%	5.00%
Sum	21.88%	75.86%	17.95%	33.33%	60.00%	85.00%
Count	8	9	9	7	3	6
Chrysophyta						
<i>Dictyocha</i> sp.			1.71%			5.00%
<i>Distephanus speculum</i> v. <i>octonarium</i>	1.56%	6.90%		4.44%		
Sum	1.56%	6.90%	1.71%	4.44%	0.00%	5.00%
Count	1	1	1	1	0	1
Cyanophyta						
<i>Trichodesmium erythraeum</i>	1.56%					
Sum	1.56%	0.00%	0.00%	0.00%	0.00%	0.00%
Count	1	0	0	0	0	0