

中华哲水蚤卵密度及其沉降速率

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摘要 : 中华哲水蚤是中国全球海洋生态系统动力学 (China-GLOBEC) 研究中的关键次级生产者, 是浮游植物与高营养级生物之间的中间纽带。为了阐明中华哲水蚤的卵沉降动力学, 采用密度梯度离心法研究了中华哲水蚤的卵密度, 研究结果表明, 在厦门湾中华哲水蚤平均卵密度为 1.0733 g cm^{-3} 。按照斯托克斯定律, 中华哲水蚤卵的沉降速率为 $43.9 \sim 67.5 \text{ m d}^{-1}$ 。对中华哲水蚤卵沉降时间与孵化时间的比较表明, 在厦门湾中华哲水蚤卵能够在孵化之前就沉降到海底。并对中华哲水蚤卵快速沉降的生态学意义展开了讨论。

关键词 : 密度 ; 沉降速率 ; 卵 ; 中华哲水蚤

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Egg density and sinking rate of a planktonic copepod *Calanus sinicus* (Copepoda : Calanoida)

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Abstract : *Calanus sinicus* is regarded as one of the key secondary producers, linking phytoplankton and higher trophic levels, in the China-GLOBEC Project. The density and sinking rate of *Calanus sinicus* eggs were studied in order to understand the depositional dynamics of eggs. The egg density of *C. sinicus* was determined by the density-gradient centrifugation with sucrose solution. The mean density of *C. sinicus* eggs was 1.0733 g cm^{-3} with a SD of 0.0087 g cm^{-3} in Xiamen Bay from December 2002 to May 2003. Based on Stokes' Law, the values of sinking rate for *Calanus sinicus* eggs were estimated, ranging from 43.9 to 67.5 m d^{-1} . The comparison of the egg deposition time and egg hatching time suggested that in most cases virtually all eggs of *C. sinicus* would settle to the bottom before their hatching in Xiamen Bay even though the eggs have high potential to hatch. The ecological significance of fast settlement of *C. sinicus* eggs was discussed.

Key Words : density ; sinking rate ; egg ; *Calanus sinicus*

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1 Introduction

The calanoid copepod *Calanus sinicus* Brodsky is distributed over the shelf waters of the South China Sea , the East China , the Yellow Sea , the Bohai Sea , the Inland Sea of Japan , and the adjacent Pacific Ocean^[1-5]. The species is one of the most important macrozooplankters in those areas in terms of biomass^[3,6-8] , and supports the production of commercially important anchovy , sand eels , and sardines^[9]. Hence , this species is regarded as one of the key secondary producers , linking phytoplankton and higher trophic levels , in the China-GLOBEC (GLOBAL ocean Ecosystems dynamics)^[10-13].

Although some biological attributes of *C. sinicus* , such as feeding^[14-16] , fecundity^[6,13,15,17] , development^[18] , respiration^[16] , diet vertical migration^[19-21] , spatio-temporal distribution^[8] , life history strategy^[11,12] , seasonal life cycle^[7] , fertilization^[22] , and metal assimilation^[23,24] have been studied for years , little has been done to determine the density and sinking rate of *C. sinicus* eggs. The gathering of information regarding the density and sinking velocity of *C. sinicus* eggs would help to understand the depositional dynamics of eggs.

2 Materials and methods

The study site (118 02.363'E ; 24 26.778'N) was located approximately in the center of Xiamen Bay , China. The water depth is 10.8 m. Samples were collected at two week intervals from December 2002 to May 2003. Water temperatures were measured with a thermometer and salinities with a hand refractometer. Chlorophyll a concentrations were measured with the fluorometric method^[25].

To measure the density of *C. sinicus* eggs , adult females were transferred into two egg incubation systems filled with sea water filtered through a 5μm sieve. The incubation systems were self-made according to the design by Burkart and Kleppel^[26] and the volume was enlarged so that enough eggs would be available. Animals were offered a mixed diet (1:1) of *Isochrysis galbana* and *Phaeodactylum tricornutum*. The concentration of the mixed diet was approximately 1.2×10^7 cell m⁻³. Egg density was determined with a density-gradient centrifugation method with sucrose solution. The density-gradient centrifugation method has been commonly used to measure the density of copepods eggs^[27-30]. Densities of the gradient were calculated as mass divided by volume ; mass was determined with an electronic scale (accuracy 0.0001g). Five different densities (1.03 – 1.15 cm⁻³) were used according to our primary study. Solutions of the gradient were carefully transferred into 15 ml centrifuge tubes (4 replicates) to make up five layers of increasing density , from top to bottom. Thirty to forty freshly spawned eggs were transferred onto the surface of the density gradient with a micropipette. A small amount of sea water was inevitably added to the gradient , but it never exceeded 1 ml. The tubes were centrifuged at 3000 r/min. for 30 min. After centrifugation each layer was carefully pipetted out , from top to bottom. Eggs settled in a particular layer were assumed to have equal density as that layer. All density measurements were made at room temperature (20℃) and we did not control the osmotic potential of the density gradient since the change was very small (a ≤1% change in egg density for a 100% change in ambient osmotic potential^[28]).

Egg sinking rates were calculated with Stokes' law^[27-30]. The Stokes' law is expressed as (1)

$$V_s = 2/9r^2g (\rho_1 - \rho_2)/\eta \tag{1}$$

Where , V_s the sinking rate , r the radius of the eggs , ρ_1 the density of the eggs , ρ_2 the density of seawater , η the kinematic viscosity of seawater. Seawater density and kinematic viscosity for Stokes' law were estimated from water temperatures and salinity^[31]. One hundred and ninty eggs of *C. sinicus* , used to measure the egg diameter , were collected on 12 April , 23 April , and 2 May , 2003. The diameter was determined with a microscope at 160 using an ocular micrometer. The mean diameter was used in Stokes' law.

To investigate the hatching time of eggs , freshly spawned eggs of *C. sinicus* were collected. Each egg was

placed in a well of a 24-well tissue culture plate filled with filtered water. Experiments were carried out at 10 , 14 , 18 , 22℃ , and 26℃. At least 50 eggs were used at each temperature. The hatching time of eggs was taken as the point at which 50% of the final number of hatchings was observed [32].

3 Result

The highest temperature was 29.3℃ in May and the lowest temperature was 14.0℃ in February in Xiamen Bay during the study period. Salinity also fluctuated seasonally. It was lower and more variable in the spring-summer because of heavy rainfall. The highest chlorophyll a concentration was 9.1 mg m⁻³ in March (Fig. 1).

The density of *Calanus sinicus* eggs was measured every two weeks from December 2002 to May 2003. The mean density of eggs was 1.0733 g cm⁻³, with a SD of 0.0087 g cm⁻³. Two peaks respectively occurred in late December and early April (Fig. 2).

The frequency distribution of the densities of 2301 eggs throughout the study period was shown in Fig. 3. Most of eggs were distributed at a density of 1.06 g cm⁻³, although eggs at all densities.

The measurement of 190 eggs showed that the mean diameter of *C. sinicus* eggs was 160.5 μm, with a SD of 8.2 μm. The sinking rate of *C. sinicus* eggs in Xiamen Bay from December to May was illustrated in Fig. 4. The values of sinking rate ranged from 43.9 to 67.5 m d⁻¹. The highest sinking rate occurred in early April, while the lowest value was observed in late January. The mean sinking rate for *C. sinicus* eggs in Xiamen Bay was 52.9 m d⁻¹, with a SD of 7.5 m d⁻¹.

Time to 50% hatching versus temperature for *Calanus sinicus* eggs was shown in Fig. 5. A power function ($y = 741.52x^{-1.2227}$, $R^2 = 0.9817$) fitted to the data showed a strong relationship.

We calculated the settling time from the surface to the bottom at the study area (10.8 m), and how it compared with the time required for hatching (Fig. 6). The hatching time was calculated from the power function derived from the Fig. 5. The egg hatching time (EHT) was long in winter when seawater temperature was low, and decreased gradually with the increase of temperature. The egg deposition time (EDT) ranged from 4.0 to 5.9 h during the study period. In all cases EHT was higher than EDT, which means that eggs of *C. sinicus* would settle to the bottom before their hatching, especially when the temperature was low.

4 Discussion

Most marine calanoids spawn their eggs directly into the water column. Since the eggs are denser than seawater, they sink, so that in shallow waters many would reach the bottom prior to hatching [27, 28, 33, 34]. Although the idea of the sinking of eggs to the bottom prior to hatching in shallow area has been proposed by many authors [27, 28, 33], little has been done to compare egg depositing time and egg hatching time directly except a recent research [29]. This

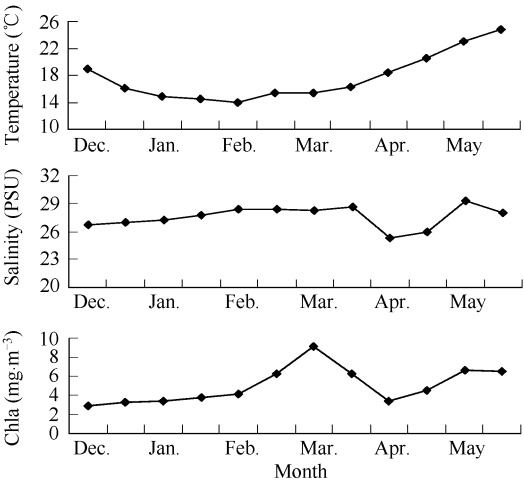


Fig. 1 Environmental variables during the study period

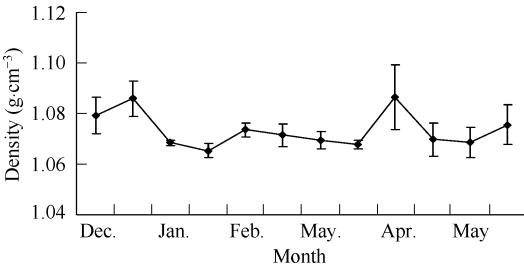


Fig. 2 Density of *Calanus sinicus* eggs in Xiamen Bay from December to May

comparison of the egg deposition time and egg hatching time suggests that in most cases virtually eggs of *C. sinicus* would settle to the bottom before their hatching in Xiamen Bay even though the eggs have high potential to hatch , which confirms the above idea. The potential for deposition of copepod eggs onto the seabed may be influenced by the depth at which spawning occurs in the water column^[28]. Zhang *et al.*^[35] reported that *Calanus sinicus* migrated into surface waters and spawned eggs at night. Thus , spawning eggs at the surface may maximize the possibility that eggs will hatch before being deposited into bottom sediments.

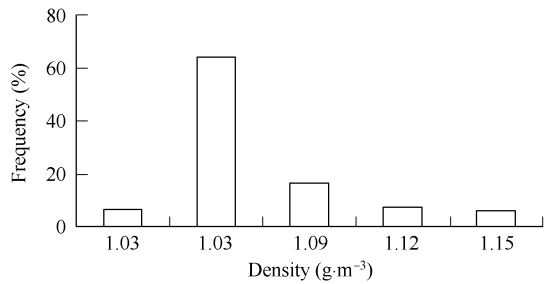


Fig. 3 Frequency distribution of *Calanus sinicus* egg density

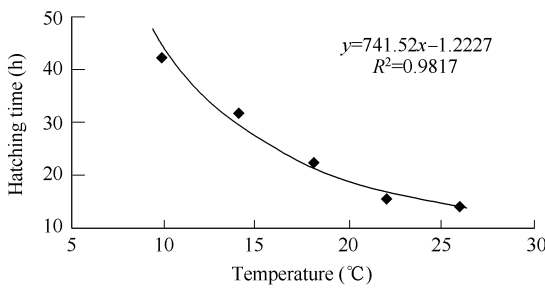


Fig. 5 Hatching time of *Calanus sinicus* eggs versus temperature

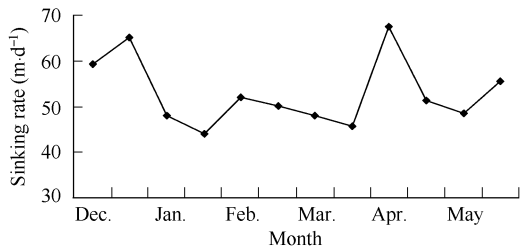


Fig. 4 Sinking rate of *Calanus sinicus* eggs in Xiamen Bay from December to May

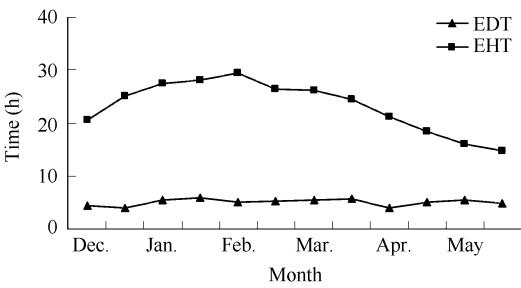


Fig. 6 Egg hatching time (EHT) and egg deposition time (EDT) of *Calanus sinicus* in Xiamen Bay

The apparent egg mortality rate in marine copepods is usually calculated as the difference between the egg production rate measured by bottle incubations and the egg production rate estimated *in situ*^[32, 36]. Thus , the apparent egg mortality rate is indeed how fast the eggs are removed from the water column^[29]. Since copepod eggs usually have higher density than sea water ,egg sinking has also been suggested as a major mechanism to remove eggs from the water column^[27, 32]. Zhang *et al.*^[37] reported that the mortality of *C. sinicus* eggs was very high (80%) in June in the Yellow Sea and they suggested that the predation of larva and juvenile of *Engraulis japonicus* was the main reason of the high mortality for *C. sinicus* eggs. However ,the larva and juvenile of *E. japonicus* are distributed in the upper 10 m in most time of the day except at noon when they sink to 20 m^[38]. Considering their sinking rate , *C. sinicus* eggs would escape from the 0 – 10 m layer within 5 h ,where larva and juvenile of *E. japonicus* distribute. Thus the loss of eggs due to predation may be limited. The sinking of eggs to the bottom prior to hatching may be one of major mechanisms that result in high mortality. Egg sinking rates in the Yellow Sea were calculated with Stokes' law. The mean density of eggs (1.0733 g cm⁻³) and diameter (160.5 μm) obtained from present study were used. The seawater and salinity are mean values of published data^[39]. The comparisons of the egg deposition time and egg hatching time for *C. sinicus* in Yellow Sea were shown in Fig. 7. The average water depth of the Yellow Sea is 44 m^[39]. Hence , *C. sinicus* egg would sink out of the water column before hatching occurred , contributing to the apparent egg mortality in the water column. Zhang^[37] observed that the mortality of *C. sinicus* egg in Station A (35)

was higher than that in Station B (55m). Our hypothesis, high mortality of eggs due to the sinking to the bottom prior to hatching, can explain the above observation. Since the depth of Station A is lower than that of Station B, the percentage of *C. sinicus* eggs that settle to the bottom before hatching in Station A would be higher than that in Station B, leading to the apparent high mortality of eggs in Station A. The hydrographic and circulation properties of the Yellow Sea are controlled by the Kuroshio Current (KUC), Taiwan Warm Current (TWC), and surface wind stress. The bottom friction layer draws KUC water across the bottom of the continental shelf into the Yangtze Relict River valley and generates upwelling along the Chinese coast^[40]. The distribution and abundance of plankton are controlled by the physical procession. Wei^[41] showed that the jet along the front and upwelling in the mixed side of the front play an important role in the transport of anchovy eggs in the Yellow Sea. Upwelling drags the sinking of *C. sinicus* eggs, while downwelling significant accelerate the sinking. Unfortunately, it is still impossible to predict the effect of upwelling/downwelling on the sinking of *C. sinicus* eggs in the Yellow Sea due to very limited knowledge on the vertical movement.

The significance of fast settlement of copepod eggs is that the post-settlement fate of the eggs instead of water column processes will determine the true egg mortality^[29]. If settled eggs can maintain survive in the sediment and return to the water column due to physical and biological suspension, these eggs will create a potentially important source for recruitment of nauplii into the plankton and the apparent egg mortality will overestimate the true egg mortality. Uye^[2] found that the most of *C. sinicus* eggs in the mud would die and some eggs on the mud could remain viable for 2 days, which means that most settled eggs would die in the field due to their weak capability of survival. Many factors would affect the density and sinking of copepod eggs. Both salinity and temperature significantly affected the density and sinking velocity of the eggs of *Arartia tonsa*^[28]. Many researches indicated that food concentration and quality affect the egg production rate and hatching success^[42]. Different hatching success of copepod eggs may indicate the different biochemical contents. So, food concentration and quality may affect the density and sinking rate of copepod eggs. However, there is no the study on this topic. The possible reason is the technical difficulty due to the small size of eggs. Miller and Marcus^[28] showed that there was no significant difference of *A. tonsa* eggs. In *C. sinicus*, a multiple-layered fertilization envelope was formed after spawning and the surface of the egg was extremely electron dense^[43]. The possible effect of the surface structure of *C. sinicus* on the sinking rate is still unknown.

It is must be acknowledged that the egg sinking rates presented here are the theoretical rates for a laminar fluid environment^[29]. Turbulence and water currents may influence the deposition of eggs in the water column. The actual sinking rate of eggs (W_s) in the natural environment can be expressed as (2):

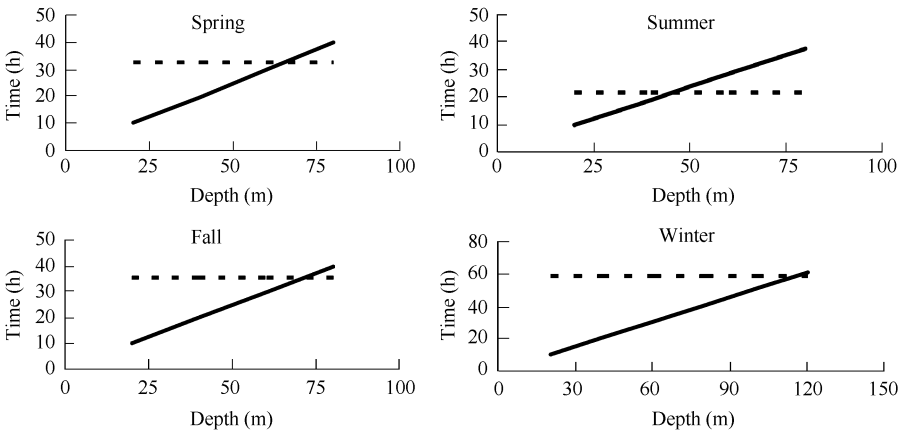


Fig. 7 Egg hatching time (---) and egg deposition time (-) predicted for *Calanus sinicus* eggs in the Yellow Sea

$$W_s = W + W'$$
 (2)

where W is the mean sinking rate (values calculated from Stokes' law) and W' is the sinking rate associated with vertical turbulent motion in the fluid. The magnitude of W' may be estimated as (3) :

$$W' = K_z / Z'$$
 (3)

where K_z is the vertical eddy diffusion coefficient , and Z' is the characteristic vertical length scale for the turbulent eddies (L)^[29,44]. Xiamen Bay is a tidally driven estuary and the water is well mixed^[45,46]. In such a condition equation (3) could be further simplified. The vertical eddy diffusion coefficient (K_z) could be caculated as (4) :

$$K_z = 2.5 \times 10^{-3} ZV$$
 (4)

where Z is the depth of the water column and V is the mean flow velocity in the water column. Z' may be approximated as $0.4Z$. W' could be simplified into (5)^[29,44] :

$$W' \approx 6.25 \times 10^{-3} V$$
 (5)

The average flow velocity in Xiamen Bay ranges from 0.1 to 0.6 m s^{-1} ^[45,46]. Thus , the magnitude of W' is estimated approximately as $54 \sim 324 \text{ m d}^{-1}$. Compared to the mean sinking rate (W) of *C. sinicus* , the value of W' is quite considerable. If the net direction of W' is down , the vertical turbulent motion would significantly accelerate the egg deposition. On the contrary , the vertical turbulent motion may make eggs keep suspension due to their up-action.

Resuspension is a common physical process that occurs everywhere in the marine environment , especially in shallow areas. Resuspension can be caused by vertical events , such as strong wind , tidal currents and biological activities. Resuspension would be expected if the bottom shear velocity scaled to (or was larger than) the sinking rate (W_s). In estuaries the bottom shear velocity may be estimated as (6)^[29,47] :

$$U^* \approx 0.0447V$$
 (6)

The magnitude of U^* in Xiamen Bay ranged 386 to 2317 m d^{-1} . Thus , eggs of *C. sinicus* are likely to be resuspended from the bottom in Xiamen Bay. The gathering of information regarding the density and sinking rate is a crucial first step to gain an understanding of depositional dynamics for egg in the field ,and will improve our insight of the population dynamics of *Calanus sinicus*.

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