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利用魚類行為—物理洋流耦合模型探討聖嬰現象對於
日本鰺在東海產卵洄游之影響

Investigating ENSO effects on the spawning migration of
Japanese anchovy in the East China Sea using a
behavior-hydrodynamic model

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Abstract




Mature individuals of Japanese anchovy (*Engraulis japonicus*) migrate from the East China Sea to the coastal water of northern Taiwan to spawn during winter. The anchovy larvae then form an important fishery resource for Taiwan. Previous studies indicate that the interannual variation of anchovy larvae catch per unit effort data exhibited a negative correlation with ENSO; however, the detail underlying mechanism explaining how ENSO affects ocean currents or environmental conditions, which in turn determine the fluctuations of anchovy larvae, remains unclear. To bridge the knowledge gap, we construct historical circulation patterns in the East China Sea and the Taiwan Strait by hydrodynamic models, and use individual-based model to represent fish behavior for simulating the migration process of Japanese anchovy. Comparing model results under various ENSO states (strong El Niño (La Niña) and moderate El Niño (La Niña) states), we find that the fluxes of Japanese anchovy populations toward Taiwan is positively correlated with the strength of China Coastal Current, which is driven by the East Asian Winter Monsoon. Specifically, in El Niño (La Niña) states, the East Asian Winter Monsoon decreases (increases) in boreal winter and weakens (strengthens) the China Coastal Current and in turn decreases (increases) the fluxes of Japanese anchovy populations migrating toward the coastal water of Taiwan. The connection between the ENSO, East Asian Winter Monsoon,

China Coastal Current, and spawning migration of Japanese anchovy suggests that large-scale environmental changes may affect reproductive biology of species through meso-scale physical environmental factors. The results also indicate that the dynamics of migration processes should be considered in fishery managements.

Keywords

ENSO, East Asian Winter Monsoon, China Coastal Current, Japanese anchovy, migration process, fish behavior-hydrodynamic model, hydrodynamic model, individual-based model

中文摘要



每年冬春之交，攝食區域位於中國東海的日本鯷成魚會洄游至位於台灣沿海的產卵場，其仔稚魚（魷仔魚）則會成為台灣沿海漁業的重要標的之一。過去研究顯示日本鯷仔稚魚的單位努力漁獲量（Catch-per-unit effort）的年間變異與聖嬰-南方震盪現象（El Niño-Southern Oscillation, ENSO）有著負相關性；然而對於 ENSO 如何影響洋流等物裡環境進而影響魷仔魚的再補充量的詳細機制，目前仍不清楚。為了釐清此問題，本研究利用物裡洋流模型（hydrodynamic model）模擬過往年份的中國東海及台灣海峽的冬季流場，同時利用個體模型（Individual-based model）來模擬日本鯷成魚的洄游行為並記錄其在模擬流場中的洄游過程。比較不同 ENSO 強度下的模擬結果，顯示到達台灣沿海海域的成魚數量與被東北季風驅動的中國沿岸流（China Coastal Current）強度呈現正相關。當強度越大的聖嬰(反聖嬰)現象發生時，東北季風減弱(增強)的情形也越明顯，進而影響中國沿岸流使之減弱(增強)，最終導致到達台灣海域的日本鯷成魚數量減少(增加)。ENSO、東北季風、中國沿岸流以及日本鯷的生殖洄游行為之間的關聯顯示了大尺度的環境變異可能藉由影響中尺度的環境物理因子傳遞至海洋生物進而影響其生殖行為。結果顯示，考慮洄游物種的漁業政策時，洄游過程所造成的影響不可忽略。

關鍵字

聖嬰-南方震盪現象、東北季風、中國沿岸流、日本鯷、洄游行為、魚類行為—物理洋流耦合模型、物裡洋流模型、基於個體模型



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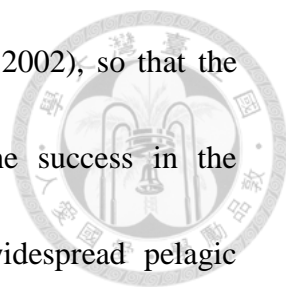


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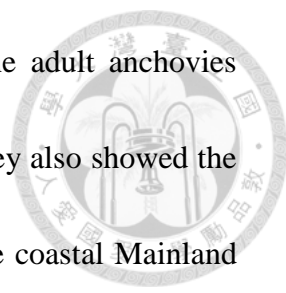
Introduction

In the East China Sea (ECS), marine populations are known to be affected by climate (Kim *et al.* 2005). Among those, Japanese anchovy (*Engraulis japonicus*) plays an important role in food web (Bakun and Parrish 1991) and represents an important fishery (Young and Chiu 1994, Chiu *et al.* 1997). The recruitment of population of Japanese anchovy is correlated with the Southern Oscillation Index (SOI) (Tsai *et al.* 1998, Hsieh *et al.* 2009). The study by Tsai *et al.* (1998) emphasized that there was a significant correlation between the catch per unit effort (CPUE) of Japanese anchovy and local SST, and the CPUE was also correlated with SOI through SST, suggesting that ENSO may affect the recruitment of Japanese anchovy through the meteorological conditions that influence coastal upwelling. However, a study using longer time series revealed that the correlation between the CPUE and SST was transient (Hsieh *et al.* 2009). This study pointed out that previous studies over-emphasized the importance of local hydrographic effects on the anchovy populations (Lee *et al.* 1995, Lee and Lee 1996, Hsia *et al.* 2004), and the climatic factors such as ENSO should be examined (Hsieh *et al.* 2009). Notably, their study suggested that the abundance fluctuations of Japanese anchovy might be affected by ENSO through modulating the circulation pattern in the ECS, which in turn affects the migration process of Japanese anchovy.



Japanese anchovy is an oceanodromous species (Chiu *et al.* 2002), so that the recruitment of Japanese anchovy is profoundly affected by the success in the spawning migration (Cushing 1975). Japanese anchovy is a widespread pelagic species mainly distributed in the northwestern Pacific Ocean, including the Sea of Japan, Yellow Sea, and ECS (Iversen *et al.* 1993), and larval anchovies are important target in the commercial fisheries in the coastal waters of Taiwan (Young and Chiu 1994, Chiu *et al.* 1997). It is known that fishing grounds are located at the coastal water of northern Taiwan (e.g. Ilan Bay) in March to May. Genetic analysis suggested that the feeding ground of the Japanese anchovy stock is located in the ECS (Yu *et al.* 2002). It is believed that some anchovies start their spawning migration from the ECS in winter and arrive at the coastal water of Taiwan for spawning in Spring (Fig. 1). After spawning, the larvae are caught, and surviving individuals undertake the feeding migration back to their feeding ground in the ECS to start the next round of life cycle (Chen and Chiu 2003). Spawning migration is a pre-spawning event and is important for recruitment. More specifically, a higher survival rate of parental fish stock after migration would lead to higher egg production (Rothschild and Fogarty 1989, Opdal *et al.* 2011). Considering the fluctuation of larva recruitment of Japanese anchovy, the effects of spawning migration cannot be ignored.

The model results by Tu *et al.* (2012) indicated that the strength of CCC aids the



spawning migration of Japanese anchovy. It is evidenced that the adult anchovies follow the CCC to arrive the Taiwan Strait (TS). The acoustic survey also showed the distribution of Japanese anchovy was extended to the TS along the coastal Mainland China in the ECS in March, 1985-1990 (Iversen *et al.* 1993). In the simulations (Tu *et al.* 2012), the authors manipulated the riverplume of the Changjiang to regulate the strength of CCC in a climatology circulation model. In their results, the adult anchovies moved southward with the CCC, and anchovies arrived at their feeding ground more easily in the simulation which had the stronger CCC, indicating that the CCC may play an important role in the spawning migration of Japanese anchovy.

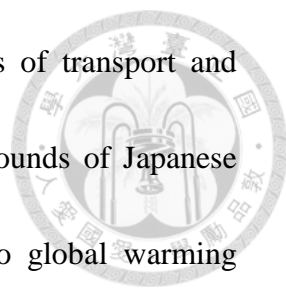
The CCC is mainly driven by the East Asian Winter Monsoon (EAWM) and enhanced by the Changjiang outflow (Lee and Chao 2003), and the EAWM had been found highly correlated with El Niño-Southern Oscillation (ENSO) (Zhang *et al.* 1997). The CCC is a southward coastal jet which develops along the east coast of Mainland China in fall and winter (Chao 1990). The CCC occurs in October, one month after the begin of EAWM, and it peaks in December but diminishes in March, when the winter monsoon is replaced by the southerly summer monsoon (Lee and Chao 2003, Isobe 2008). The East Asian Monsoon is one of most energetic monsoon circulation systems and dominates the local weather in the East Asian region (Chang and Lau 1982), and it shows the reversal of winds in summer and winter. The East

Asian Monsoon is affected by ENSO through a Pacific–East Asian teleconnection.

The lower-tropospheric anticyclone/cyclone shifting system located in the western North Pacific is the key to bridge ENSO in the eastern Pacific and the EAWM (Wang *et al.* 2000). The warm ENSO events occur in boreal winter are often accompanied with a weaker EAWM, and vice versa (Tornita and Yasunari 1996, Zhang *et al.* 1997).

According to previous studies, ENSO had a significant negative correlation with the CPUE of Japanese Anchovy (Hsieh *et al.* 2009). In our research, we hypothesize the mechanism that ENSO influences the abundance of Japanese anchovy is linked by the meso-scale physical factors: First, the ENSOs affect the strength of EAWM. Second, the strength EAWM determines the southward velocity and the extension of CCC. As a consequence, the CCC influences the success rate that adult anchovies arrive at the coastal water of northern Taiwan, owing to the successful migration of Japanese anchovy aided by the CCC.

To test the hypothesis, we use a coupled biological–physical model, and it is necessary to establish the past realistic circulation in our hydrodynamic model. Numerous studies showed that biological–physical model becomes a valuable and important tool to study dispersal and migration of marine organisms with the advances in computation and hydrodynamic modeling (Capella *et al.* 1992, Rose 1993, Cowen *et al.* 2006). Moreover, previous research showed that using



biological–physical model is convenient to compare differences of transport and distribution pattern due to climate change (e.g. The spawning grounds of Japanese sardine were predicted to shift towards more north areas due to global warming (Okunishi *et al.* 2012)). Correlation between the Japanese anchovy and the circulation in the ECS has been demonstrated by simulation models that driven by the climatology data and scenario tests (Tu *et al.* 2012). However, to compare the differences of migration of Japanese anchovy in various ENSO years requires simulating historical circulation.

Here, we use the historical data for surface wind velocity over the ECS and the circulation information of ECS to reconstruct the past circulation in the ECS, and then simulate the migration process of Japanese anchovy in our hydrodynamic models. Comparing the results of different ENSO states may improve our understandings of ENSO effects on the recruitment of Japanese anchovy, and provide advices for fishery managements.

Materials and Methods

Historical data analysis

In this study, we used Oceanic Niño Index (ONI) as an indicator for ENSO states (i.e. El Niño and La Niña events). In our study, the definition for the range of CCC from north to south is between 31°N and 25.5°N , which is the region from the Changjiang estuary to the northern boundary of the TS. The zonal width of CCC concludes 10 kilometers from the China coastline.

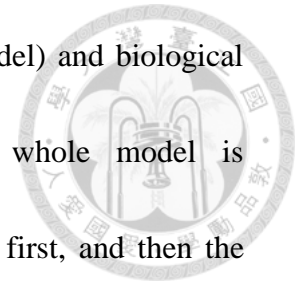
A consistent relationship has been found in the historical data of ONI, the EAWM and the CCC in 2003 - 2013 (Figs. 2a-c). The linear correlation coefficient between the ONI and the EAWM is 0.6548 (p-value= 0.0288), and between the monsoon and the CCC is 0.6831 (p-value= 0.0205). These results indicate that the strength of EAWM decreased during the El Niño phase, and the strength of CCC can be affected by the EAWM.

Model description

The simulation region is between 24°N - 33°N and 119°W - 124°W , which contains most part of the ECS and the TS. The years chosen for simulation include two strong EL Niño years (i.e. 2003, 2010), two strong La Niña years (i.e. 2008, 2011), a moderate EL Niño year (i.e. 2007) and a moderate La Niña year (i.e. 2012). The



models contain two parts: physical model (i.e. hydrodynamic model) and biological model (i.e. migration process of Japanese anchovy). The whole model is hierarchically constructed. The hydrodynamic sub-model is built first, and then the biological sub-model is coupled to the results of the physical models (Willis 2011).

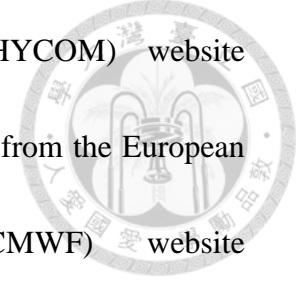


The simulation of physical model for each year starts from the December 1st of the previous year and end in March. The simulation period for the biological models starts from the January 1st and lasts for 60 days. This decision is based on the larval anchovy fishery. According to the fishery survey, the maximum CPUE lays in March, and the larvae's age is about 15–30 days old (Chiu and Chen 2001), meaning that the adult anchovies must arrive at the spawning ground before March.

A. Hydrodynamic model

The physical model in this study is configured with the Regional Ocean Modeling System (ROMS), which is a hydrostatic, primitive-equation model with a free surface, terrain-following vertical coordinate (Haidvogel *et al.* 2000, Marchesiello *et al.* 2003). The past study (Shchepetkin and McWilliams 2005) described the detail about the algorithms of ROMS. For the ECS and TS region the domain extends from 24°N-33°N and from 119°W-124°W with a horizontal resolution of 1/50° and includes 20 vertical levels (terrain-following curvilinear coordinates). The initial condition and the boundary condition are determined using

the data from the Hybrid Coordinate Ocean Model (HYCOM) website (<http://hycom.org>). The driving forces include surface wind stress from the European Centre for Medium-Range Weather Forecasts (ECMWF) website (<http://www.ecmwf.int/>) and the constant Changjiang outflow. For focusing on the effect of EAWM affecting the CCC, the Changjiang runoff in the models is set as the annual average inflow: 0.029 Sv (Zhang *et al.* 1990).



B. Biological model

The biological model in this study describes the migration process of Japanese anchovy. The model is based on Lagrangian framework to record the particles location and movement, and it is coupled with the individual-based model to describe the swimming behaviors of adult anchovies in the migration.

The behavior model basically follows (Tu *et al.* 2012). The behavior model contains two parts: swimming speed and the local orientation patterns. The swimming speed is always constant at 30 cm/s, and the anchovies are oriented by current velocity (Eqn. 1) or temperature gradient (eqns. 2-3).

$$V = 30 \text{ cm/s} \quad (1)$$

$$u_{S_1} = V \times \frac{u_c}{\sqrt{u_c^2 + v_c^2}} \quad v_{S_1} = V \times \frac{v_c}{\sqrt{u_c^2 + v_c^2}} \quad (2)$$

$$\nabla T = \frac{\partial T}{\partial x} i + \frac{\partial T}{\partial y} j \quad (3(a))$$

$$GM = \sqrt{(\partial T / \partial x)^2 + (\partial T / \partial y)^2} \quad (3(b))$$

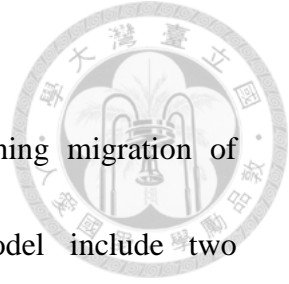
$$u_{S_2} = V \times \frac{(\partial T / \partial x)}{GM} i \quad v_{S_2} = V \times \frac{(\partial T / \partial x)}{GM} j \quad (3(c))$$

V is the magnitude of fish swimming velocity; u_c , v_c are the velocity of the current; u_s , v_s separately represent x, y component of fish swimming velocity, and T is temperature. These equations represent the swimming speed and different strategies in determination of migration orientation. Here, Eqn.2 assumes that fish change their migration direction follow the current, and Eqn.3 supposes that the orientation of migration is mainly determined by temperature. Many simulation studies also indicate that temperature play an important role to determine the migration direction in Japanese anchovy (Wang *et al.* 2013) and similar species, Japanese sardine (Okunishi *et al.* 2009). We assumed that anchovies swim in optimal cruise speed equivalent to a unit body length per second (Weihs 1973). The swimming behavior in Eqn.3 indicates the fish head to local maximum temperature. For this behavior, we assumed that fish have ability to find the optimal temperature for spawning (Takasuka *et al.* 2005).

The orientation of adult anchovies in this study is ruled by three equations: Adult anchovies swim along with the current (Eqn. 2) after the beginning of the migration, but change their behavior to follow the temperature gradient to the local maximum temperature (Eqns.3a-c) when they sense the optimal temperature for spawning. In our study, we set the threshold temperature for adult anchovies to change their orientation rules to be 24°C.

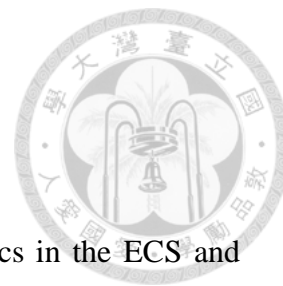
Sensitivity analyses

Considering fluctuations in the initial conditions of spawning migration of Japanese anchovy, the sensitivity analyses of biological model include two components: initial locations and starting dates. In the sensitivity test of initial locations, the tracers are released at 30°N and 32°N, which are the northernmost and southernmost distribution of anchovies in the January in the ECS according to the acoustic surveys (Iversen *et al.* 1993). In the sensitivity test of starting dates, the start location are the same (31°N) but the tracers are released at January 5th in each years, which is 5-day delay compared to the original simulation. The tracers with final location south of 24.7°N, north of 25.7°N, and between 120.8 and 121.8°E are considered as close to Taiwan enough to find the suitable spawning ground.



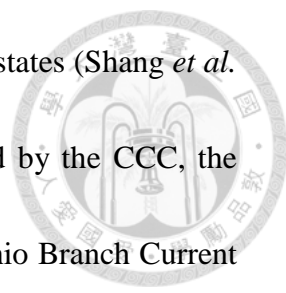
Results

The simulation results of physical models



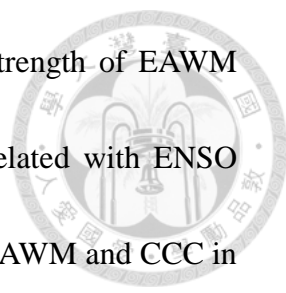
The physical models represent the hydrographic characteristics in the ECS and revealed the interannual variation. The CCC can be observed in all simulation results, and the source of jet starts from the Changjiang mouth and is formed by the Changjiang Diluted Water (Figs. 3a-f). The Changjiang Diluted Water with low salinity forms the strong density gradient when it enters the ECS (Figs. 4a-f). The Changjiang Diluted Water turns right and forms a southward jet called the CCC. The CCC causes a intrusion of cold water into warmer sea area in the models, and the same phenomenon can be observed in the satellite data (Lee and Chao 2003, Chang *et al.* 2006). According to the 2 months (i.e. January and February) average of near surface sea temperature (1-5m) and circulation velocity (Figs. 3a-f, 5a-f), the strength and the range of CCC exhibited interannual variation in simulation results. The CCC extended more in meridional way in strong La Niña years (i.e. 2008, 2011), and the strength of CCC decreased in El Niño years (i.e. 2003, 2007) (Figs. 3a-f, 5a-f). Furthermore, in El Niño years, the CCC may even disappear (Figs. 6a-f).

The patterns and features of currents in the Taiwan Strait (TS) are highly consistent with previous observations (Lin *et al.* 2005) and the numerical study for the general current patterns (Wu *et al.* 2007). The TS is under the influences of the three



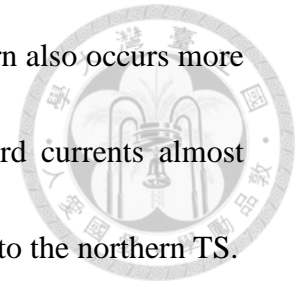
currents (Fig. 7) modulated by the strength of monsoon and ENSO states (Shang *et al.* 2005). In the model results, the surface circulations are composed by the CCC, the extension of South China Sea Warm Current (SCSWC) and Kuroshio Branch Current (KBC) in winter (Figs. 8a-f). The CCC intrudes from the north along the coast of Mainland China in the western TS, and the CCC sometimes forms a branch flowing into the central TS and makes a "U" turn northeastward due to the blocking of the Changyun Rise (Fig. 9). The "U" form branch is also observed in satellite images (Li *et al.* 2006, Chang *et al.* 2009). A branch of the KBC passes the Penghu Channel and flow northeastward along the western coast of Taiwan, and usually forms an anticyclonic meander upper the Changyun Rise to bypass the shallow area. Sometimes the current has a branch bypasses the western of Penghu Island and flow into the central TS. In our study, we call this branch current, KBETC, and it occupies the eastern TS during the most of time. The extension of South China Sea Warm Current (SCSWC) offers the northward current in the western and central TS. Besides, an anticyclonic eddy may occur in the northwestern area of Changyun Rise in the central TS sometimes (Fig. 9). The general circulation in the study shows agreement with the review paper (Hu *et al.* 2010), but the currents may extend, diminish or even disappear in the TS.

According to these results, the differences of circulation patterns between El



Niño years and La Niña years are caused by the fluctuation in strength of EAWM which is affected by ENSO. The EAWM strength is highly correlated with ENSO (Figs. 2a-b), and there is good correlation between the strength of EAWM and CCC in the model results ($r= 0.953$, $p\text{-value}= 0.0032$) (Fig. 11b-c). Meanwhile, comparing the dynamics of the EAWM and the circulations in the ECS and TS suggests that the EAWM not only strengthens and extends the CCC, but also suppress the northward flux in the TS. The southward water velocity increases as the EAWM increases, and the CCC also intrudes into the TS due to the strengthened EAWM. The KBETC is suppressed by EAWM and is blocked at the south of the Changyun Rise, and most influx from the Kuroshio Current follows the SCSKB. Also, when EAWM is strong, the diminishment of SCSWC in the western TS can be observed frequently. In contrast, when the EAWM is weak, the CCC stops at the northern TS, and the SCSWC and KBETC dominate the TS. Concluding the monsoon effects on the circulations, northward currents almost dominate the whole TS in El Niño states, while the intrusion of CCC is limited only to the northern TS. In contrast, the SST is lower and the northward flux decreased in the TS in La Niña years (Figs. 8a-f), which is consistent with the past study (Kuo and Ho 2004). In La Niña years, the CCC and the extension of SCSWC show antagonistic relationship in the western TS, which means the extension of CCC causes the diminishment of SCSWC in the western TS.

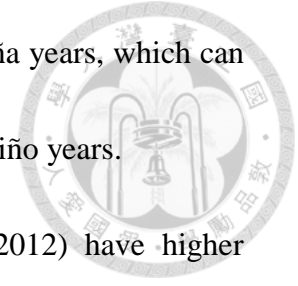
Besides, the branch of CCC forming a northeastward "U" shape turn also occurs more frequently in the La Niña years. In El Niño years, the northward currents almost dominate the whole TS, while the intrusion of CCC is limited only to the northern TS.



The simulation results of biological models


The tracer trajectories indicate the migration routes of Japanese anchovy, conforming to the speculation and model results from past studies (Yu *et al.* 2005, Tu *et al.* 2012). More importantly, the results of this study show increasing trend in the fluxes of Japanese anchovy populations in La Niña years (Figs. 10, 12a-f). Except the results in year 2010 and 2012, most tracers move southwestward along the coast of Mainland China, meaning that the moving direction of the tracers is the same as the CCC. However in 2010 and 2012, only about half of the tracers follow the direction of the CCC, and only the tracers starting at the nearshore area can catch the CCC. Almost all tracers that follow the CCC can reach the northern coastal area of Pingtan Island (i.e. part of Fujian Province), but some of them in year 2003 and 2010 (i.e. strong El Niño years) cannot enter the TS due to their slow movement, making them unable to bypass the Pingtan Island during the spawning season. Beside the abundance, the timing that adult anchovies enter into the TS (Figs. 12a-f) show difference in the El Niño and La Niña years. The tracers show about 10 days late for

entering into the TS in the El Niño years compared with the La Niña years, which can be explained by the smaller current velocity in the CCC in the El Niño years.



Only the tracers in La Niña years (i.e. 2008, 2011 and 2012) have higher percentage of arrival at the coastal water of Taiwan (Fig. 10), but none of the tracers can bypass the north tip of Taiwan to reach the Ilan Bay (Figs. 12c, e, and f). Most tracers that arrive at the spawning area go southward but leave the coastal area of Mainland China when they bypass Pingtan Island and enter the TS. The tracer trajectories present "U" shape turn in the central TS, and this change in the moving direction is oriented by the branch of the CCC in the central TS, which occurs more often in the La Niña states. In the end, the tracers move along the western coast of Taiwan to reach the coastal water of northern Taiwan. In contrast, very few tracers approach the coastal water of northern Taiwan in El Niño years (i.e. 2003, 2007 and 2010) (Fig. 10), and most tracers are limited to the western TS (Figs. 12a, 12b, 12d). The tracer trajectories form "V" shape turn in the coastal water of Mainland China, and then the tracers turn northeastward, indicating that tracers are impeded by the northward currents dominating the most part of TS in El Niño. Consequently, most tracers have no chance to reach the eastern TS.

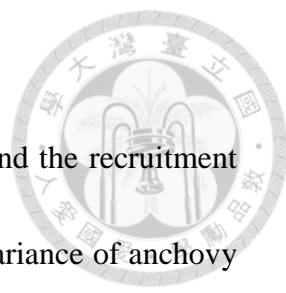
Sensitivity analyses



The sensitivity analysis on initial locations indicate that the effect of spawning ground shifting is not significant to the abundance of Japanese anchovy that arrive at their spawning ground (Figs. 13a-b). In this simulation, the north and south boundary of the anchovy's feeding ground was used. The results suggest that the physical condition of anchovy overwintering ground aid adult anchovy to follow the CCC and arrive at their spawning area. When tracers were released at 32°N, although there were less tracers following the CCC, the tracer trajectories that followed with the CCC are still very similar as the original simulations (Fig. 13b).

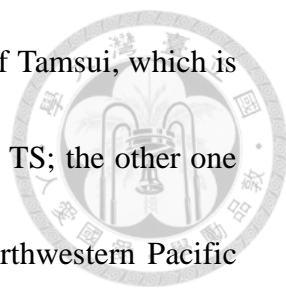
The sensitivity test of the particle-released starting date shows that the number of tracers reaching the coastal waters of Taiwan were higher in La Niña years (i.e. 2008, 2011, and 2012) when tracers were released at January 5th (Fig. 14). Although the abundance of tracers that arrive at the coastal waters of Taiwan are different, the simulation that tracers were released at January 5th also showed the same trend that Japanese anchovy arrived at their spawning ground more easily in La Niña years.

Discussion



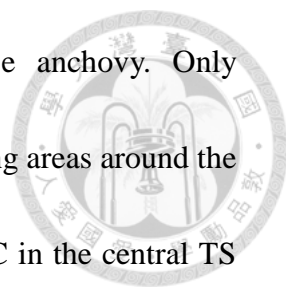
A previous study has shown the correlation between ENSO and the recruitment of Japanese anchovy, but ENSO can only explained <10% of the variance of anchovy CPUE (Hsieh *et al.* 2009). The low-correlation may be due to the decadal variation of ENSO–EAWM relationship. The historical data shows strong correlation between ENSO and EAWM in year 2003-2013 (Figs. 2a-b), conforming the past studies that ENSO can deeply affect the strength of EAWM (Chongyin 1990, Wang 2006). The strong (weak) EAWM are generally associated with La Niña (El Niño) (Zhang *et al.* 1997). Although it also has been found that the EAWM and ENSO are not consistently highly correlated in late 1970s by some studies (Zhou *et al.* 2007, He 2013). The recent paper (He and Wang 2013) showed ENSO and the EAWM are in a high-correlation period in the recent decades. Their study indicates the ENSO–EAWM relationship is modulated by the Pacific Decadal Oscillation, and the authors suggest that ENSO might deeply affect the EAWM during 2002 - 2012. This period of high correlation is basically the same as our study period.

The tracer trajectories show a good agreement in temporal-spatial distribution of Japanese anchovy with acoustic surveys (Iversen *et al.* 1993), and the simulation results also have consistency in location and timing with existing fishing grounds of Japanese anchovy in the Taiwan Strait. In winter, there are two fishing grounds in the



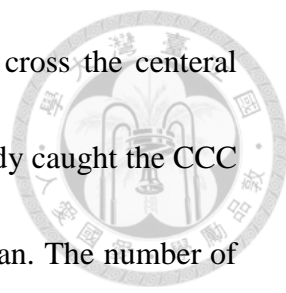
coastal water of northern Taiwan: one locates at the coastal water of Tamsui, which is the western fishing ground for larva anchovies in the northwestern TS; the other one locates at Ilan Bay, which is the eastern fishing ground in the northwestern Pacific Ocean (Chen *et al.* 2010). In addition, the fishery in the coastal water of Fujian Province also target the adults and larvae of Japanese anchovy and the fishing season generally starts in February (Jiang and Zheng 1984). All the simulation migration routes match the fishing season and pass or stay in the area of Fujian Province's fishing ground. Only the individuals with migration routes in the La Niña years arrive at the western fishing ground (the coastal water of Tamsui) of Taiwan before the end of February, while no tracer reaches Ilan Bay (eastern fishing ground around Taiwan) in any simulation (Fig. 10).

Our results demonstrate the advantage of the biological-physical model in testing the possible migration routes affected by different circulation patterns and clarify the important environment factors that orient the swimming direction of anchovies. Although the previous study suggest that strong thermal front is the key factor that orient anchovies to cross the TS (Tu *et al.* 2012), the most important factor that lead anchovies to arrive at the coastal water of Tamsui is the "U" shape branch current from the CCC in this study. It demonstrates the necessity of using the realistic data to drive hydrodynamic model and the dynamic of circulation is the critical factor that

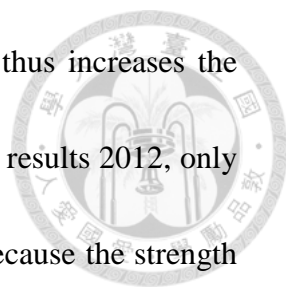


determine the success in the spawning migration of Japanese anchovy. Only anchovies that cross the TS could have chance to arrive the spawning areas around the Taiwan. Occurrence of the "U" shape branch current from the CCC in the central TS is the only pathway that anchovies can take to cross the central TS which is almost dominated by northward currents during early spring. The "U" shape branch current from the CCC usually occurs when both the stronger CCC and weaker northward SCSWC and KBETC occur (Fig. 9). This means the strength of CCC is important for migration of Japanese anchovy, but the dynamic of circulation in TS is the direct factor influencing the success rate of anchovy arrival at the coastal water of Taiwan. The strong CCC and the weak northward currents are manipulated by the strong EAWM, which cannot be presented in climatology data. Thus, the realistic data show the value in this study.

According to figure 14, the sensitivity analysis of the particle-released starting date clearly distinguish how the strength of CCC and the circulation patterns in the TS affect the migration process of Japanese anchovy. The results suggest two things: First, if the northward currents dominant the TS, the Japanese anchovies will face the huge obstacle in their migration process. Meanwhile, the circulation patterns in TS is the main reason that lead adult Japanese anchovies to arrive at the coastal waters of Taiwan more easily in La Niña years compared with El Niño years. Second, when the



circulation patterns in the TS are suitable for adult anchovies to cross the central Taiwan Strait, the stronger CCC aids adult anchovies that had already caught the CCC have higher chance to arrive at their spawning ground around Taiwan. The number of tracers released at January 5th arrived at the coastal water of Taiwan is higher in the La Niña years, but there is no significant difference in El Niño years. In the sensitivity test, the CCC was stronger to adult anchovies in sensitivity test for all years, but the circulation patterns in the TS mainly manipulated by the EAWM is no significant different to the original result. The results suppose that the appropriate circulation patterns in the TS is the necessary condition for Japanese anchovies to arrive at their spawning area around Taiwan, and anchovies will have difficulty to cross the central TS when the northward currents dominate the whole area (e.g. the El Niño years: 2003, 2007, and 2010). The results in La Niña years shows a good agreement that the CCC strength increases the fluxes of Japanese anchovy populations migrating toward the coastal water of Taiwan. The tracers released at January 5th were transported by the stronger CCC in first 15 days compared to the tracers released at January 1st. The reason that the CCC got stronger gradually before January 15th in every year is because that our model does not have not enough time to spin up to stable before January 15th. In our model, the strength of Changjiang outflow increases day after days before January 15th, which is caused by the unstable state of Changjiang. The



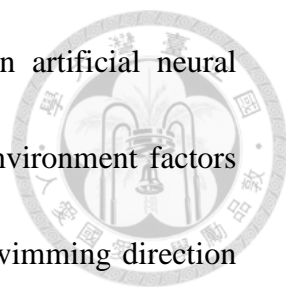
strong CCC aids more adult anchovies to enter into the TS, and thus increases the individuals to arrive at the coastal water of Taiwan. However in the results 2012, only a few more individuals that arrived at the spawning area. This is because the strength of CCC is stronger in 2012 than other La Niña years, and most tracers in 2012 that cannot arrive at the spawning ground are those tracers that cannot followed the CCC in the original simulation; as such, the effect of CCC is not significant in the result in 2012.

Although the currents play the key factor that determine whether anchovies can cross the TS, the temperature gradient is also important to aid anchovies to find the spawning ground. In this study, we also design another fish behavior model that anchovies only swim along with the current to clarify the mechanism of orientation of Japanese anchovy. Comparing the results based on different fish behavior models (Figs. 15a-b), the trajectory differences indicate that the adult anchovies are mainly oriented by the currents in most time in the model results, but follow the temperature gradient after the individuals cross the TS and temperature gradient can lead anchovies to find the spawning ground more preciously.

In our results, no tracer reaches Ilan Bay in any case, suggesting that either the biological or the physical model needs improvements. Focusing on the area of Northern Taiwan, the circulations in our hydrodynamic models show a eastward

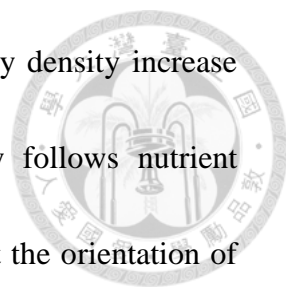
coastal current follow the northern coastal of Taiwan (Figs. 16a-c), which is consistent with empirical observations (Tang *et al.* 2000), and temperature in the Pacific Ocean is higher than the TS. The coastal current and the temperature gradient may facilitate anchovies to reach the Ilan Bay (east spawning ground) from the TS. However, no tracer catches the coastal current due to the distance between the tracers and the coast, indicating the biological model needs to be improved.

Although our biological models may catch the key factors that orient the Japanese anchovies in the migration process, this primitive model seems to oversimplify fish biology. Previous studies on capelin and cod (Huse *et al.* 2004), Japanese sardine (Okunishi *et al.* 2009) and Icelandic capelin (Barbaro *et al.* 2009) showed other approaches that consider different factors to construct the swimming behavior of migratory fish. The research of capelin and cod in the Barents Sea (Huse *et al.* 2004) used an individual-based model to describe fish swimming behavior, and coupled it with observed temperature distribution. In fish swimming behavior model, movement patterns contained the stochastic movement and the directed movement, the directed movement was determined before each simulation and was independent from the environment cues, and threshold temperature activated the directed movement. The research partially captured the spatial dynamics of both species. The model study of Japanese sardine in the western North Pacific (Okunishi *et al.* 2009)



used the bioenergetics model, a genetic algorithm (GA), and an artificial neural network (ANN) to simulate the migration of Japanese sardine. Environment factors (e.g. day length, temperature and solar orientation) affected the swimming direction which was determined by ANN. ANN requires observation data for the training process, so sufficient data are necessary for this kind simulation of migration. The research of capelin in the Iceland Sea (Barbaro *et al.* 2009) used the observed temperature and constant current data as environment information, and the capelins were oriented by temperature gradient and capelins adjusted their swimming direction due the position or swimming direction of neighboring capelins. Notably, the swimming speed regulated by anomaly temperature gradient and fish schooling were considered.

In our biological models, temperature gradient is the factor that orients anchovies when they are close to coastal Taiwan; however, many other factors can influence migration of Japanese anchovy, including the ecosystem components (lower trophic levels), bioenergetics of fish or nutrient distribution. The research on European anchovy in Mediterranean that included a bioenergetics growth model linked with a lower trophic level ecosystem model reproduces the growth and many biological processes of European anchovy (Politikos *et al.* 2011). Besides temperature, foraging is another important factor affecting the swimming direction of fishes. The prey



distribution profoundly affects the location of spawning; high prey density increase the larval growth rate and survival rate, and the prey density follows nutrient distribution. The simulation models shows that nutrients can affect the orientation of Japanese sardine (Okunishi *et al.* 2009). Using the models considering nutrients may lead more anchovies to follow with the CCC, and the anchovies that cross the TS also have higher chance to arrive at the coastal area of northwestern Taiwan (i.e. Tamsui river estuary). Moreover, the anchovies may move closer to the Tamsui river estuary, which may lead them to have a higher chance to catch the current which bypasses the northern tip of Taiwan and goes eastward, and later arrive at Ilan Bay. In addition, we used constant swimming velocity in our models, while the field observation showed that the ability of adjusting swimming speeds play an important role in the spawning migration of salmon (Hinch and Bratty 2000). This suggests that the ability of adjusting swimming speed is as important as the orientation, and it should be considered in the future models. Although a model that includes ecosystem components, bioenergetics of fish and improvements of fish swimming behavior may reproduce better on the spatial-temporal dynamics of Japanese anchovy, our primitive model can still clearly present the possible mechanism that ENSO affects the population dynamic of Japanese anchovy and provide information for fisheries management.

Conclusion

This study shows ENSO can profoundly affect the circulation patterns in the ECS and Taiwan Strait, which in turn affects the spawning migration of Japanese anchovy. Specifically, the EAWM decreased in the El Niño years, and caused the dominance of the northward current in the TS and weakened the CCC in the ECS. The strong EWAM in La Niña years lead to a circulation pattern that aided the anchovies to migrate cross the TS. The results suggests that the adult Japanese anchovies have a higher chance to arrive at the spawning ground near the coast of Taiwan in La Niña years. Consider ENSO effects on the recruitment of Japanese anchovy is necessary for fishery management policy. Accumulating evidence indicates that large-scale environmental variations have caused fluctuations of marine populations (Barber and Chavez 1986, Philander *et al.* 1989, Mantua and Hare 1997, Di Lorenzo *et al.* 2008). In fact, studies have indicated fluctuations of marine populations are better predicted by large-scale climate patterns than local factors (Stenseth *et al.* 2003). The dynamics of complex patterns in the climate can affect ecological factors in both direct and indirect pathways (Stenseth *et al.* 2003). Thus, we suggest that understanding the mechanisms underlying how large-scale climate affects populations can enhance the accuracy of predictions of marine ecosystems, which is needed for management policy (Ottersen *et al.* 2010).





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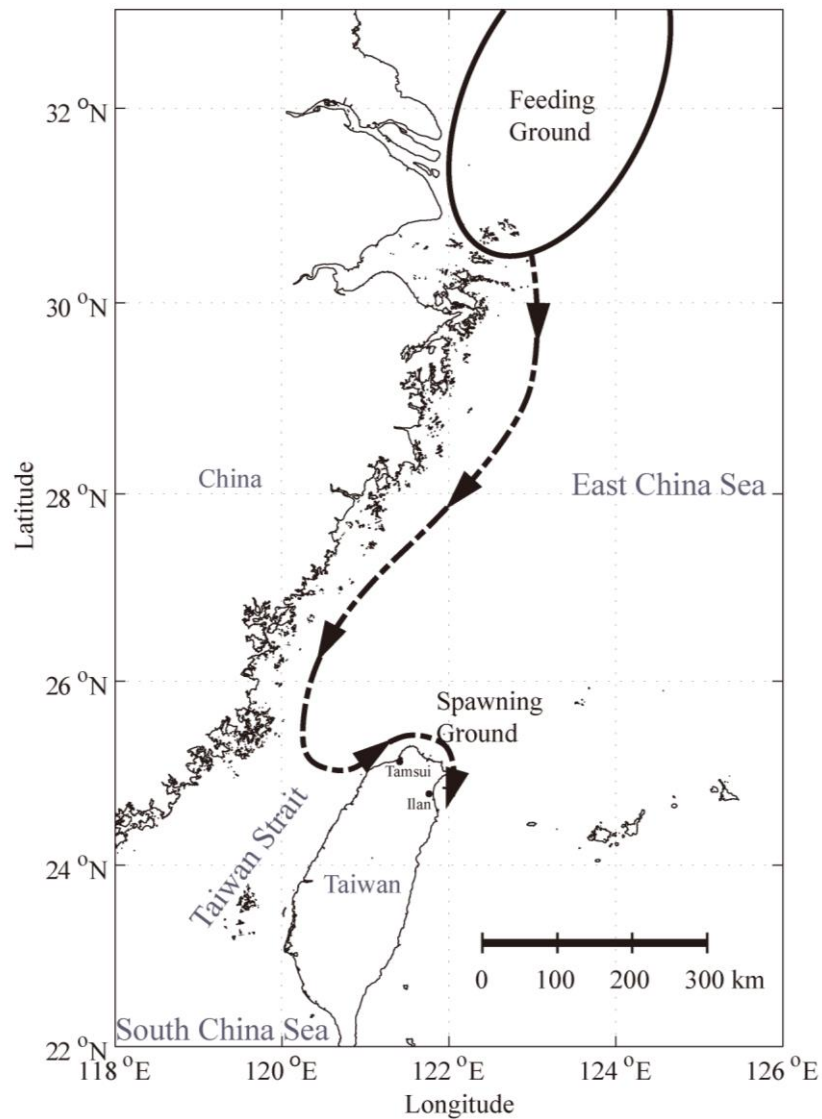


Figure 1. Hypothetical spawning migration route of Japanese anchovy from the coastal area nearby the Yangtze River mouth to the coastal area of Taiwan. Adult anchovies follow the China Coastal Current into the Taiwan Strait, and cross the Taiwan Strait to arrive at the coastal area of northern Taiwan. Tamsui and Ilan coastal areas are known spawning grounds.

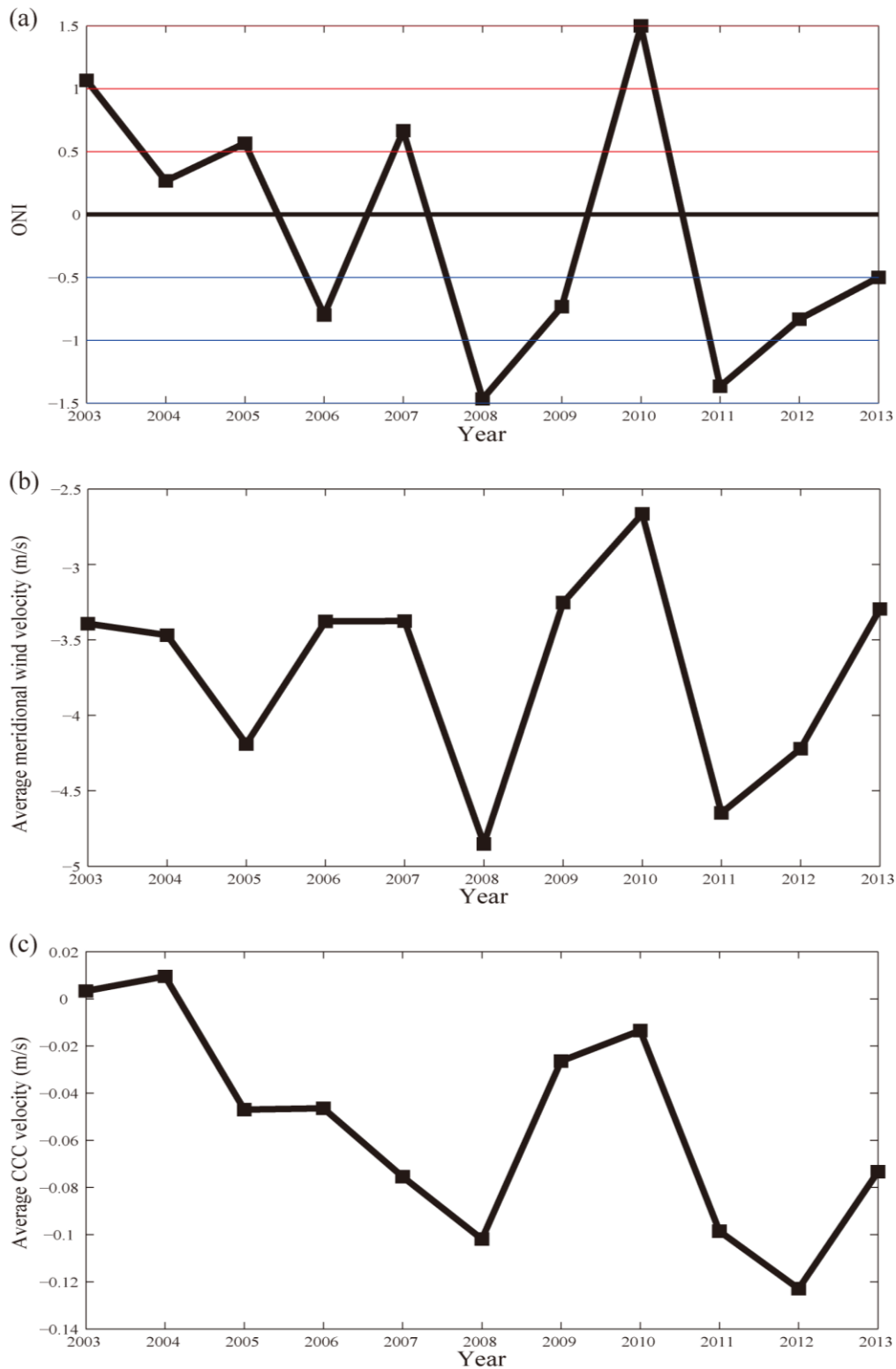


Figure 2. The historical data of (a) Oceanic Niño Index (ONI), (b) Averaged meridional wind velocity and (c) the averaged velocity of China Coastal Current, where positive values indicate southward flows. Plotted are averaged data from January to February.

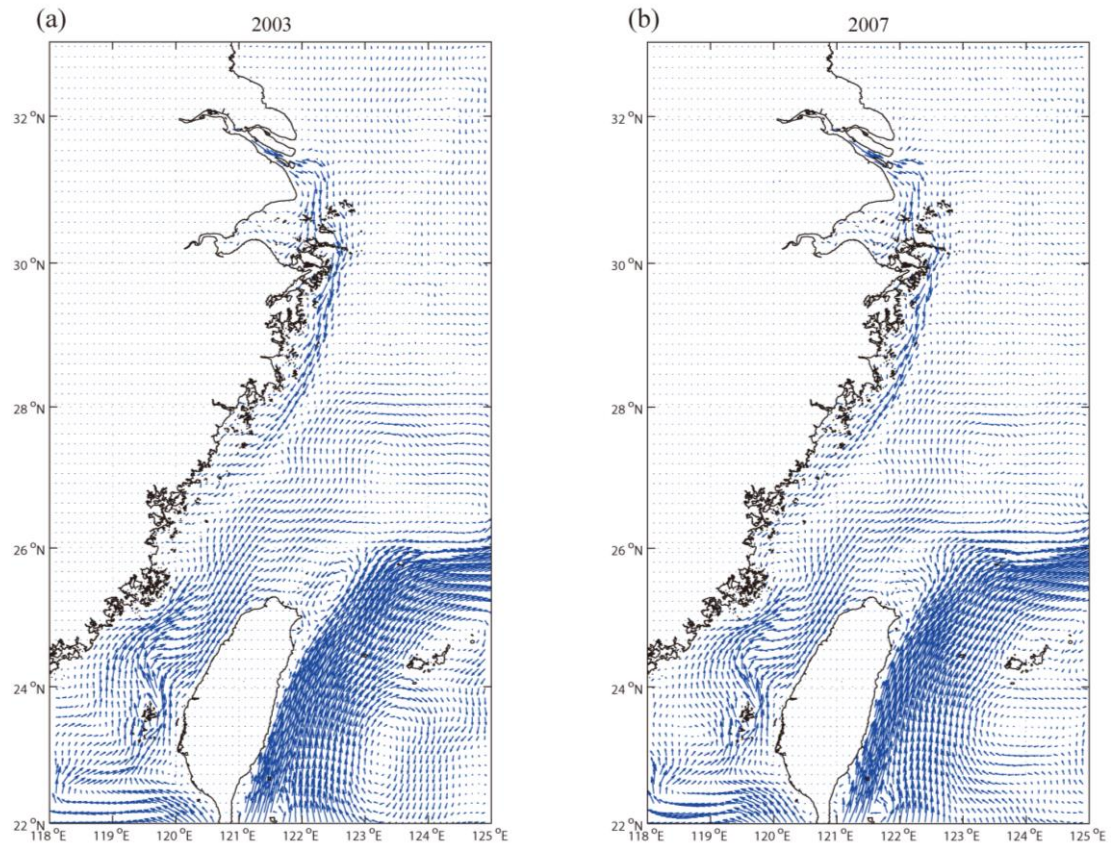


Figure 3. Model results of near-surface (averaged from 1 to 5 m) current velocity in the East China Sea averaged from January to February for (a) 2003, strong El Niño, and (b) 2007, moderate El Niño.

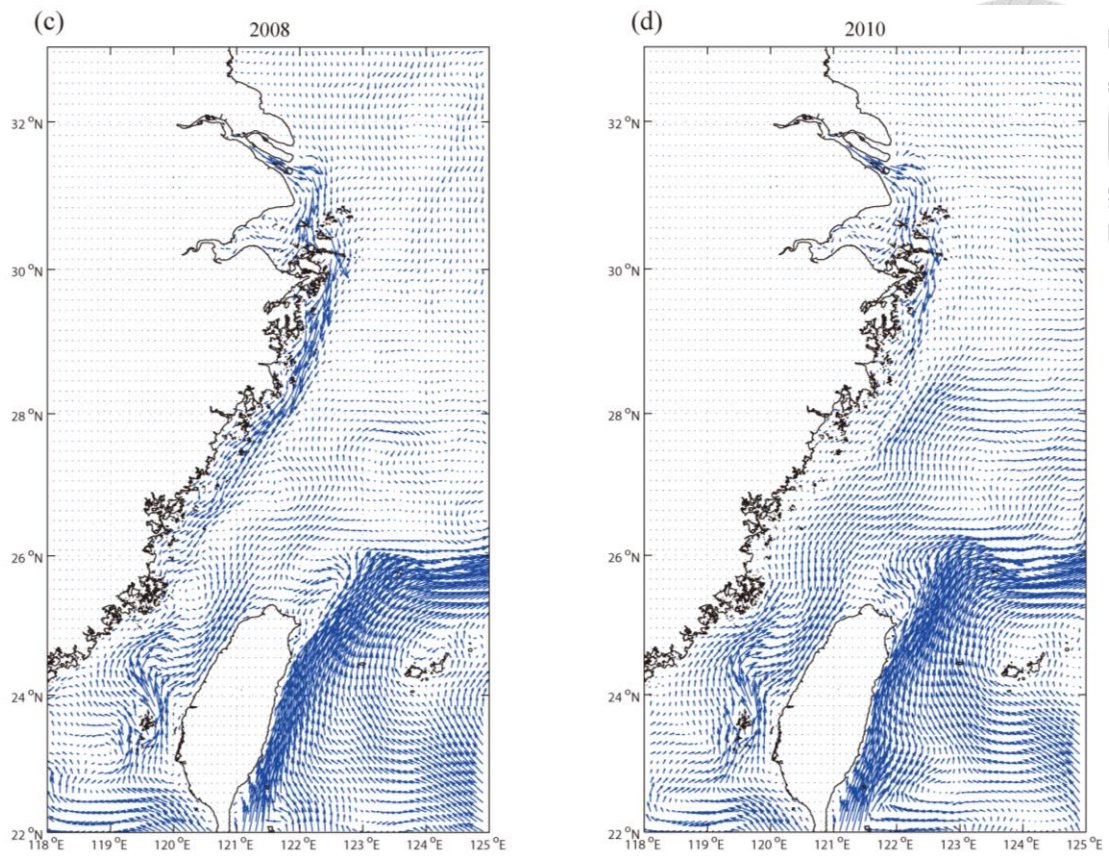


Figure 3 (continued). Model results of near-surface (averaged from 1 to 5 m) current velocity in the East China Sea averaged from January to February for (c) 2008, strong La Niña and (d) 2010, strong El Niño.

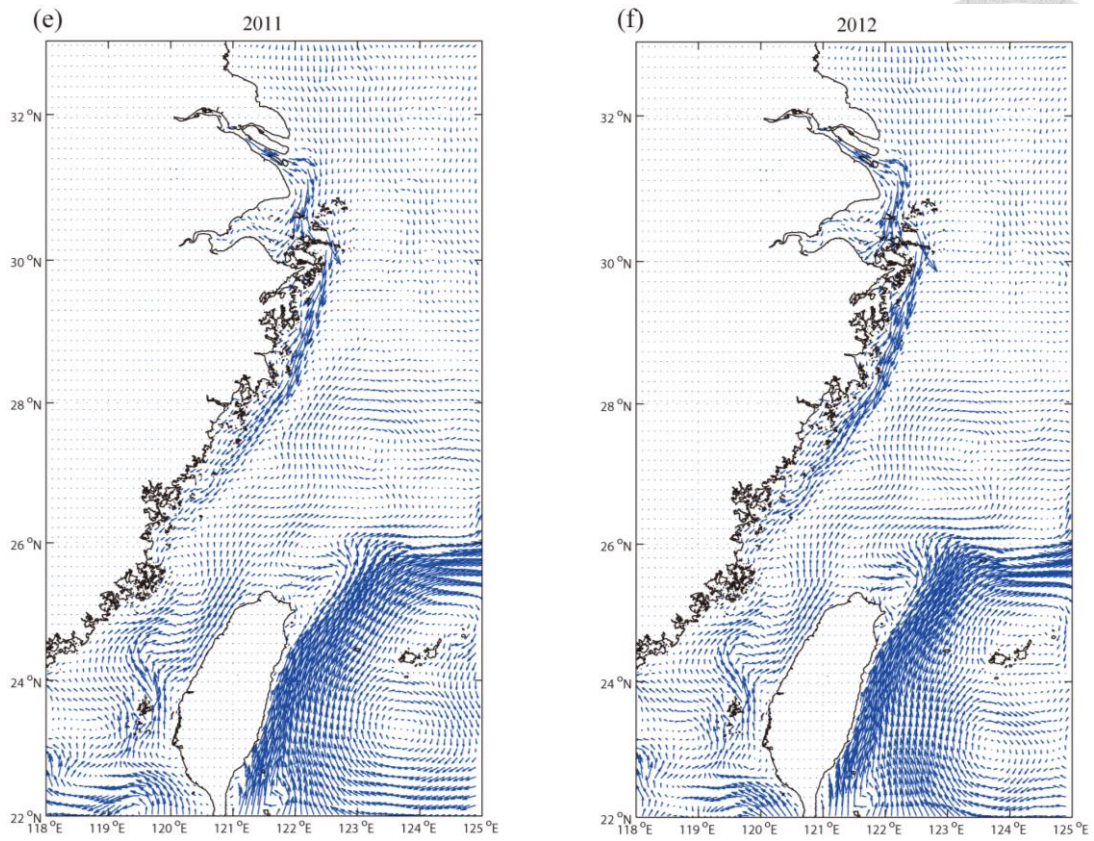


Figure 3 (continued). Model results of near-surface (averaged from 1 to 5 m) current velocity in the East China Sea averaged from January to February for (e) 2011, strong La Niña and (f) 2012, moderate La Niña.

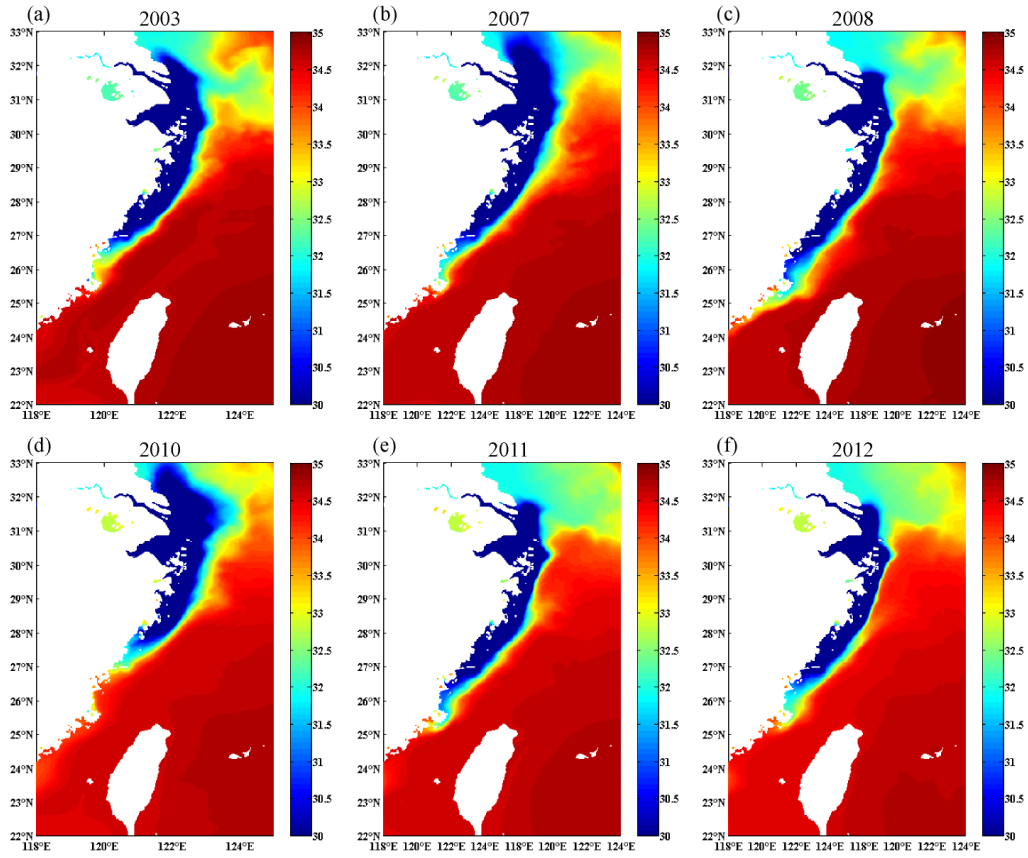


Figure 4. Model results of near-surface (averaged from 1 to 5 m) salinity distribution in the East China Sea averaged from January to February for (a) 2003, strong El Niño, (b) 2007, moderate El Niño, (c) 2008, strong La Niña, (d) 2010, strong El Niño, (e) 2011, strong La Niña, and (f) 2012, moderate La Niña.

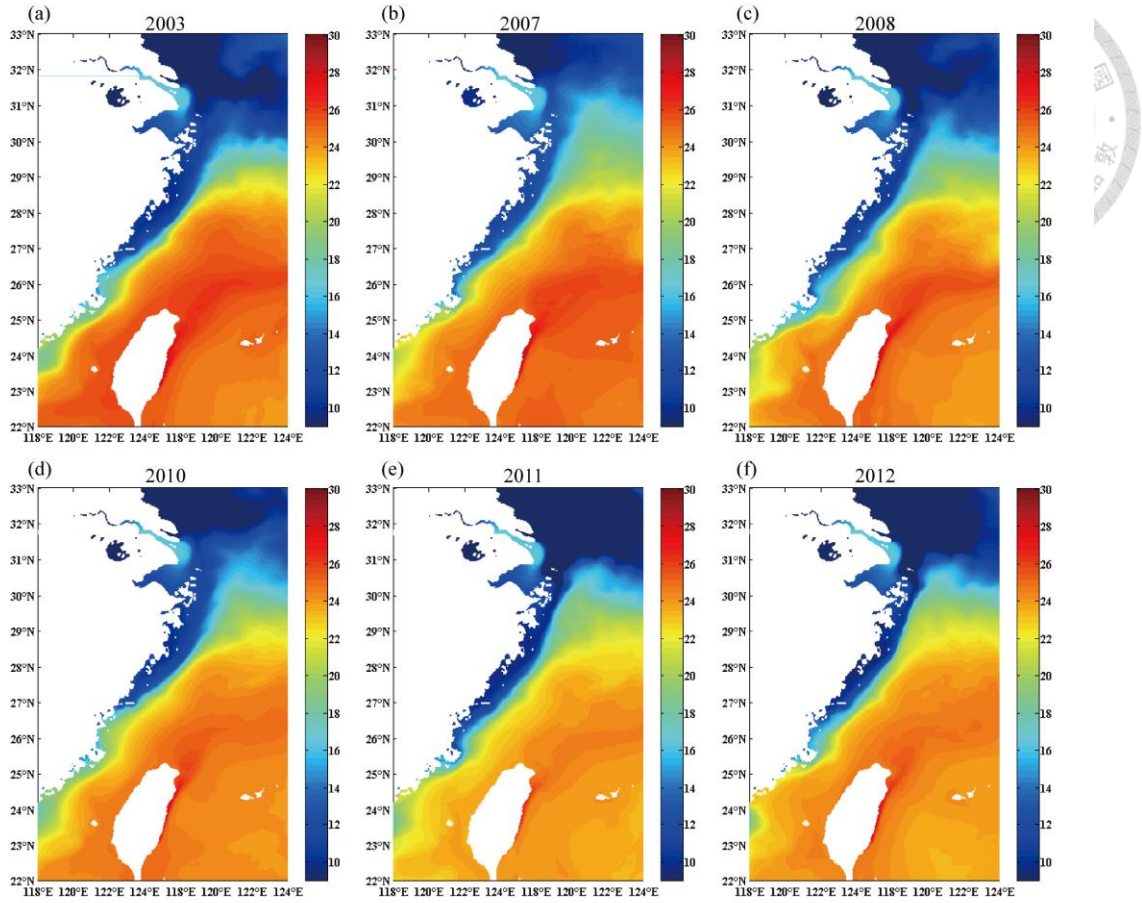


Figure 5. Sea surface temperature (averaged from 1 to 5 m) in the East China Sea averaged from January to February for (a) 2003, strong El Niño, (b) 2007, moderate El Niño, (c) 2008, strong La Niña, (d) 2010, strong El Niño, (e) 2011, strong La Niña, and (f) 2012, moderate La Niña.

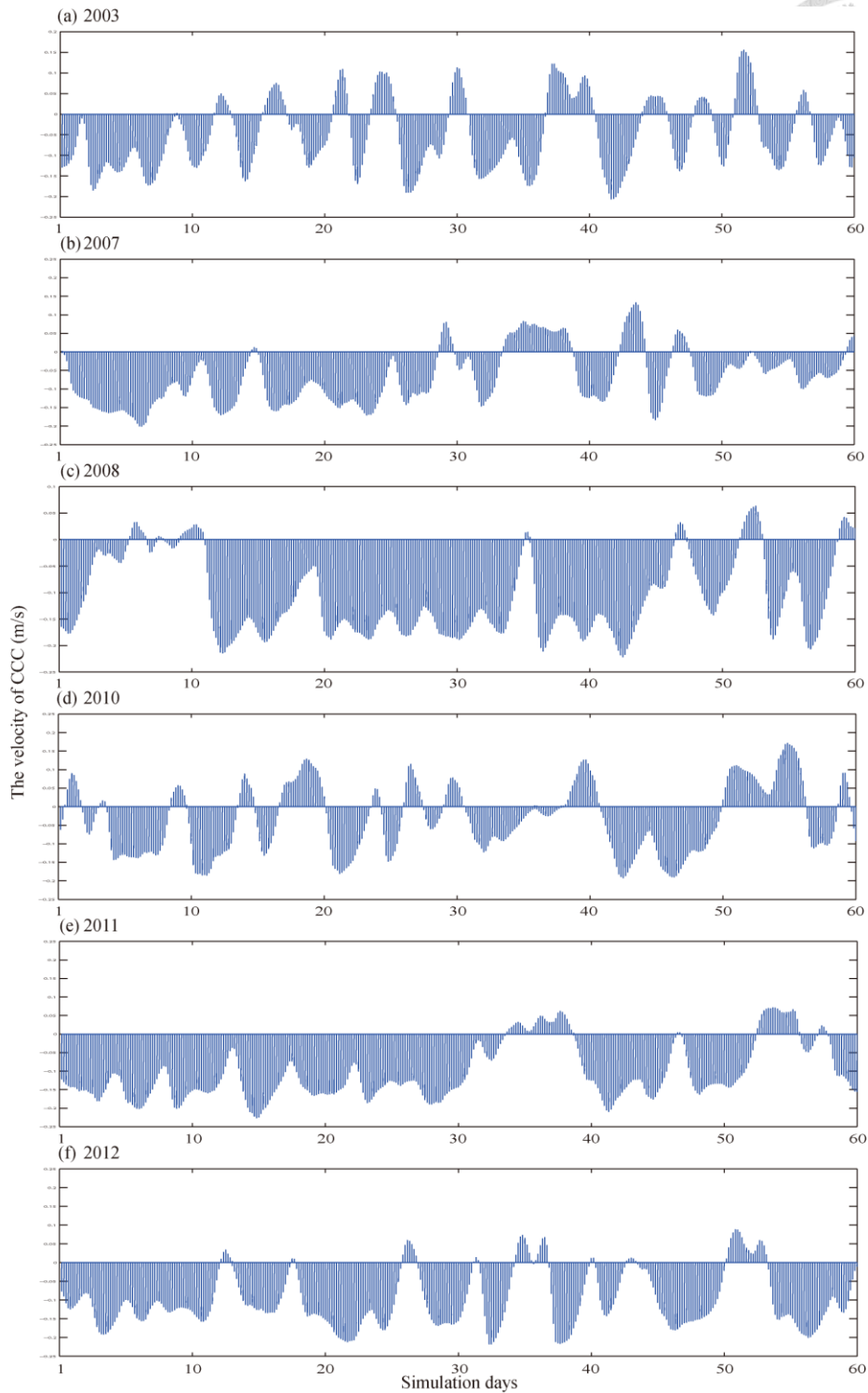


Figure 6. Model results of the velocity and the direction of the current in the coastal area of Mainland China (the location of the CCC) starting from January 1st for (a) 2003, strong El Niño, (b) 2007, moderate El Niño, (c) 2008, strong La Niña, (d) 2010, strong El Niño, (e) 2011, strong La Niña, and (f) 2012, moderate La Niña. The negative values indicate southward flows.

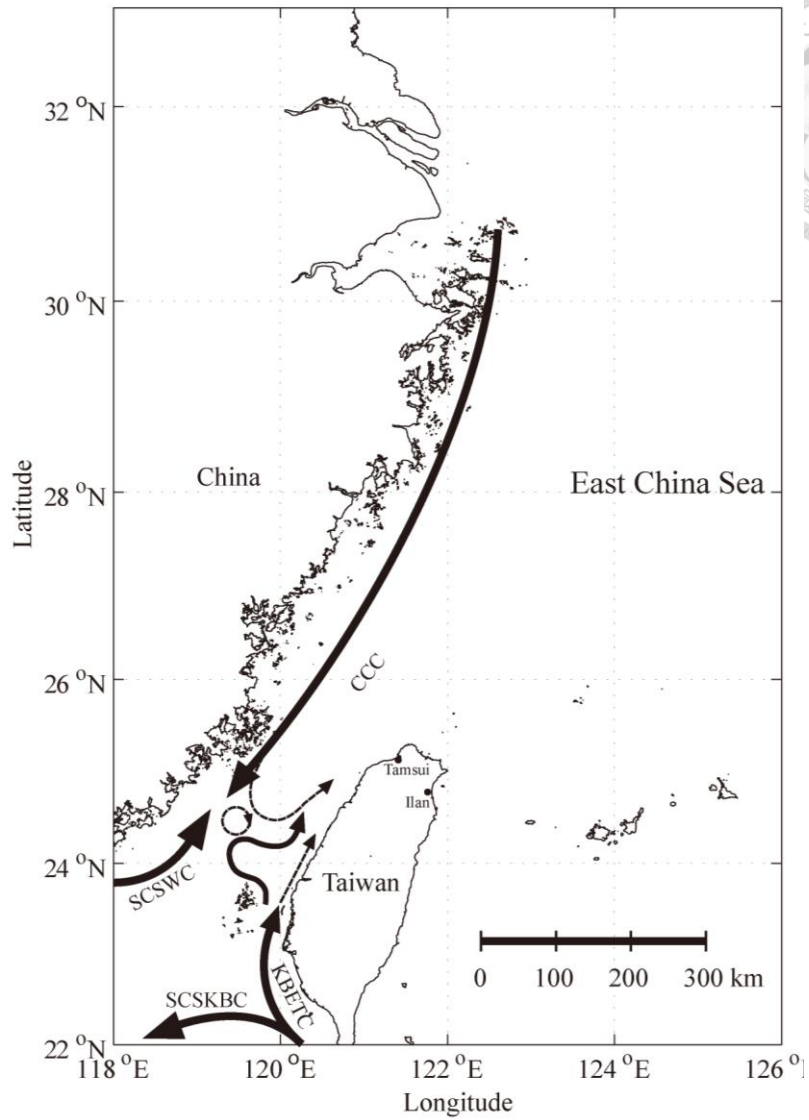


Figure 7. The general circulation pattern in the hydrodynamic model in Winter. CCC, China Coastal Current; SCSWC, South China Sea Warm Current; KBETC, Kuroshio Branch Current along with the coast of Taiwan in the Taiwan Strait; SCSKBC, Kuroshio Branch Current to the South China Sea.

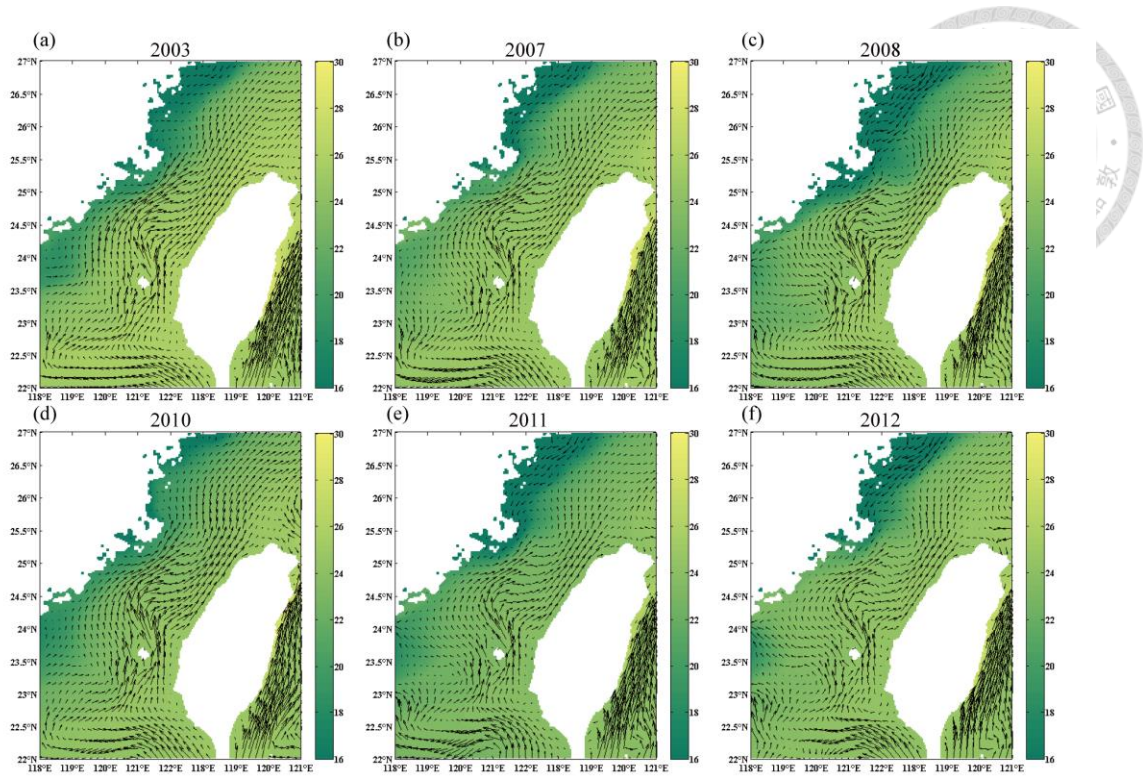


Figure 8. Near-surface (averaged from 1 to 5 m) current velocity and SST in the Taiwan Strait averaged from January to February in year (a) 2003, strong El Niño, (b) 2007, moderate El Niño, (c) 2008, strong La Niña, (d) 2010, strong El Niño, (e) 2011, strong La Niña, and (f) 2012, moderate La Niña.

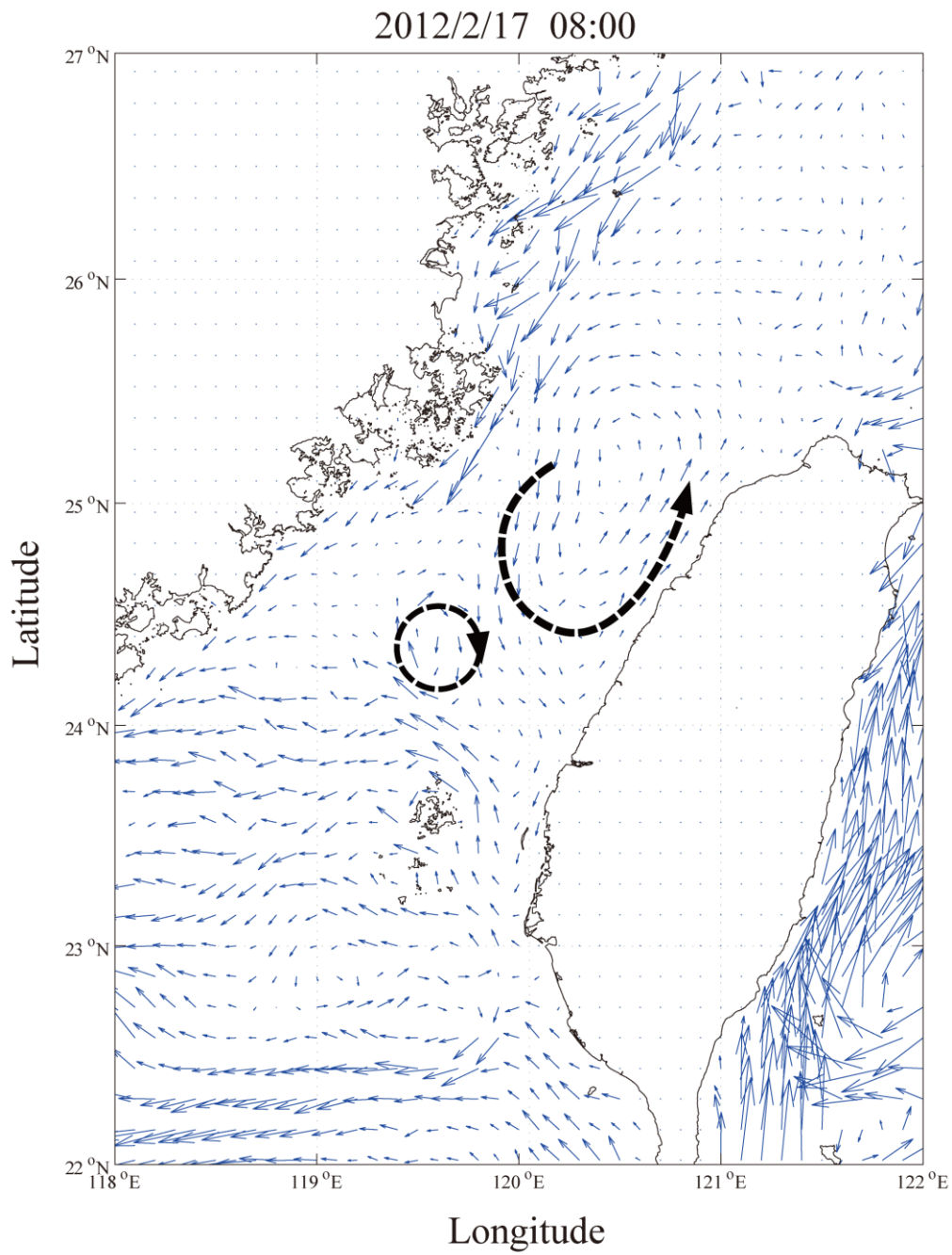


Figure 9. Schematic illustrating the "U" shape current in the central of Taiwan Strait and the anticyclonic eddy in the northwestern area of Changyun Rise generated from the hydrodynamic model.

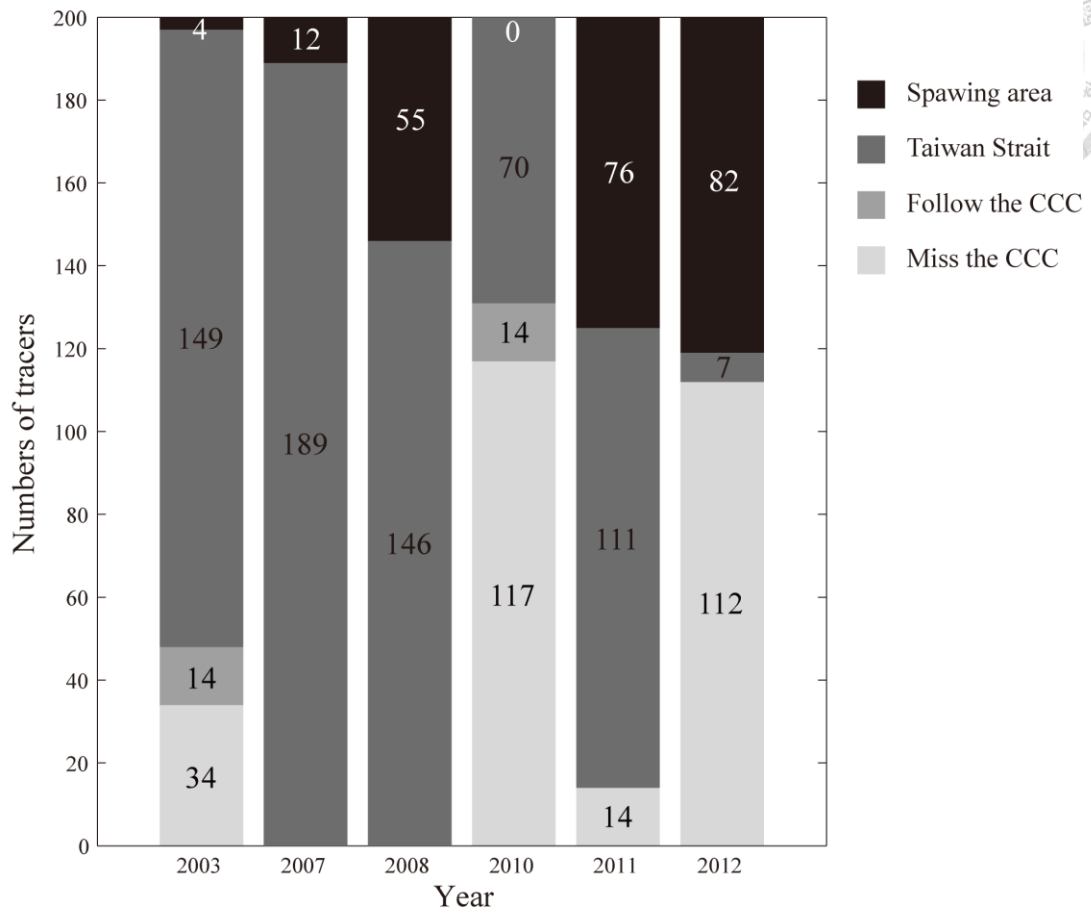


Figure 10. Variation in final destinations of the tracers in the end of simulations among years.

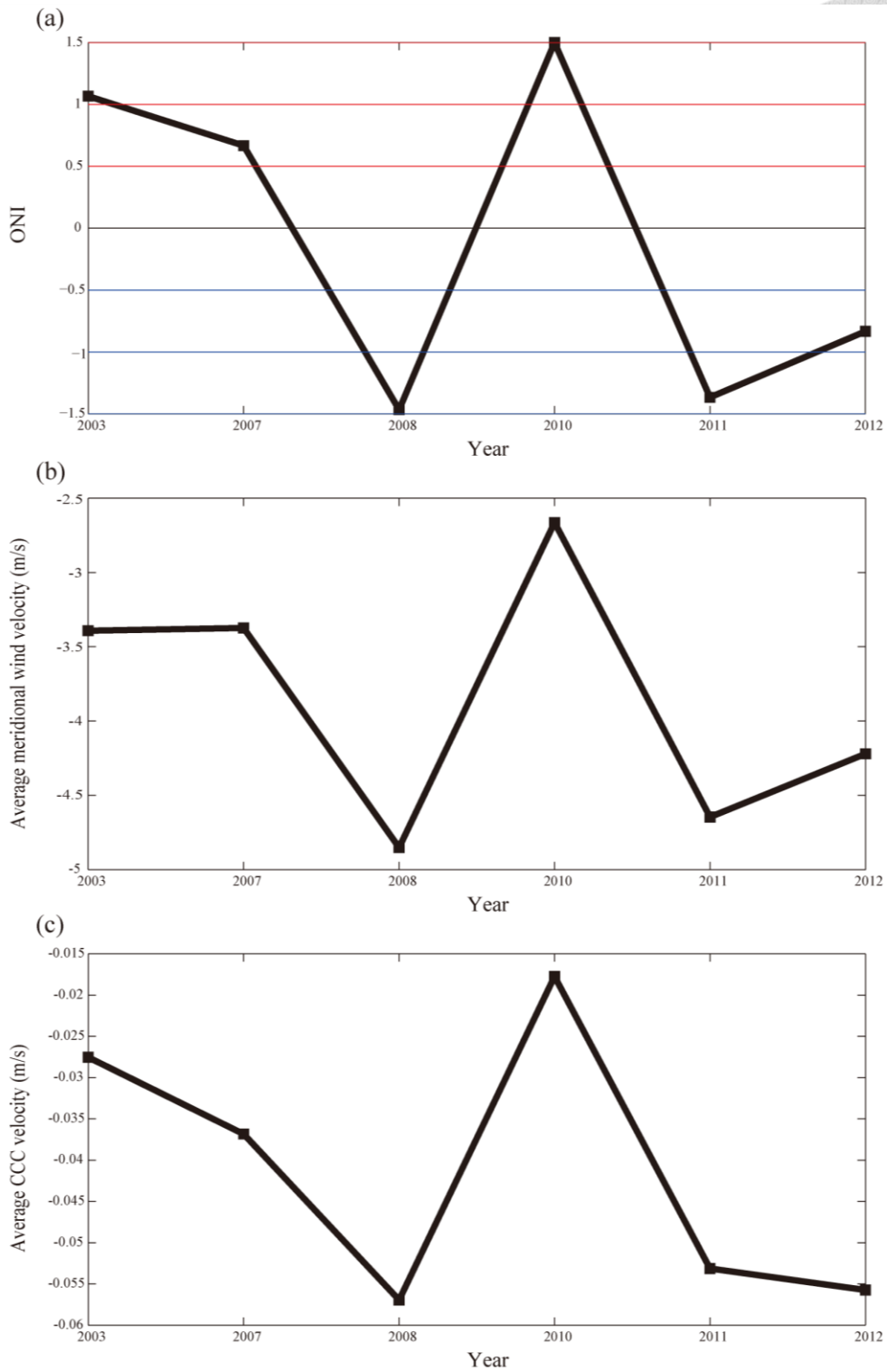


Figure 11. The simulation results of the strength variation of the CCC from ROMS, and it has positive correlation with ONI and EAWM. (a) ONI, (b) meridional wind velocity and the simulation results for (c) the averaged velocity of China Coastal Current from January to February.

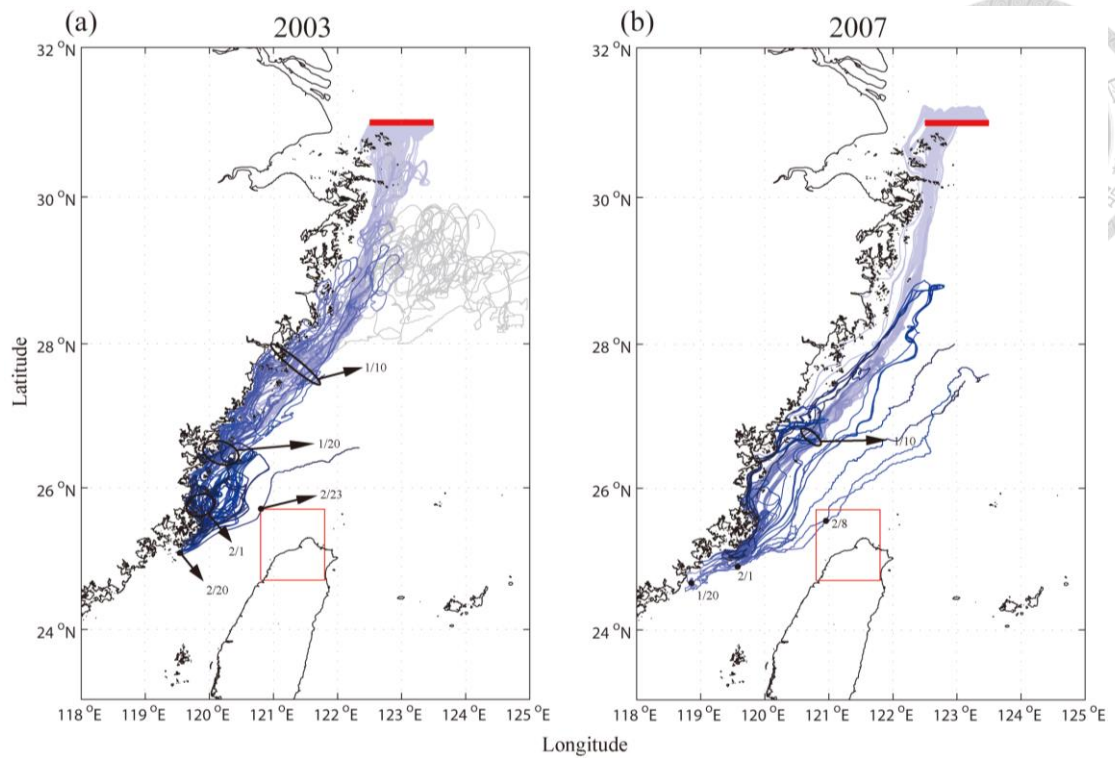


Figure 12. The tracer trajectories in year (a) 2003, strong El Niño and (b) 2007, moderate El Niño. The heavy red line represents the starting location. The red rectangular enclosed the area deemed as successful arrival of Japanese anchovy in this study, which is defined as the 50 kilometers around the Tamsui river estuary. Color of trajectories indicates time of simulation, with darker color representing later stages. The gray trajectories represent the tracers that miss the CCC.

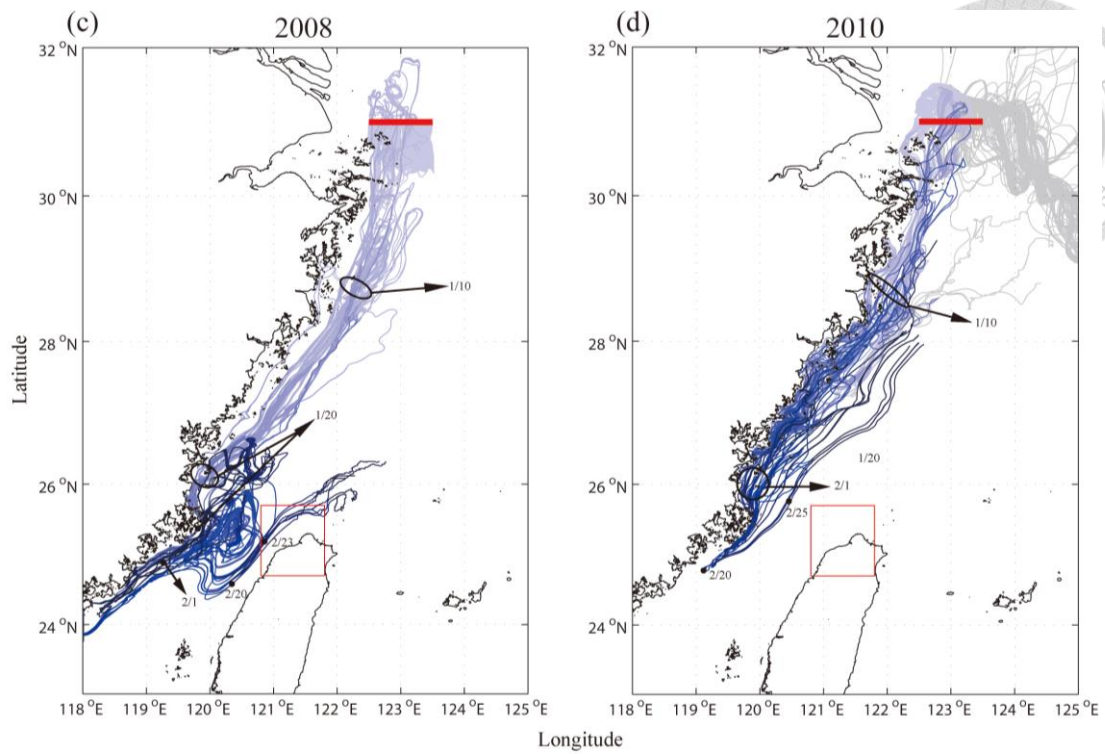


Figure 12 (continued). The tracer trajectories in year (c) 2008, strong La Niña and (d) 2010, strong El Niño. The heavy red line represents the starting location. The red rectangular enclosed the area deemed as successful arrival of Japanese anchovy in this study, which is defined as the 50 kilometers around the Tamsui river estuary. Color of trajectories indicates time of simulation, with darker color representing later stages. The gray trajectories represent the tracers that miss the CCC.

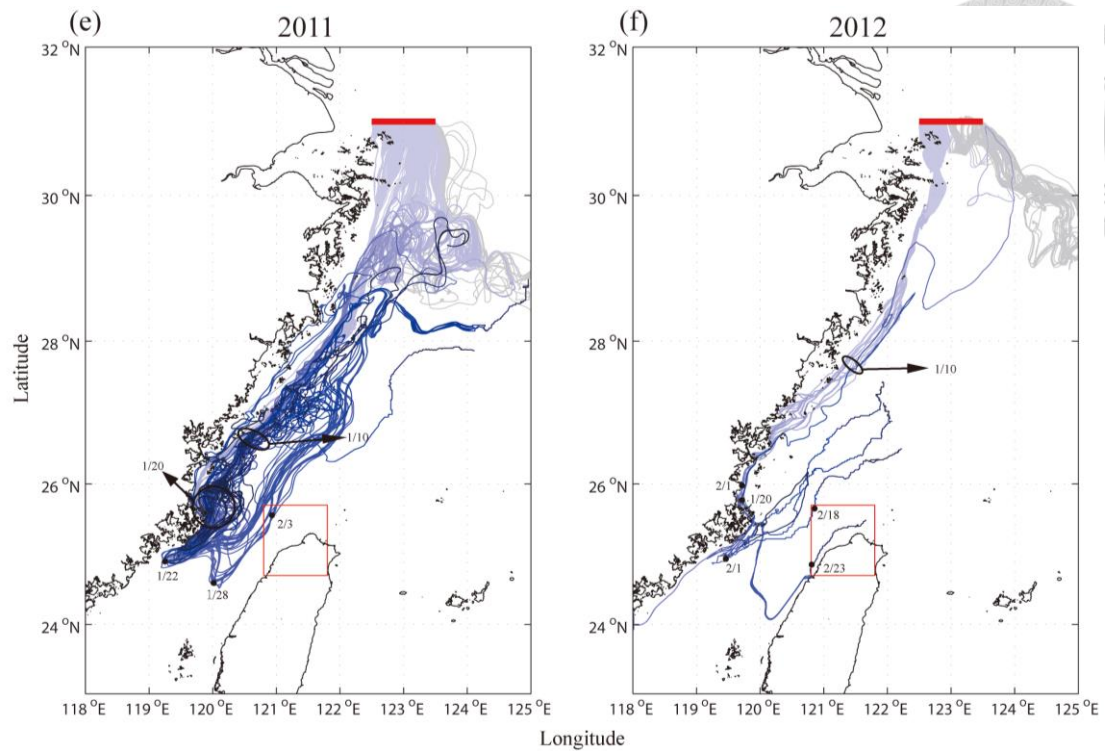


Figure 12 (continued). The tracer trajectories in year (e) 2011, strong La Niña and (f) 2012, moderate La Niña. The heavy red line represents the starting location. The red rectangular enclosed the area deemed as successful arrival of Japanese anchovy in this study, which is defined as the 50 kilometers around the Tamsui river estuary. Color of trajectories indicates time of simulation, with darker color representing later stages. The gray trajectories represent the tracers that miss the CCC.

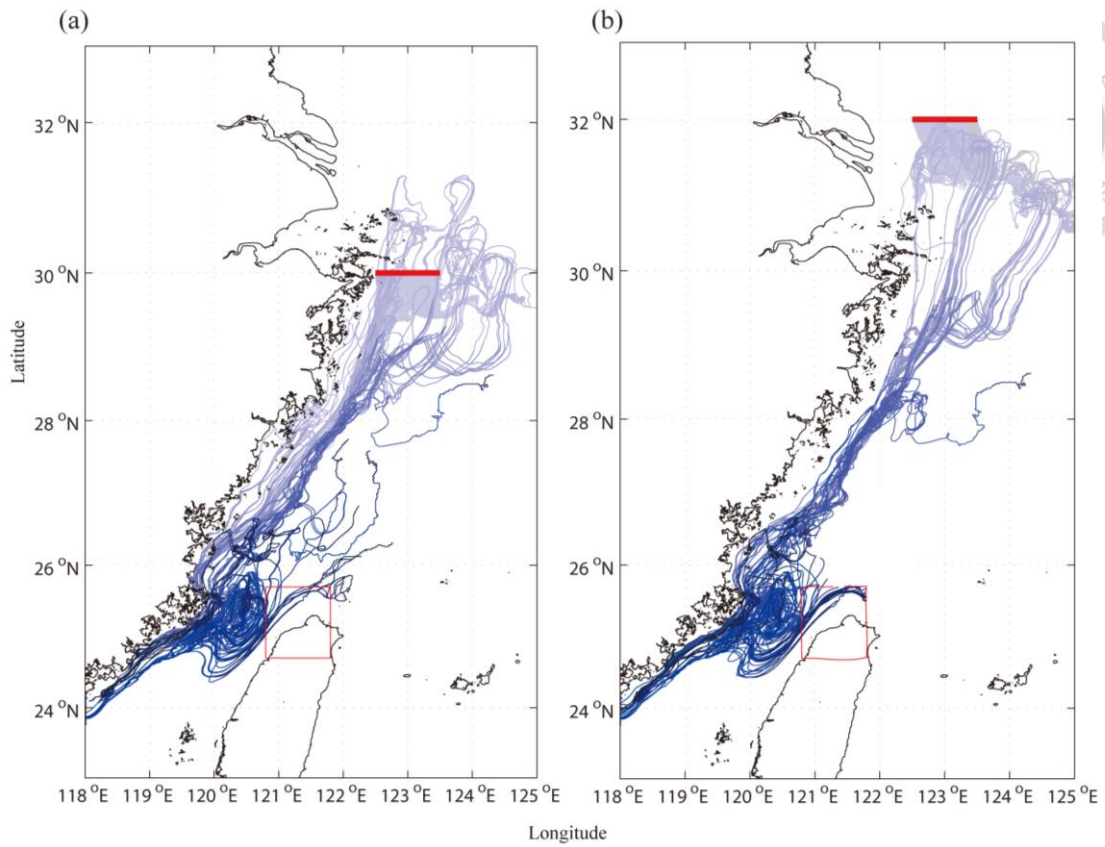


Figure 13. The tracer trajectories with different initial locations, using the results of 2008 as an example: (a) 30°N and (b) 32°N. The heavy red line represents the starting location. The red rectangular enclosed the area deemed as successful arrival of Japanese anchovy in this study, which is defined as the 50 kilometers around the Tamsui river estuary. Color of trajectories indicates time of simulation, with darker color representing later stages.

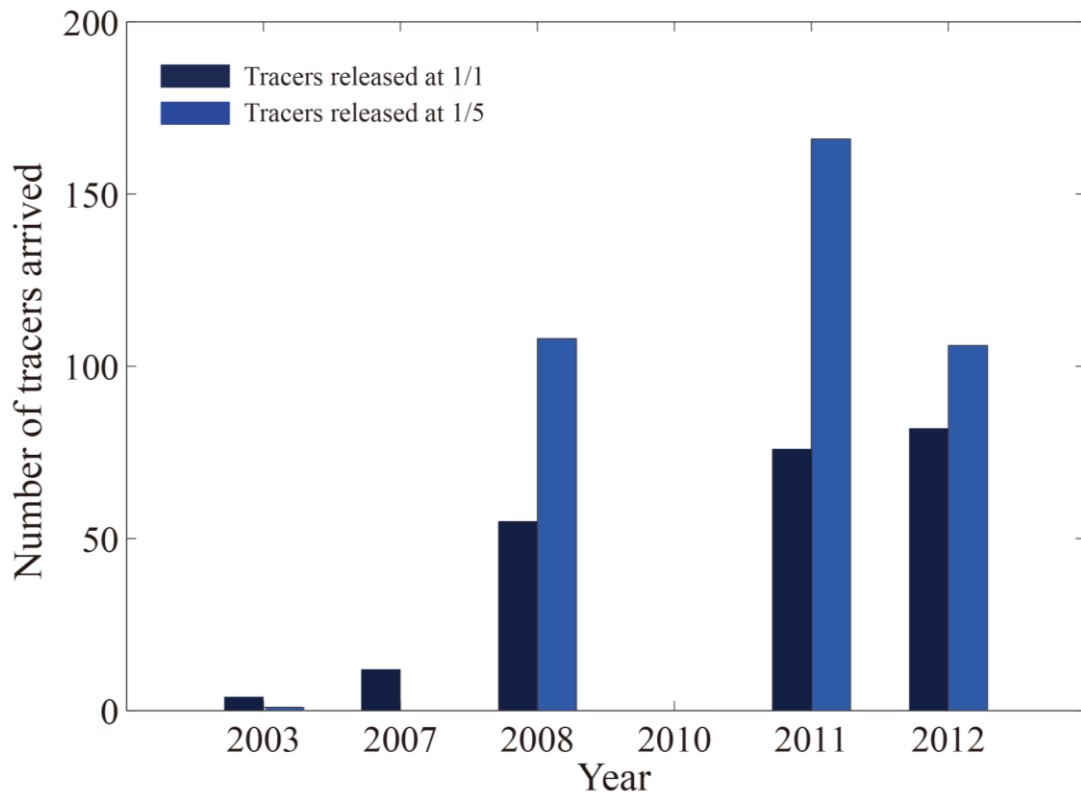


Figure 14. Summary statistics of simulations with different initial days.

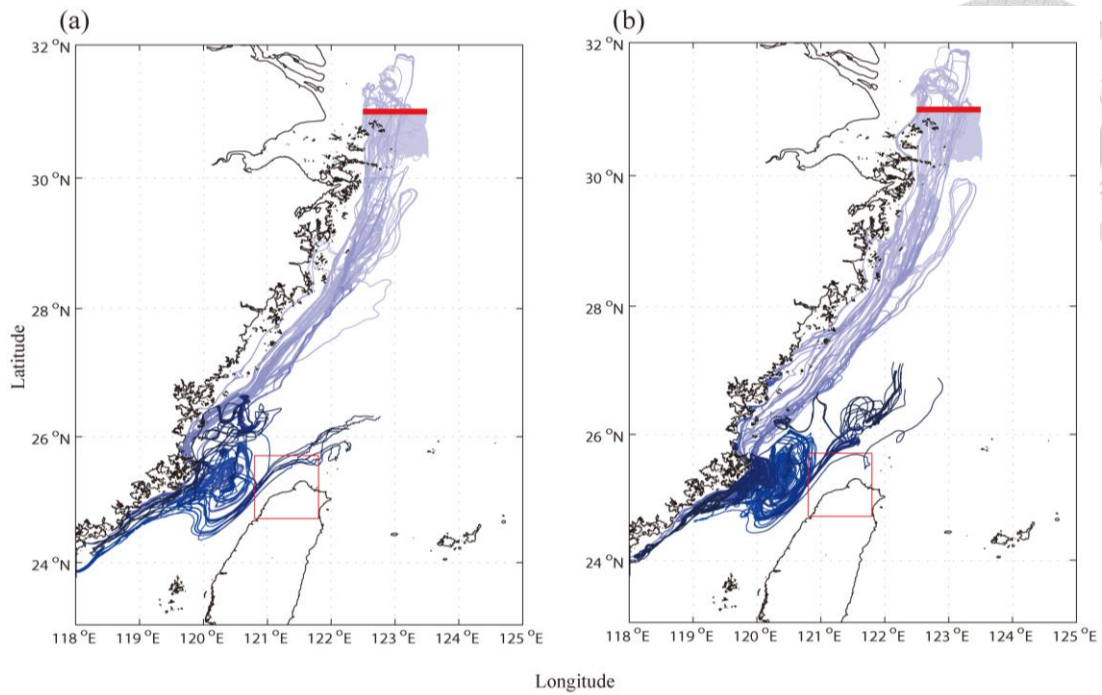


Figure 15. The tracer trajectories from different modeling scenarios, using the results of 2008 as an example: (a) anchovies swim along with the current but change their behavior to follow the temperature gradient when sense the threshold temperature, and (b) anchovies only swim along with the current. The heavy red line represents the starting location. The red rectangular enclosed the area deemed as successful arrival of Japanese anchovy in this study, which is defined as the 50 kilometers around the Tamsui river estuary. Color of trajectories indicates time of simulation, with darker color representing later stages.

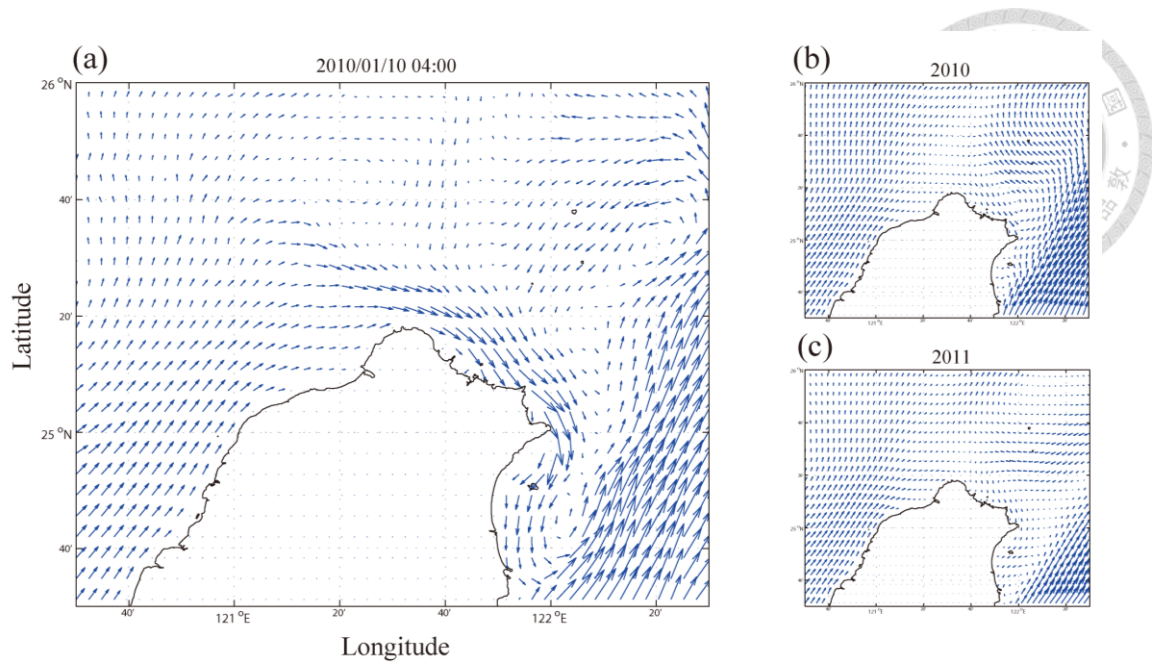


Figure 16. The current along with the northern coastal of Taiwan, which flows eastward in most time. (a) A snap shot at 2010/01/10, 04:00, (b) the two month average circulation in 2010 and (c) two month average circulation in 2011.