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Distribution and role of the genus *Oithona* (Copepoda: Cyclopoida) in the South China Sea

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KEYWORDS

Oithona; Sea currents; Temperature; Larval fishes; Fish spawns Summary The relationships between the small cyclopoid copepod *Oithona* and hydrological factors, phytoplankton and ichthyoplankton were evaluated using the data obtained in the central South China Sea (SCS) in summer 2014. The genus abundance ranged from 6.00 ind. m⁻³ to 93.75 ind. m⁻³ with high abundance band occurring in the branch of SCS Monsoon Jet. The lower temperature and higher salinity in the surface water of the band than other zones indicated that deep water intrusion was a positive factor for aggregation of the genus. The community structure of the genus was dominated by *Oithona plumifera* and *Oithona similis* made up 97% of the genus abundance associated with *Oithona tenuis*. The result of db-RDA analysis showed that the community structure of the genus was affected by temperature, Chl *a*, larval fishes and fish spawns, and temperature was the most important limiting factor. The result of GAMs analysis showed that abundance of *O. tenuis*, and copepodites were affected by Chl *a*, larval fishes and fish spawns; abundance of *O. similis* was affected by Chl *a* and fish spawns; and abundance of *O. plumifera* was affected by Chl *a* and larval fishes. Therefore, we suggest that the branch of SCS

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Monsoon Jet and deep water intrusion favor aggregation of plankton in the central SCS in summer. We confirm that the temperature is the limiting factor to the reproduction of the genus *Oithona* in tropic seas and the genus *Oithona* is a food-web linker between primary production and larval fishes in the central SCS.

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1. Introduction

The genus Oithona Baird, 1843 is the most numerous pelagic copepod in the world ocean and a dominant group of the small planktonic marine copepods, represented in very high numbers and being a significant contributor to secondary production (Nielsen and Andersen, 2002; Paffenhöfer, 1993; Saiz et al., 2003). Small copepods are often the dominant zooplankton and have an important role in regenusting and exporting nutrients (Hopcroft and Roff, 1996; Hopcroft et al., 1998; McKinnon and Ayukai, 1996; Zamora-Terol et al., 2014a). The group play a linking role in marine food webs with feeding on the phytoplankton and microbial components and is being preyed on by larger zooplankton and several pelagic ichthyoplankton (Castro et al., 2010; Spinelli et al., 2012; Van Noord et al., 2013). Small planktonic copepods are the main component of the first feeding diet of many pelagic fishes and richer than other feeding food in nutrition (Ajiboye et al., 2011; Shansudin et al., 1997; Spinelli et al., 2012).

Physical environment determines the spatial distribution of the genus copepods. Aggregateion of the genus is affected by hydrodynamics at Kenton coast in South Africa (Porri et al., 2007). Oithona nana Giesbrecht, 1892 is the most abundant copepod species from late summer until early winter in Southampton Water (Williams and Muxagata, 2006). Oithona atlantica Farran, 1908 occurs in Arctic waters only during warm years and the abundance of O. atlantica was positively correlated with the temperature in Atlantic waters (Dvoretsky and Dvoretsky, 2015). Abundance, reproductive and mortality rates of Oithona similis Claus, 1866 correlated strongly with the water temperature in cold seas (Dvoretsky and Dvoretsky, 2009; Dvoretsky, 2012). The abundance characteristics of O. similis are negatively correlated with salinity and the winter index of the North Atlantic Oscillation index (Dvoretsky and Dvoretsky, 2015).

The genus *Oithona* are omnivorous copepods that primarily consumes protozooplankton, dinoflagellates, diatoms and organic detritus (Castellani et al., 2008; Kattner et al., 2003; Lonsdale et al., 2000; Nakamura and Turner, 1997; Pond and Ward, 2011). *Oithona* spp. ingested dinoflagellates and ciliates preferentially to other prey items of the nano- and micro-plankton assemblage in tropical waters of North Queensland, Australia. Ciliates and heterotrophic dinoflagellates are the main food source of the genus *Oithona* in Buzzards Bay during the warm season (Nakamura and Turner, 1997). Ciliates, particularly non-loricate ciliates, contributed substantially to the carbon ration of the genus *Oithona* in the Ross Sea, Antarctica, during an austral summer (Lonsdale et al., 2000).

The genus *Oithona* feed on the larvae of some small-size fish species, such as Clupeidae, Gadidae and Osmeridae

(Nunn et al., 2012). O. nana Giesbrescht, 1982 is in the diet of anchovy Engraulis encrasicolus Linnaeus, 1758 larvae in the north-west Mediterranean (Tudela et al., 2002) and Oithona davisae Ferrari and Orsi, 1984 is in the food diet of larval Japanese anchovy Engraulis japonicas Temminck and Schlegel, 1846 in Ariake Bay, Japan (Islam and Tanaka, 2009). Small copepods is the important first feeding food of capelin Mallotus villosus Müller, 1776 in summer in the Barents Sea (Pedersen and Fossheim, 2008). Three important commercially exploited whitefish cod (Gadus morhua Linnaeus, 1758), haddock (Melanogrammus aeglefinus Linnaeus, 1758) and whiting (Merlangius merlangus Linnaeus, 1758) prefer to prey on O. similis in the intermediate stage between larval stage and juveniles stage in the Irish Sea, especially haddock (Rowlands et al., 2008).

The genus Oithona are one of the most abundant copepod genus in trophical and polar seas (Chew and Chong, 2011; Chew et al., 2015; Dvoretsky and Dvoretsky, 2015; Hunt and Hosie, 2006a,b; Hwang et al., 2010; McKinnon et al., 2005; Pinkerton et al., 2010; Rezai et al., 2004; Wang et al., 2015). The number of studies of the genus Oithona in tropical waters is very scarce, mainly limited to the north SCS and the adjacent coastal zone (Zamora-Terol et al., 2014a,b). To our knowledge, the genus Oithona is one of the dominant genus in the coast of Malaysia and Vietnam (Chew and Chong, 2011; Rezai et al., 2004; Truong et al., 2013). Hwang et al. (2010) have investigated the distribution of the genus Oithona in the northeast South China Sea (SCS). Dahms et al. (2015) have analyzed the biogeographic distribution of the genus Oithona in the waters around Taiwan Island. The feeding and egg production of Oithona plumifera Baird, 1843, Oithona attenuata Farran, 1913, O. nana, Oithona dissimilis Lindberg, 1940, Oithona simplex Farran, 1913 and Dioithona oculata Farran, 1913 have been addressed in tropical and subtropical waters (Ambler et al., 1999; Hopcroft and Roff, 1996, 1998; Mckinnon and Klumpp, 1998; Zamora-Terol et al., 2014a). And the relationship between larval fishes and the genus Oithona is not clear in tropical seas.

SCS with a maximum depth deeper than 5000 m is the largest tropical marginal sea in the West Pacific Ocean. The seasonal circulation is mostly driven by monsoon winds. Prevailing southwest monsoon, SCS Monsoon Jet, flow to the north along the west coast, and the jet divides into two branches at 14.7°N, one flows to the northeast (Fig. 1) and one flows to the east in summer (Bao et al., 2005; Liao et al., 2006). Copepod horizontal distribution follows the surface current in SCS (Hwang et al., 2014; Wang et al., 2015). Larval flying fishes, lightfishes and dolphinfishes are three dominant groups of larval fishes in the tropical Pacific Ocean (Loeb, 1979; Vilchis et al., 2009). Flying fishes and lightfishes prefer to prey on zooplankton and feed up the

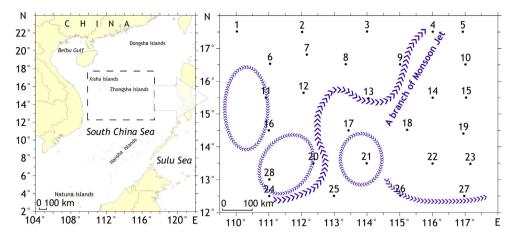


Figure 1 Map showing the area investigated and the approximate positions of stations (the surface current was drew following Liao et al. (2006), Bao et al. (2005), Xiang et al. (2015) and the water current pictures were downloaded from National Marine Environmental Forecasting Center of China).

commercially exploited fish, tuna and jumbo squid (Gong et al., 2015; Rosas-Luis et al., 2011; Van Noord et al., 2013). The relationship between small zooplankton and larval fishes that is important to accurately estimate fishery potential production and mass and energy transfer in marine food web is not clear in SCS. In this study, we evaluated the relationship between the genus *Oithona* and larval fishes basing on adults and copepidotes of the genus *Oithona* distribution investigated and hydrological factors and phytoplankton impacting on the genus analyzed in the central SCS in summer, for the similar seasonal abundance of the genus *Oithona* and ichthyoplankton in tropical seas (Du et al., 2016; León-Chávez et al., 2010).

2. Material and methods

2.1. Sampling

Samplings were performed in SCS with 28 stations from July 26 to August 17 in 2014. The area explored extended from 12° to 18°N and 110° to 118°E (Fig. 1). Zooplankton samples were collected by vertical hauls from surface to 200 m layer. The genus Oithona was analyzed from the samples collected with the middle deep-water plankton net (160 μm mesh size, 0.5 m mouth diameter, and 2.8 m total length) and fish spawns and larval fishes were analyzed from the samples collected with the large deep-water plankton net (505 μm mesh size, 0.8 m mouth diameter, and 2.8 m total length). Hydrographic data were collected quasi-simultaneously to zooplankton sampling using CTD48M made by the SeaSun-Tech company, including temperature (Temp), salinity (Sal) and chlorophyll a (Chl a).

2.2. Data analysis

The abundance distributions were performed using Surfer 10.0. Prior to the other analysis, the abundance of species was log-transformed, and the hydrographic data were divided to 4 water columns classified by depth of 25 m from surface to 100 m layer, including 0–25 m, 25–50 m,

50-75 m. and 75-100 m. The Pearson correlation between the genus Oithona and the impact factors including fish spawns, larval fishes, temperature, salinity and Chl a were analyzed in R 3.25. Hierarchical cluster analysis to present the distribution of the genus Oithona community, Principal component analysis (PCA) to analyze the dominated degree of each species in the genus Oithona community and distance-based redundancy analysis (db-RDA) to analyze the relationships between the genus Oithona community and impact factors were performed with the Bray-Curtis similarity matrix using the package BiodiversityR in R 3.25. The genus Oithona affected by phytoplankton and larval fishes analyzed with A generalized additive model (GAM, using package mgcv in R 3.25) that is a nonparametric regression technique offering advantages over conventional regression techniques without being tied to a particular functional relationship and restricted in assumptions about the underlying statistical distribution of the data.

3. Results

3.1. Spatial distance of temperature, salinity and chlorophyll a

The average temperature ranged from 20.42°C in the $75-100\,\text{m}$ water column to 28.98°C in the $0-25\,\text{m}$ water column with the remarkable spatial distribution difference (Table 1). The average temperature in the southwest corner (st. 24 and st. 28) was lowest in every water column.

The average salinity ranged from 32.10% in the 0-25 m water column to 33.35% in the 75-100 m water column (Table 1). The average salinity in the southwest corner (st. 24 and st. 28) was higher than in the surrounding waters in every water column.

The average Chl a concentration ranged from 0.22 mg m $^{-3}$ in the 0–25 m water column to 0.98 mg m $^{-3}$ in the 50–75 m water column (Table 1). The average Chl a concentration had only remarkable horizontal distribution difference in the 25–50 m water column, with the significantly higher values in the southwest corner.

Table 1 The distributions of temperature, satinfty and Chi a by water column.								
	Water column	Water column						
	0–25 m	25-50 m	50-75 m	75-100 m				
Temperature [°C]	$\textbf{28.98} \pm \textbf{0.9}$	$\textbf{26.51} \pm \textbf{2.2}$	22.82 ± 1.8	20.42 ± 1.4				
Salinity [‰]	$\textbf{32.10} \pm \textbf{0.4}$	$\textbf{32.48} \pm \textbf{0.4}$	$\textbf{33.15} \pm \textbf{0.4}$	$\textbf{33.35} \pm \textbf{0.5}$				
Chl $a \text{ [mg m}^{-3}\text{]}$	$\textbf{0.22} \pm \textbf{0.1}$	$\textbf{0.63} \pm \textbf{0.7}$	$\textbf{0.98} \pm \textbf{0.3}$	$\textbf{0.58} \pm \textbf{0.1}$				

Table 1 The distributions of temperature, salinity and Chl *a* by water column.

3.2. Abundance of the genus *Oithona*, copepodites and ichthyoplankton

The genus *Oithona* abundance ranged from 6.00 ind. m^{-3} at st. 1 to 93.75 ind. m^{-3} at st. 9, with high abundance band along northeast from 12.5°N, 111°E to 17.5°N, 116°E (Fig. 2). Copepodites of the genus *Oithona* (copepodites) had the similar horizontal abundance distribution to the genus, with the highest abundance at st. 9 (83.33 ind. m^{-3}) and the lowest at st.18 (4.17 ind. m^{-3}). Abundance of fish spawns ranged from 1.00×10^{-2} ind. m^{-3} at st. 2 to 216.67×10^{-2} ind. m^{-3} at st. 9. Abundance of larval fishes ranged from 1.25×10^{-2} ind. m^{-3} at st. 2 to 275.00×10^{-2} ind. m^{-3} at st. 24.

3.3. The genus Oithona composition

Altogether 9 taxa were encountered, including *O. similis*, *O. plumifera*, *Oithona longispina* Nishida, Tanaka and Omori,

1977, O. attenuata, Oithona fallax Farran, 1913, O. simplex, O. tenuis Rosendorn, 1917, Oithona vivida Farran, 1913 and Oithona rigida Giesbrecht, 1896 (Fig. 3). And average abundance of O. plumifera, O. similis and O. tenius contributed to 97% of the genus Oithona abundance respectively were 13.7, 15.8 and 5.87 ind. ${\rm m}^{-3}$.

Hierarchal cluster analysis showed three communities (Fig. 4). Stations in the high abundance band were included in a single group (Group 3), st. 1 was only included in Group 1, and the others were included in Group 2. Species composition among groups was little different, and abundance variance dominated to classify three communities. The genus *Oithona* (non-including *O. attenuata* and *O. vivida*), copepodites, fish spawns and larval fishes were most abundant in Group 3 (Fig. 5). The average temperature of Group 3 was lowest in 0–25 m and 25–50 m water columns, and the average salinity and Chl *a* were highest in the columns (Fig. 5).

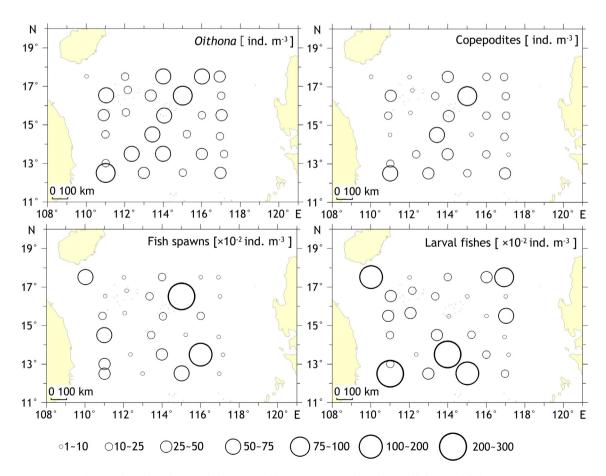


Figure 2 Abundance of the genus Oithona, copepodites, larval fishes and fish spawns.

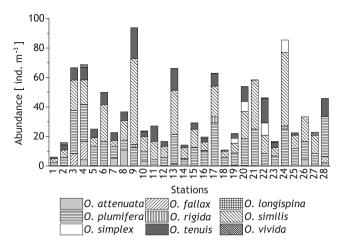


Figure 3 Abundance compositions of the genus Oithona.

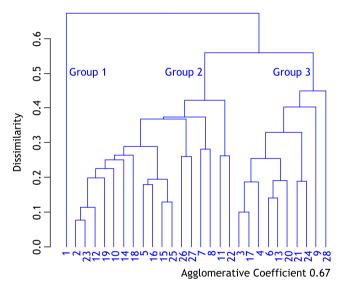


Figure 4 Hierarchical clustering of the genus *Oithona* community.

PCA showed that *O. similis* and *O. plumifera* dominated the community structure (Fig. 6). Stations in Group 2 had higher similarity than in Group 3.

3.4. Relationships between the genus *Oithona* community and impact factors

The Pearson analysis showed that the significant abundance correlation between *Oithona* spp. and *O. plumifera*, *O. similis* and *O. tenuis* accorded with the high contribution of the three dominant taxa (Table 2). The correlations between copepodite and *Oithona* spp., *O. plumifera* and *O. similis* were significant. The significant correlation between *O. similis* and *O. plumifera* indicated that their horizontal distributions were similar. The correlation between *O. tenuis* and larval fishes was negative significant. The correlations between temperature and *O. plumifera*, copepodite were negative significant. The correlations

between Chl a and Oithona spp., O. plumifera and copepodite were significant.

db-RDA analysis showed that the four factors (temperature, Chl *a*, larval fishes, and fish spawns) expressed 35.4% of the genus *Oithona* community structure (Fig. 7). Temperature expressed 13.9% of the community structure, the others expressed 21.5%.

Results of GAMs analysis showed that those GAMs were fit to explain the relationships between species in the genus and predators and prey (Table 3, Fig. 8). Abundance of O. plumifera, O. similis, O. tenuis and copepodites was affected strongly by Chl a concentration. Abundance of O. plumifera, O. tenuis and copepodite tends to increase with the Chl a concentration. Chl a had bottom-up control to O. similis. When the Chl a concentration was below 1.0 mg m $^{-3}$ control turned to top-down at Chl $a > 1.0 \text{ mg m}^{-3}$. O. plumifera, O. tenuis and copepodite were affected by larval fish. Larval fish had bottom-up control to O. tenuis when larval fishes abundance was below 1.26 ind. m^{-3} , then turned to top-down. The relationship between copepodite and fishes spawn had the opposite trend. The control power of larval fish to O. plumifera was not strong. O. similis and O. tenuis were also affected by fishes spawn, and the relationships were poorer than copepodite.

4. Discussion

4.1. Distribution of the genus Oithona

The genus Oithona is widely distributed in the world ocean (Paffenhöfer, 1993). In the central SCS, 9 taxa was encountered, in accords with 8 taxa identified around Taiwan waters (Dahms et al., 2015). Dominant taxa have contributed at least 95% to abundance of the genus Oithona and O. similis has the similar dominant level in the central SCS and the northeast SCS (Dahms et al., 2015). However, dominant taxa were different in the two regions. O. fallax, Oithona setigera Dana, 1849 and O. similis were dominant taxa around Taiwan waters (Dahms et al., 2015). O. similis is a cosmopolitan species, O. atlantica Farran, 1908 and O. frigida Giesbrecht, 1902 are O. similis, which was proven by molecular genetic methods (Wend-Heckmann, 2013). O. plumifera is usually the dominant taxa in a tropical waters, such as the tropical region of the Pacific Ocean (Zalkina, 1970), the central Great Barrier Reef (Williams et al., 1988), Mediterranean (Fernández de Puelles et al., 2014; Fragopoulu and Lykakis, 1990), the oligotrophic tropical waters of the Brazil Current (Lopes et al., 1999), the south coast of South Africa (Porri et al., 2007), the tropical Atlantic (Champalbert et al., 2008), the coastal area of Vietnam (Truong et al., 2013) and the north SCS (Zhou et al., 2013). O. tenuis is distributed throughout the subtropical and tropical seas in high abundance, which agrees with the dominant character of O. tenuis in the central SCS (Nishida, 1985). O. setigera is also a dominant species in the tropical Pacific Ocean, such as in an upwelling zone in Chile (Escribano et al., 2007; Nishida, 1985). We suggest that the genus Oithona assemblages would be the same in SCS and surmise that the difference is a result of confusing O. similis with O. fallax and O. setigeras with O. plumifera (Nishida, 1985).

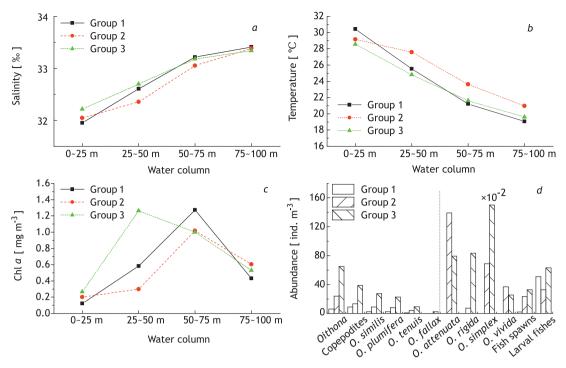


Figure 5 Comparison of salinity, temperature, Chl *a* and abundance of the genus *Oithona*, copepodites, larval fishes and fish spawns by group.

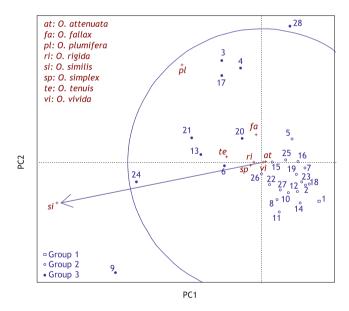


Figure 6 PCA performed on the genus Oithona community.

4.2. Impact between the genus *Oithona* and hydrological factors

Copepod horizontal distribution follows the surface current in SCS, especially the copepods collected by the middle net (Hwang et al., 2014; Wang et al., 2015). The high abundance band of the genus *Oithona* occurred in the branch of the South China Sea Monsoon Jet and it indicates the similar result in the central SCS (Liao et al., 2006). Ke et al. (2014) has suggested that spatial distribution of phytoplankton and hydrologic factors are significantly influenced by the surface

current patterns and river discharges in the Southern shelf of SCS. Mesozooplankton distribution is usually determined by currents in other regions as well. Majority of mesozooplankton significant species are most abundant to the north of the Azores Current in the Azores waters (Head et al., 2002). Mesozooplankton abundance is lower in the Kuroshio Current area than in the other regions of the north SCS (Hwang et al., 2007). The spatial distribution of the *O. similis* abundance and production is determined by the physical environment in the central Baltic Sea (Hansen et al., 2004). Thus the genus *Oithoina* distribution would be affected by the branch current of the jet in the central SCS in summer.

The relationship between the groups of the genus community and temperature, salinity indicates that relatively low temperature and high salinity in 0–25 m and 25–50 m of water columns assisted the reproduction of the genus *Oithona* in the central SCS. In upwelling zones, surface temperature is often lower than in surrounding zones, and surface salinity is higher (Xiang et al., 2015). The deep water intrusion may be an important factor affecting the genus *Oithona* abundance in the central SCS. The nitricline is depressed as downwelling occurs off northwest Luzon, resulting in very low chlorophyll concentrations (Chen et al., 2006). The prosperity of diatoms in the Malacca Strait may be promoted mainly by the sufficient nutrients brought by the deep-water intrusion or river inflow (Ke et al., 2016).

The relationship between the genus community and temperature, as well as the lower temperature in the high abundance band indicates that temperature is the main factor limiting the genus *Oithona* in the central SCS in summer. The meso-copepod abundance is negatively correlated with temperature in Patagonian frontal system (SW Atlantic Ocean) in spring and Dolgaya Bay (Barents Sea) in summer (Dvoretsky and Dvoretsky, 2010; Spinelli et al.,

	Oithona	O. plumifera	O. similis	O. tenuis	Copepodites
Oithona	1.000	,			
O. plumifera	0.839**	1.000			
O. similis	0.687**	0.415*	1.000		
O. tenuis	0.413**			1.000	
Copepodites	0.785**	0.618**	0.525**		1.000
Larval fishes				-0.469^{**}	
Temp.		-0.443 [*]			-0.453 [*]
Chl a	0.461*	0.466*			0.407*

Note: Temp/Chl a: Temperature/Chl a concentration in the 0-100 m water column.

Correlation is significant at the 0.01 level (2-tailed).

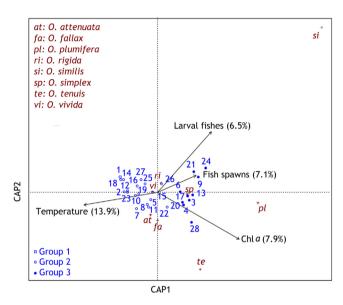


Figure 7 db-RDA performed on the genus Oithona community and impact factors.

2012). On the contrary, the genus Oithona abundance is positively correlated with temperature in polar seas (Dvoretsky and Dvoretsky, 2009; Ward et al., 2007; Zamora-Terol et al., 2014b). The negative correlation between O. plumifera and copepodite and temperature indicates that O. plumifera and copepodite are more sensitive to temperature than O. similis and O. tenuis in the central SCS. Similarly, O. atlantica is positively correlated with the temperature in the Barents Sea and O. similis is negatively correlated (Dvoretsky and Dvoretsky, 2015). The significant correlation between O. similis and temperature is also not found in polar seas (Dvoretsky and Dvoretsky, 2015; Metz, 1995).

4.3. Impact between the genus Oithona and phytoplankton

The genus Oithona is more abundant in the zone with higher phytoplankton abundance in the central SCS in summer. The significant positive correlations between Chl a and the genus Oithona, O. plumfera and copepodites have indicated that the phytoplankton was an important carbon resource for the genus Oithona in CSCS. Small Oithona spp. (<0.5 mm standard length) feeds mainly on nanoplankton (Pond and Ward, 2011; Turner, 1986). The primary production is channeled with the genus by microzooplankton (Lee et al., 2013). Fatty acid biomarker analysis has indicated that diatoms are an important food source for the genus Oithona in the Southern Atlantic Ocean (Pond and Ward, 2011).

In the study, the abundance of O. similis is forced topdown by phytoplankton when Chl a concentration was over 1.0 mg m^{-3} in the central SCS. The highest abundance of O. similis is at 1.1 mg m $^{-3}$ Chl a in Southern Atlantic Ocean (Pond and Ward, 2011). Low phytoplankton concentrations (Chl $a < 1.0 \text{ mg m}^{-3}$) limited reproductions of *Rhicalanus* gigas at South Georgia (Ward and Shreeve, 1999). The genus Oithona abundance is the lowest during the phytoplankton blooms and the temporal distribution is opposite to Calanus chilensis in the upwelling zone in Chile (Escribano et al., 2007). Large-sized mesozooplankton (>1 mm standard length) dominated the total biomass and contributed more than 50% of the herbivory in the north SCS (Chen et al., 2015). We suggest that the food competition between O. similis and larger calanoids (>2 mm standard length) decreases the abundance of O. similis in the high phytoplankton abundance zones of the central SCS.

4.4. Impact between the genus Oithona and ichthyoplankton

The genus Oithona and nauplii are an important group in larval fish diet, especially first-feeding larval fish (Sánchez-Velasco, 1998). The genus Oithona was a main group in dietary components of larval Pacific cod in March and April in Mutsu Bay, Japan (Takatsu et al., 1995). Copepodite of O. similis were an important feeding food of age-0 Walleye pollock in the southeastern Bering Sea in summer (Strasburger et al., 2014). The relationship between O. plumifera, O. tenuis, copepodites and larval fishes indicate that O. plumifera, O. tenuis and copepodites are preyed on by larval fish in the central SCS.

The similar effect of fish spawns on the genus Oithona community and copepodites with larval fishes indicates that the genus Oithona was in dietary components of larval fishes. Sailfish spawns oceanographic features provide a favorable feeding environment for their larvae (Richardson et al., 2009). The biochemical composition of Engraulis ringgens

Correlation is significant at the 0.05 level (2-tailed).

Table 3 Regression coefficients of parameters including Chl a, fish larvae and spawns on the dominant taxa and copepodites of the genus Oithona. The coefficients were calculated by GAMs. The relative goodness of fit of a model was indicated by the generalized cross validation (GCV) and Akaike information criterion (AIC). The deviance of the weight-specific ingestion rate explained by predictors involved is also shown as DE.

	DE	GCV	CIV	R
O. plumifera	29.6%	0.06	-0.04	0.511
O. similis	64.0%	0.96	8.04	0.748
O. tenuis	63.8%	0.10	11.1	0.752
Copepodites	54.7%	0.07	0.45	0.692

spawn in the upwelling system of the Chile coast was beneficial for young larvae in winter (Castro et al., 2010). High densities of anchovy spawn in coincidence with larger calanoids (>1 mm standard length) could be indicative of the presence of spawning group anchovies feeding on in the Patagonian frontal system (SW Atlantic Ocean) (Spinelli et al., 2012). Argentine hake Merluccius hubbsi spawn associate with small copepods (<1 mm total length) including a dominant species O. similis which is an important first-feeding food of Argentine hake M. hubbsi in the Argentine Sea (Temperoni et al., 2014). Spawns of flyfish and Bregmaceros spp. Thompson, 1840 are two common groups in the central SCS (Chen, 1979). Copepods were the major food of flyfish and larvae (Lipskaya, 1987; Van Noord et al., 2013). The relationship between copepodites and fish spawns indicates

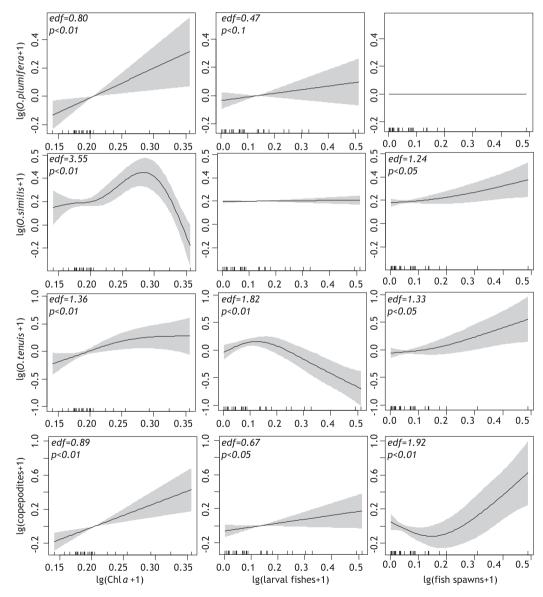


Figure 8 Partial effects of Chl a concentration and abundance of fish larvae and spawns on abundance of O. plumifera, O. similis, O. tenuis and copepodites of the genus Oithona. Relative strengths of individual predictors in different models were compared by estimated degrees of freedom (edf) and significance (p). The units of Chl a concentration and abundance of dominant taxa and copepodites of the genus Oithona and fish larvae and spawns were mg m⁻³ and ind. mg m⁻³.

that the main food of first feeding larval fish is of <0.5 mm standard length (Viñas and Ramíres, 1996). *O. similis* preyed on by larval fishes could indicate that *O. similis* is smaller than 1 mm standard length and has related with fish spawns.

5. Conclusion

The genus abundance ranged from 6.00 ind. m⁻³ to $93.75 \text{ ind. m}^{-3}$ with high abundance band occurred in the branch of SCS Monsoon Jet. The lower temperature and higher salinity in the surface water of the band than in other zones indicated that deep water intrusion was a positive factor for aggregation of the genus. The community structure of the genus was dominated by O. plumifera and O. similis, which made up 97% of the genus abundance associated with O. tenuis. The community structure of the genus was affected by temperature, Chl a, fish larvae and spawns. Temperature was the most important limiting factor that was negatively correlated with abundance of O. plumifera and copepodites of the genus. Results of GAMs analysis showed that abundance of O. plumifera, O. similis, O. tenuis and copepodites were affected by Chl a; abundance of O. plumifera, O. tenuis and copepodites were affected by larval fishes; and abundance of O. similis, O. tenuis and copepodites were affected by fish spawns. Abundance of O. similis was the highest when Chl a concentration was 1.0 mg m^{-3} . Therefore, we suggest that the branch of SCS Monsoon Jet and deep water intrusion favor an aggregation of plankton and O. similis do not compete with large copepods during the phytoplankton bloom in the central SCS in summer. We confirm that the temperature is the limiting factor for the reproduction of the genus Oithona in tropic seas and the genus Oithona is a food-web linker between primary production and larval fishes in the central SCS.

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References

- Ajiboye, O., Yakubu, A.F., Adams, T.E., Olaji, E.D., Nwogu, N.A., 2011. A review of the use of copepods in marine fish larviculture. Rev. Fish Biol. Fish. 21 (2), 225–246, http://dx.doi.org/10.1007/ s11160-010-9169-3.
- Ambler, J.W., Ferrari, F.D., Fornshell, J.A., Buskey, E.J., 1999. Diel cycles of molting, mating, egg sac production and hatching in the swarm forming cyclopoid copepod *Dioithona oculata*. Plankt. Biol. Ecol. 46 (2), 120–127.
- Bao, L., Lu, Y., Wang, Y., Xu, H., 2005. Seasonal variations of upper ocean circulation over the South China Sea from satellite altime-

- try data of many years. Chin. J. Geophys. 48, 543-550, (in Chinese).
- Castellani, C., Irigoien, X., Mayor, D.J., Harris, R.P., Wilson, D., 2008. Feeding of *Calanus finmarchicus* and *Oithona similis* on the microplankton assemblage in the Irminger Sea, North Atlantic. J. Plankton Res. 30 (10), 1095—1116, http://dx.doi.org/10.1093/plankt/fbn074.
- Castro, L.R., Claramunt, G., González, H.E., Krautz, M.C., Llanos-Rivera, A., Méndez, J., Schneide, W., Scoto, S., 2010. Fatty acids in eggs od anchoveta *Engraulis ringens* during two contrasting winter spawning seasons. Mar. Ecol.-Prog. Ser. 420, 193–205, http://dx.doi.org/10.3354/meps08819.
- Champalbert, G.A., Kouamé, B., Pagano, M., Marchal, E., 2008. Feeding behavior of adult *Vinciguerria nimbaria* (Phosichthyidae), in the tropical Atlantic (0°–4°N, 15°W). Mar. Biol. 156, 79–95, http://dx.doi.org/10.1007/s00227-008-1067-z.
- Chen, Z., 1979. Fish larvae and spawns in Xishao Islands and Zhongsha Islands waters. Fish. Sci. Technol. Inf. 4, 11–13, (in Chinese).
- Chen, C.C., Shiah, F.K., Chung, S.W., Liu, K.K., 2006. Winter phytoplankton blooms in the shallow mixed layer of the South China Sea enhanced by upwelling. J. Mar. Syst. 59 (1–2), 97–110, http://dx.doi.org/10.1016/j.jmarsys.2005.09.002.
- Chen, M., Liu, H., Song, S., Sun, J., 2015. Size-fractionated mesozooplankton biomass and grazing impact on phytoplankton in northern South China Sea during four seasons. Deep Res Pt. II 117, 108–118, http://dx.doi.org/10.1016/j.dsr2.2015.02.026.
- Chew, L.L., Chong, V.C., 2011. Copepod community structure and abundance in a tropical mangrove estuary, with comparisons to coastal waters. Hydrobiologia 666 (1), 127–143, http://dx.doi.org/10.1007/s10750-010-0092-3.
- Chew, L.L., Chong, V.C., Ooi, A.L., Sasekumar, A., 2015. Vertical migration and positioning behavior of copepods in a mangrove estuary: interactions between tidal, diel light and lunar cycles. Estuar. Coast. Shelf Sci. 152, 142–152, http://dx.doi.org/10.1016/j.ecss.2014.11.011.
- Dahms, H.U., Tseng, L.C., Hwang, J.S., 2015. Biogeographic distribution of the cyclopoid copepod genus *Oithona* from mesoscales to global scales. J. Exp. Mar. Biol. Ecol. 467, 26–32, http://dx.doi.org/10.1016/j.jembe.2015.02.009.
- Du, F., Wang, L., Wang, X., Ning, J., Gu, Y., Li, Y., 2016. Assemblage and abundance of Oithona and environmental factors in Nansha Islands waters, South China Sea. Oceanol. Limnol. Sin. 106–116, http://dx.doi.org/10.11693/hyhz20160700143 (in Chinese with English abstract).
- Dvoretsky, V.G., 2012. Seasonal mortality rates of *Oithona similis* (Cyclopoida) in a large Arctic fjord. Polar Sci. 6 (3—4), 263—269, http://dx.doi.org/10.1016/j.polar.2012.09.001.
- Dvoretsky, V.G., Dvoretsky, A.G., 2009. Life cycle of *Oithona similis* (Copepoda: Cyclopoida) in Kola Bay (Barents Sea). Mar. Biol. 156, 1433—1446, http://dx.doi.org/10.1007/s00227-009-1183-4.
- Dvoretsky, V.G., Dvoretsky, A.G., 2010. Mesozooplankton structure in Dolgaya Bay (Barents Sea). Polar Biol. 33 (5), 703–708, http://dx.doi.org/10.1007/s00300-009-0748-5.
- Dvoretsky, V.G., Dvoretsky, A.G., 2015. Interannual variations in abundance and biomass of planktonic copepods Oithona in the barents sea. Biol. Bull. 42 (5), 449–457, http://dx.doi.org/10.1134/S1062359015050052.
- Escribano, R., Hidalgo, P., González, H., Giesecke, R., Riquelme-Bugueño, R., Manríquez, K., 2007. Seasonal and inter-annual variation of mesozooplankton in the coastal upwelling zone off central-southern Chile. Prog. Oceanogr. 75 (3), 470—485, http://dx.doi.org/10.1016/j.pocean.2007.08.027.
- Fernández de Puelles, M.L., Macias, V., Vicente, L., Molinero, J.C., 2014. Seasonal spatial pattern and community structure of zooplankton in waters off the *Baleares archipelago* (Central Western Mediterranean). J. Mar. Syst. 138, 82–94, http://dx.doi.org/10.1016/j.jmarsys.2014.01.001.

- Fragopoulu, N., Lykakis, J.J., 1990. Vertical distribution and nocturnal migration of zooplankton in relation to the development of the seasonal thermocline in Patraikos Gulf. Mar. Biol. 104, 381–387, http://dx.doi.org/10.1007/BF01314340.
- Gong, Y., Chen, Z., Zhang, Z., Jiang, Y., 2015. Feeding habits of Diaphus chrysorhynchus from continental slope region in northern South China in autumn. South Chin. Fish. Sci. 90—107, (in Chinese).
- Hansen, F.C., Möllmann, C., Schütz, U., Hinrichsen, H.H., 2004. Spatio-temporal distribution of *Oithona similis* in the Bornholm Basin (Central Baltic Sea). J. Plankton Res. 26 (6), 659–668, http://dx.doi.org/10.1093/plankt/fbh061.
- Head, R.N., Medina, G., Huskin, I., Anadon, R., Harris, R.P., 2002. Phytoplankton and mesozooplankton distribution and composition during transects of the Azores Subtropical Front. Deep Res Pt. II 49, 4023–4034, http://dx.doi.org/10.1016/S0967-0645(02) 00140-6.
- Hopcroft, R.R., Roff, J.C., 1996. Zooplankton growth rates: diel egg production in the copepods Oithona, Euterpina and Corycaeus from tropical waters. J. Plankton Res. 18 (5), 789—803, http://dx.doi.org/10.1093/plankt/18.5.789.
- Hopcroft, R.R., Roff, J.C., 1998. Zooplankton growth rates: the influence of size in nauplii of tropical marine copepods. Mar. Biol. 132 (1), 87–96, http://dx.doi.org/10.1007/s002270050374.
- Hopcroft, R.R., Roff, J.C., Lombard, D., 1998. Production of tropical copepods in Kingston Harbour, Jamaica: the importance of small species. Mar. Biol. 130 (4), 593–604, http://dx.doi.org/10.1007/s002270050281.
- Hunt, B.P.V., Hosie, G.W., 2006a. The seasonal succession of zooplankton in the Southern Ocean south of Australia, Part I: The seasonal ice zone. Deep Res Pt. I 53, 1182—1202, http://dx.doi. org/10.1016/j.dsr.2006.05.001.
- Hunt, B.P.V., Hosie, G.W., 2006b. The seasonal succession of zooplankton in the Southern Ocean south of Australia, Part II: The Sub-Antarctic to Polar Frontal Zones. Deep Res Pt. I 53 (7), 1203—1223, http://dx.doi.org/10.1016/j.dsr.2006.05.002.
- Hwang, J.S., Dahms, H.U., Tseng, L.C., Chen, Q.C., 2007. Intrusions of the Kuroshio Current in the northern South China Sea affect copepod assemblages of the Luzon Strait. J. Exp. Mar. Biol. Ecol. 352 (1), 12–27, http://dx.doi.org/10.1016/j. jembe.2007.06.034.
- Hwang, J.S., Kumar, R., Dahms, H.U., Tseng, L.C., Chen, Q.C., 2010. Interannual, seasonal, and diurnal variations in vertical and horizontal distribution patterns of 6 *Oithona* spp. (Copepoda: Cyclopoida) in the South China Sea. Zool. Stud. 49, 220—229.
- Hwang, J.S., López-López, L., Molinero, J.C., Tseng, L.C., Chen, Q. C., Hung, J.J., 2014. Copepod assemblages in the northern South China Sea during inter-monsoon transition periods. J. Sea Res. 86, 43–48, http://dx.doi.org/10.1016/j.seares.2013.10.012.
- Islam, M.S., Tanaka, M., 2009. Diet and prey selection in larval and juvenile Japanese anchovy *Engraulis japonicus* in Ariake Bay, Japan. Aquat. Ecol. 43 (2), 549-558, http://dx.doi.org/ 10.1007/s10452-008-9207-6.
- Kattner, G., Albers, C., Graeve, M., Schnack-Schiel, S.B., 2003. Fatty acid and alcohol composition of the small polar copepods, *Oithona* and *Oncaea*: indication on feeding modes. Polar Biol. 26 (10), 666–671, http://dx.doi.org/10.1007/s00300-003-0540-x.
- Ke, Z., Tan, Y., Ma, Y., Huang, L., Wang, S., 2014. Effects of surface current patterns on spatial variations of phytoplankton community and environmental factors in Sunda shelf. Cont. Shelf Res. 82, 119—127, http://dx.doi.org/10.1016/j.csr.2014.04.017.
- Ke, Z., Tan, Y., Huang, L., 2016. Spatial variation of phytoplankton community from Malacca Strait to southern South China Sea in May of 2011. Acta Ecol. Sin. 36 (3), 154–159, http://dx.doi.org/ 10.1016/j.chnaes.2016.03.003.
- Lee, D.B., Choi, K.H., Ha, H.K., Yang, E.J., Lee, S.H., Lee, S., Shin, H.C., 2013. Mesozooplankton distribution patterns and grazing impacts of copepods and *Euphausia crystallorophias* in the

- Amundsen Sea, West Antarctica, during austral summer. Polar Biol. 36 (8), 1215—1230, http://dx.doi.org/10.1007/s00300-013-1314-8
- León-Chávez, C.A., Sánchez-Velasco, L., Beier, E., Lavín, M.F., Godínez, V.M., Färber-Lorda, J., 2010. Larval fish assemblages and circulation in the Eastern Tropical Pacific in Autumn and Winter. J. Plankton Res. 32 (4), 397–410, http://dx.doi.org/10.1093/plankt/fbp138.
- Liao, G., Yuan, Y., Wang, Z., 2006. The three dimensional structure of the circulation in the South China Sea during the summer of 1998. Acta Oceanol. Sin. 28, 15–25, (in Chinese).
- Lipskaya, N.Y., 1987. Feeding of flyingfish (Exocoetidae) lar-vae and fingerlings in the region of the Peruvian up-welling. J. Ichthyol. 27 (3), 108—116.
- Loeb, V.J., 1979. Larval fishes in the zooplankton community of the North Pacific Central Gyre. Mar. Biol. 53 (2), 173—191, http://dx.doi.org/10.1007/bf00389188.
- Lonsdale, D.J., Caron, D.A., Dennett, M.R., Schaffner, R., 2000. Predation by *Oithona* spp. on protozooplankton in the Ross Sea, Antarctica. Deep Res Pt. II 47 (15–16), 3273–3283, http://dx.doi.org/10.1016/S0967-0645(00)00068-0.
- Lopes, R.M., Brandini, F.P., Gaeta, S.A., 1999. Distribution patterns of epipelagic copepods off Rio de Janeiro (SE Brazil) in summer 1991/1992 and winter 1992. Hydrobiologia 411, 161–174, http://dx.doi.org/10.1023/a:1003859107041.
- McKinnon, A.D., Ayukai, T., 1996. Copepod egg production and food resources in Exmouth Gulf, Western Australia. Mar. Freshw. Res. 47 (4), 595–603, http://dx.doi.org/10.1071/MF9960595.
- Mckinnon, A.D., Klumpp, D.W., 1998. Mangrove zooplankton of North Queensland, Australia I. Plankton community structure and environment. Hydrobiologia 362, 127—143, http://dx.doi.org/10.1023/A:1003186601878.
- McKinnon, A.D., Duggan, S., De'ath, G., 2005. Mesozooplankton dynamics in nearshore waters of the Great Barrier Reef. Estuar. Coast. Shelf Sci. 63 (4), 497–511, http://dx.doi.org/10.1016/j. ecss.2004.12.011.
- Metz, C., 1995. Seasonal variation in the distribution and abundance of *Oithona* and *Oncaea* species (Copepoda, Crustacea) in the southeastern Weddell Sea, Antarctica. Polar Biol. 15 (3), 187–194, http://dx.doi.org/10.1007/BF00239058.
- Nakamura, Y., Turner, J.T., 1997. Predation and respiration by the small cyclopoid copepod *Oithona similis*: how important is feeding on ciliates and heterotrophic flagellates? J. Plankton Res. 19 (9), 1275–1288, http://dx.doi.org/10.1093/plankt/ 19.9.1275.
- Nielsen, T.G., Andersen, C.M., 2002. Plankton community structure and production along a freshwater-influenced Norwegian fjord system. Mar. Biol. 141 (4), 707—724, http://dx.doi.org/10.1007/s00227-002-0868-8.
- Nishida, S., 1985. Taxonomy and distribution of the famliy Oithonidae (Copepoda, Cyclopoida) in the Pacific and Indian Oceans. Bull. Ocean Res. Inst. Univ. Tokyo 20, 1–167.
- Nunn, A.D., Tewson, L.H., Cowx, I.G., 2012. The foraging ecology of larval and juvenile fishes. Rev. Fish Biol. Fish. 22 (2), 377–408, http://dx.doi.org/10.1007/s11160-011-9240-8.
- Paffenhöfer, G.A., 1993. On the ecology of marine cyclopoid copepods (Crustacea, Copepoda). J. Plankton Res. 15 (1), 37–55, http://dx.doi.org/10.1093/plankt/15.1.37.
- Pedersen, T., Fossheim, M., 2008. Diet of 0-group stages of capelin (*Mallotus villosus*), herring (*Clupea harengus*) and cod (*Gadus morhua*) during spring and summer in the Barents Sea. Mar. Biol. 153 (6), 1037–1046, http://dx.doi.org/10.1007/s00227-007-0875-x.
- Pinkerton, M.H., Smith, A.N.H., Raymond, B., Hosie, G.W., Sharp, B., Leathwick, J.R., Bradford-Grieve, J.M., 2010. Spatial and seasonal distribution of adult *Oithona similis* in the Southern Ocean: predictions using boosted regression trees. Deep Res Pt. I 57 (4), 469–485, http://dx.doi.org/10.1016/j.dsr.2009.12.010.

- Pond, D.W., Ward, P., 2011. Importance of diatoms for Oithona in Antarctic waters. J. Plankton Res. 33 (1), 105–118, http://dx.doi.org/10.1093/plankt/fbq089.
- Porri, F., McQuaid, C.D., Froneman, W.P., 2007. Spatio-temporal variability of small copepods (especially *Oithona plumifera*) in shallow nearshore waters off the south coast of South Africa. Estuar. Coast. Shelf Sci. 72 (4), 711–720, http://dx.doi.org/10.1016/j.ecss.2006.12.006.
- Rezai, H., Yusoff, F.M., Arshad, A., Kawamura, A., Nishida, S., Ross, O.B.H., 2004. Spatial and temporal distribution of copepods in the Straits of Malacca. Zool. Stud. 43 (2), 486–497.
- Richardson, D.E., Llopiz, J.K., Leaman, K.D., Vertes, P.S., Muller-Karger, F.E., Cowen, R.K., 2009. Sailfish (*Istiophorus platypterus*) spawning and larval environment in a Florida Current frontal eddy. Prog. Oceanogr. 82 (4), 252–264, http://dx.doi.org/10.1016/j.pocean.2009.07.003.
- Rosas-Luis, R., Tafur-Jimernez, R., Alegre-Norza, A.R., Castillo-Valderrama, P.R., Cornejo-Urbina, R.M., Salinas-Zavala, C.A., Sanchez, P., 2011. Trophic relationships between the jumbo squid (*Dosidicus gigas*) and the lightfish (*Vinciguerria lucetia*) in the Humboldt Current System off Peru. Sci. Mar. 75 (3), 549–557, http://dx.doi.org/10.3989/scimar.2011.75n3549.
- Rowlands, W.L., Dickey-Collas, M., Geffen, A.J., Nash, R.D.M., 2008. Diet overlap and prey selection through metamorphosis in Irish Sea cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), and whiting (*Merlangius merlangus*). Can. J. Fish. Aquat. Sci. 65 (7), 1297—1306, http://dx.doi.org/10.1139/F08-041.
- Saiz, E., Calbet, A., Broglio, E., 2003. Effects of small-scale turbulence on copepods: the case of *Oithona davisae*. Limnol. Oceanogr. 48 (3), 1304–1311, http://dx.doi.org/10.4319/lo.2003.48.3.1304.
- Sánchez-Velasco, L., 1998. Diet composition and feeding habits of fish larvae of two co-occurring species (Pisces: Callionymidae and Bothidae) in the North-western Mediterranean. ICES J. Mar. Sci. 55 (2), 299–308, http://dx.doi.org/10.1006/jmsc.1997.0278.
- Shansudin, L., Yusof, M., Azis, A., Shukri, Y., 1997. The potential of certain indigenous copepod species as live food for commercial fish larval rearing. Aquaculture 151 (1–4), 351–356, http://dx. doi.org/10.1016/S0044-8486(96)01490-1.
- Spinelli, M.L., Pájaro, M., Martos, P., Esnal, G.B., Sabatini, M., Capitanio, F.L., 2012. Potential zooplankton preys (Copepoda and Appendicularia) for *Engraulis anchoita* in relation to early larval and spawning distributions in the Patagonian frontal system (SW Atlantic Ocean). Sci. Mar. 76 (1), 39–47, http://dx.doi.org/ 10.3989/scimar.2012.76n1039.
- Strasburger, W.W., Hillgruber, N., Pinchuk, A.I., Mueter, F.J., 2014. Feeding ecology of age-0 walleye pollock (*Gadus chalcogrammus*) and Pacific cod (*Gadus macrocephalus*) in the southeastern Bering Sea. Deep Res Pt. II 109, 172–180, http://dx.doi.org/10.1016/j.dsr2.2013.10.007.
- Takatsu, T., Nakatani, T., Mutoh, T., Takahashi, T., 1995. Feeding habits of Pacific cod larvae and juveniles in Mutsu Bay, Japan. Fish. Sci. 61 (3), 415—422.
- Temperoni, B., Viñas, M.D., Martos, P., Marrari, M., 2014. Spatial patterns of copepod biodiversity in relation to a tidal front system in the main spawning and nursery area of the Argentine hake *Merluccius hubbsi*. J. Mar. Syst. 139, 433—445, http://dx.doi.org/10.1016/j.jmarsys.2014.08.015.
- Truong, T.S.-H., Nguyen, C., Lam, N.-N., Jensen, K.T., 2013. Seasonal and spatial distribution of mesozooplankton in a tropical estuary, Nha Phu, South Central Viet Nam. Biologia (Bratisl.) 69 (1), 80–91, http://dx.doi.org/10.2478/s11756-013-0289-9.
- Tudela, S., Palomera, I., Quilez, G., 2002. Feeding of anchovy Engraulis encrasicolus larvae in the north-west Mediterranean.

- J. Mar. Biol. Assoc. U. K. 82, 349–350, http://dx.doi.org/10.1017/S0025315402005568.
- Turner, T., 1986. Zooplankton feeding ecology: contents of fecal pellets of the cyclopoid copepods *Oncaea venusta*, *Corycaeus amazonicus*, *Oithona plumifera*, and *O. simplex* from the Northern Gulf of Mexico. Mar. Ecol. 7 (4), 289—302, http://dx.doi.org/10.1111/j.1439-0485.1986.tb00165.x.
- Van Noord, J.E., Lewallen, E.A., Pitman, R.L., 2013. Flyingfishes feeding ecology in the eastern Pacific: prey partitioning within a speciose epipelagic community. J. Fish Biol. 83 (2), 326—342, http://dx.doi.org/10.1111/jfb.12173.
- Vilchis, L.I., Balance, L.T., Watson, W., 2009. Temporal variability of neustonic ichthyoplankton assemblages of the eastern Pacific warm pool: can community structure be linked to climate variability? Deep Res Pt. I 56 (1), 125–140, http://dx.doi.org/10.1016/j.dsr.2008.08.004.
- Viñas, M.D., Ramíres, F.C., 1996. Gut analysis of first-feeding anchovy larvae from Patagonian spawning area in relation to food availability. Arch. Fish. Mar. Res. 43 (3), 231–256.
- Wang, L., Du, F., Li, Y., Ning, J., Guo, W., 2015. Community characteristics of pelagic copepods in Nansha area before and after onset of Southwest Monsoon. South Chin. Fish. Sci. 11 (5), 47–66, (in Chinese).
- Ward, P., Shreeve, R.S., 1999. The spring mesozooplankton community at South Georgia: a comparison of shelf and oceanic sites. Polar Biol. 22 (5), 289—301, http://dx.doi.org/10.1007/s003000050422.
- Ward, P., Whitehouse, M., Shreeve, R., 2007. Plankton community structure south and west of South Georgia (Southern Ocean): links with production and physical forcing. Deep Res Pt. I 54 (11), 1871–1889, http://dx.doi.org/10.1016/j.dsr.2007.08.008.
- Wend-Heckmann, B., 2013. *Oithona similis* (Copepoda: Cyclopoida)

 A Cosmopolitan Species? Universität Bremen, Bremen, 1–175.
- Williams, J.A., Muxagata, E., 2006. The seasonal abundance and production of *Oithona nana* (Copepoda:Cyclopoida) in Southampton Water. J. Plankton Res. 28 (11), 1055—1065, http://dx.doi.org/10.1093/plankt/fbl039.
- Williams, D.M., Dixon, P., English, S., 1988. Cross-shelf distribution of copepods and fish larvae across the central Great Barrier Reef. Mar. Biol. 99 (4), 577–589, http://dx.doi.org/10.1007/BF00392565.
- Xiang, R., Fang, W., Lu, Y., Huang, X., Zhou, S., 2015. Observed three-dimensional structures of a cold eddy and an eastward jet in the western South China Sea during September 2014. J. Trop. Ocean 34 (6), 1–10, (in Chinese).
- Zalkina, A.V., 1970. Vertical distribution and diurnal migration of some Cyclopoida (Copepoda) in the tropical region of the Pacific Ocean. Mar. Biol. 5 (4), 275–282.
- Zamora-Terol, S., Kjellerup, S., Swalethorp, R., Saiz, E., Nielsen, T. G., 2014a. Population dynamics and production of the small copepod *Oithona* spp. in a subarctic fjord of West Greenland. Polar Biol. 37 (7), 953–965, http://dx.doi.org/10.1007/s00300-014-1493-v.
- Zamora-Terol, S., McKinnon, A.D., Saiz, E., 2014b. Feeding and egg production of *Oithona* spp. in tropical waters of North Queensland, Australia. J. Plankton Res. 36 (4), 1047–1059, http://dx.doi.org/10.1093/plankt/fbu039.
- Zhou, L., Tan, Y., Huang, L., Lian, X., Qiu, D., Ke, Z., 2013. Size-based analysis for the state and heterogeneity of pelagic ecosystems in the northern South China Sea. J. Oceanogr. 69 (4), 379—393, http://dx.doi.org/10.1007/s10872-013-0180-x.