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Linkages between the biomass of *Scomber japonicus* and net primary production in the southern East China Sea

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Abstract

Fish biomass is a critical component of fishery stock assessment and management and it is often estimated from ocean primary production (OPP). However, the relationship between the biomass of a fish stock and OPP is always complicated due to a variety of trophic controls in the ecosystem. In this paper, we examine the quantitative relationship between the biomass of chub mackerel (*Scomber japonicus*) and net primary production (NPP) in the southern East China Sea (SECS), using catch and effort data from the Chinese mainland large light-purse seine fishery logbook and NPP derived from remote sensing. We further discuss the mechanisms of trophic control in regulating this relationship. The results show a significant non-linear relationship exists between standardized CPUE (Catch-Per-Unit-Effort) and NPP (*P*<0.05). This relationship can be described by a convex parabolic curve, where the biomass of chub mackerel increases with NPP to a maximum and then decreases when the NPP exceeds this point. The results imply that the ecosystem in the SECS is subject to complex trophic controls. We speculate that the change in abundance of key species at intermediate trophic levels and/or interspecific competition might contribute to this complex relationship. **Key words:** southern East China Sea, net primary production, *Scomber japonicus*, biomass

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1 Introduction

Fish biomass is a critical component of fishery stock assessment and management and it is often estimated from ocean primary production (OPP) by using trophic dynamic models that assume bottom-up control (Pauly and Christensen, 1995; Lu et al., 2000; Wang et al., 2005; Friedland et al., 2012). However, the relationship between fish biomass and OPP is always complicated by the various types of trophic control such as top-down or waspwaist control (Frank et al., 2005; Ji et al., 2010; Ware and Thomson, 2005; Bakun, 2006). Therefore, a better understanding of trophic linkages between OPP and fish biomass is critical to fisheries stock assessment and management. Trophic linkages are especially relevant given recent trends towards ecosystem-based fisheries management (Pikitch et al., 2004), because they can be used to illustrate an ecosystem's state and its carrying capacity, which is critical to maintaining sustainable exploitation and for developing more parsimonious ecosystem models (Chassot et al., 2007).

The chub mackerel (*Scomber japonicus*) in the southern East China Sea (SECS) is an important fishery resource and is intensively exploited by the light-purse seine fisheries from China (including Taiwan), Japan and Korea. Since this stock is overfished and subject to overfishing, it is urgent to conduct fishery stock assessment and develop a rational fishery management plan to keep this resource sustainable (Cheng and Lin, 2004; Li et al., 2011). Trophic dynamic models are incorporated into chub mackerel stock assessment (Lu et al., 2000). However, there are great uncertainties in the results, because the assumptions of bottom-up control and a positive relationship between OPP and fish biomass that are implicit in these models may be violated and in-situ OPP that have limitations in temporal and spatial scale are often used (Lu et al., 2000; Vernet and Smith, 2007).

Remote sensing of ocean color provides an effective method for deriving OPP (Forget et al., 2007) and a reasonable estimation of OPP based on different algorithms has been available since a new era of ocean color remote sensing was initiated by the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) mission in 1997 (Acker et al., 2002; Forget et al., 2007; Friedland et al., 2012). Relative to in-situ measures of OPP, remote sensing provides a consistent method for estimating OPP at high temporal resolution, over large areas and long time periods (Vernet and Smith, 2007). The long-term and large-scale satellite-acquired OPP data provide an opportunity to examine the dynamics of fish biomass with regard to trophic control mechanisms in the ecosystem (Friedland et al., 2012).

In this study, we use chub mackerel commercial catch and effort data from the Chinese mainland large light-purse seine fishery logbook and net primary production (NPP) derived from remote sensing to examine linkages between the biomass of chub mackerel and NPP on chub mackerel fishing grounds in the SECS and we discuss the mechanisms of trophic control in this ecosystem. Studying trophic linkages is expected to

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improve our knowledge of the ecosystem and help guide chub mackerel stock assessment and fishery management.

2 Materials and methods

2.1 Fisheries data

Commercial catch and effort data for chub mackerel from 1998 to 2012 are from the Chinese mainland large light-purse seine fishery logbook. The names of fishing vessels, fishing locations, date, catch and the number of hauls are recorded in the data. The fishing effort of this fishery in offshore waters of the East China Sea was distributed south of 30°N along the shelf break frontal area from 1998 to 2004, but since 2005 there has been some effort north of 30°N. Therefore, to make CPUE (Catch-Per-Unit-Effort) and area fished comparable throughout the time series, we established a study area in the SECS based on fishing locations from 1998 to 2004 (Fig. 1). The study area represents the center of fishing activities for the time series and covers the main chub mackerel spawning, nursery and fishing grounds in the region (Hiyama et al., 2002; Yukami et al., 2012).

2.2 Net primary production data

NPP products, which are derived from SeaWiFS and MO-DIS (Moderate Resolution Imaging Spectroradiometer) data using the VGPM (Vertically Generalized Production Model) algorithm, were acquired from Oregon State University (http:// www.science.oregonstate.edu/ocean.productivity/). The temporal resolution of NPP products is monthly and the spatial resolution is $10' \times 10'$. The SeaWiFS-based NPP is available from 1998 to 2007 and MODIS-based NPP from 2003 to 2012.

2.3 Data processing

2.3.1 Fisheries data processing

CPUE is calculated as follows:

$$CPUE_{y,m,l,g} = \frac{C_{y,m,l,g}}{F_{y,m,l,g}},$$
(1)

where $C_{y,m,l,g}$ and $F_{y,m,l,g}$ are the catch and number of hauls in year *y*, month *m* and lunar calendar *l* for fishing company *g*. To improve the CPUE and make it as a better proxy for biomass (Maunder and Punt, 2004), it is standardized using a generalized linear model (GLM) as follows:

$$\eta(u) = y + g + l + l^2, \qquad (2)$$

$$u = E(CPUE_{v,m,l,g} + 1.0), \qquad (3)$$

where η is the link function and *E* is the expectation. The error structure of the GLM is assumed to follow a gamma distribution (Guan, 2008). The product of the CPUE standardization is the year effects estimated by the model. The year effect for 1998 is set at 1.0 and the standardized CPUE for all other years is relative to this baseline value.

In order to evaluate the results of the CPUE standardization, nominal CPUE (NCPUE) is defined as:

$$NCPUE_{y} = \frac{C_{y}}{F_{y}},$$
(4)

where C_{v} and F_{v} are the total catch and total hauls in year y.

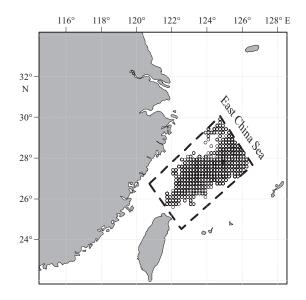


Fig.1. Study area and fishing locations of the Chinese mainland large light-purse seine fishery in the southern East China Sea from 1998 to 2012.

2.3.2 Net primary production data processing

The monthly total NPP (MNPP) in the study area is calculated as:

$$MNPP_{y,m} = \sum_{i \subseteq F_{\Lambda}} NPP_{y,m,i} S_i D_m , \qquad (5)$$

where S_i is the area of the pixel *i*, D_m is the number of days in month *m*, $NPP_{y,m,i}$ is the NPP of pixel *i* in month *m* and year *y*, and F_A is the study area in Fig. 1.

The monthly total NPP is summed over months, resulting in a yearly total NPP (YNPP) using Eq. (6).

$$YNPP_{y} = \sum_{m=1}^{12} MNPP_{y,m}$$
 (6)

A comparison of the two types of MNPP data, which were derived respectively from SeaWiFS and MODIS and overlapped from 2003 to 2007, shows a systematic deviation. Therefore, the MODIS-based MNPP can not be used directly to extend the SeaWiFS-based YNPP time series by Eq. (6). To account for this deviation, a linear relationship between the two data sets is estimated. Using this linear relationship and MODIS-based MNPP, we extend the SeaWiFS-based YNPP time series from 2007 to 2012.

2.3.3 Polynomial regression analysis

We use polynomial regression to examine the relationship between SeaWiFS-based YNPP and standardized CPUE. The level of significance is set at 0.05.

3 Results

3.1 Standardized CPUE

The year effects estimated by the GLM are all significant (P<0.001) and indicate much year-to-year variability in the

biomass of the stock (Fig. 2). Although there exists a significant linear correlation between standardized and nominal CPUE (r=0.98, P<0.001; Fig. 2), there is a relatively large difference between the two CPUEs in 1998.

3.2 The YNPP time series

There was a significant linear relationship between Sea-WiFS-based and MODIS-based MNPPs across the overlapping years (*P*<0.001; Fig. 3). Using this linear relationship, the MO-DIS-based MNPPs from 2008 to 2012 are adjusted to the Sea-WiFS scale and a complete SeaWiFS-based YNPP time series

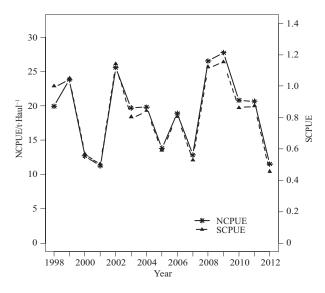


Fig.2. The yearly fluctuation of standardized CPUE (SCPUE) and nominal CPUE (NCPUE).

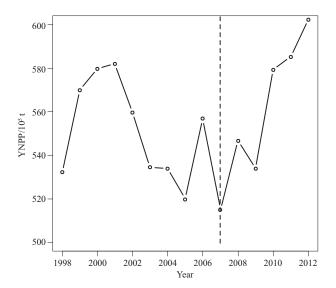


Fig.4. Yearly net primary production in the study area (YNPP). Data to the left of the dashed line was derived from SeaWiFS data, and to the right of the dashed line was estimated from MODIS data according to the linear relationship.

from 1998 to 2012 is obtained (Fig. 4). Figure 4 shows the considerable interannual variability in YNPP.

3.3 Relationship between YNPP and standardized CPUE

There was no significant linear relationship between standardized CPUE and YNPP (P>0.05). However, YNPP has a significant quadratic polynomial relationship with standardized CPUE (P<0.01). The relationship can be described by a convex parabolic curve, where the biomass of chub mackerel increases with NPP to a maximum and then decreases when the NPP exceeds this point (Fig. 5).

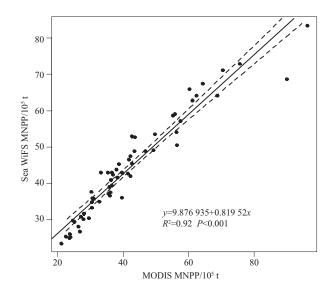


Fig.3. Linear relationship between monthly net primary productivity in the study area (MNPP) based on SeaWiFS and MODIS data. Dashed lines were 95% confidence interval for the regression line.

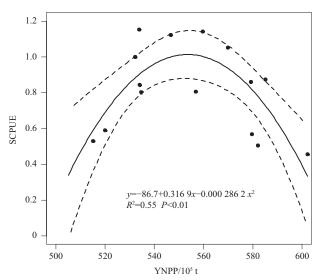


Fig.5. Yearly fishing area net primary production (YNPP) plotted against standardized CPUE (SCPUE). Dashed lines were 95% confidence interval for the regression line.

4 Discussion

4.1 CPUE standardization

Because the fishing efficiencies of various companies are different and moon phase has considerable effects on catch (Guan, 2008), we use a GLM to standardize CPUE to remove those effects, stabilize catchability, and create a standardized CPUE that is a sufficient proxy for the biomass of chub mackerel (Maunder and Punt, 2004). Other variables were also considered for inclusion in the GLM (e.g., sea surface temperature and month), but they did not statistically improve the standardization model, and so are not used.

Although moon phase has a considerable effect on the fishing efficiency, it does not describe much interannual variability in catchability because the distribution of fishing effort in each phase of the moon is similar for each year. Thus, its influence is limited on year effects. Catchability, however, fluctuates yearto-year due to the presence or absence of particular fishing companies. For example, the fishing efficiency of the Liaoning Ocean Fishery Company is high (Guan, 2008), but the company did not operate in the area in 1998 which probably reduced the nominal CPUE in that year. Correspondingly, the biomass of the fish stock would be underestimated by the nominal CPUE. The standardized CPUE accounts for these differences in catchability (Fig. 2), thus we prefer to use this index for the analyses.

4.2 Satellite-derived net primary production

Many different algorithms are used to estimate NPP from remote sensing data (Friedland et al., 2012). We used NPP estimated by the VGPM algorithm (Behrenfeld and Falkowski, 1997), because we believe it provides a better estimate given the high sea surface temperature (SST) in the study area (Behrenfeld and Falkowski, 1997; Feng et al., 1999). The 6th order polynomial employed by the VGPM algorithm that describes the relationship between the maximum photosynthetic rate and temperature exhibits a peak near 20°C, followed by a decline with further increases in temperature. This functional relationship is suitable in regions of high SST. Although increasing temperature usually increases photosynthesis, high temperatures are often associated with nutrient limitations that inhibit phytoplankton growth (Behrenfeld and Falkowski, 1997; Forget et al., 2007; Wang et al., 2008). Also, increasing temperature can increase the respiration of phytoplankton and limit the accumulation of photosynthetic products. Guan et al. (2005) used this polynomial to estimate ocean primary production off China and achieved good results. Further, the results from Friedland et al. (2012) also show the VGPM algorithm to have higher estimation accuracy in the higher temperature water.

Since the sensors on satellites are never exactly the same, the products vary by satellite (Fig. 3). As such, in order to use data from multiple satellites in the same analyses, an algorithm needs to be developed to correct the systematic difference between sensors. Typically there is a good relationship between measurements taken by different satellites in the same region, and in this study we are able to accurately correct the difference between SeaWiFS-based and MODIS-based MNPPs (Fig. 3).

4.3 Dynamics of biomass of chub mackerel

During the study period, there are two continuously increasing segments in the YNPP time series: one from 1998 to 2001 and the other from 2009 to 2012 (Fig. 4). Correspondingly, the standardized CPUE decreases from 1.00 in 1998 to 0.50 in 2001 and from 1.15 in 2009 to 0.46 in 2012. Fishing mortality is not likely to have caused this cyclical fluctuation in the biomass of chub mackerel, since fishing effort is not correlated to the cycle of the biomass over this period (Guan, 2008; Li et al., 2011). As such, the fluctuation in the biomass of chub mackerel is more likely to be controlled by the environment and the convex parabolic relationship between the biomass and net primary production shows how the trophic linkages within this ecosystem affect the dynamics of this fishery resource. Other research also shows the changes in the oceanic ecological environment such as regime shifts (Hwang, 1999; Hiyama et al., 2002; Yatsu et al., 2005; Guan et al., 2011) have an important influence on the biomass dynamics of chub mackerel, but the specific links that control these relationships are not yet well understood.

Although we show here that environment directly influences the biomass dynamics of chub mackerel, this is not to say that fishing does not affect the population. Fishing, in addition to removing the chub mackerel biomass, also truncates the age and size structure of the population (Cheng and Lin, 2004). Shifting the structure of the population towards younger and smaller individuals can reduce the capacity of the population to resist environmental change and make the population more susceptible to dramatic fluctuations in abundance (Hsieh et al., 2006). Despite the intense fishing pressure, chub mackerel has a high reproductive capacity (Zheng et al., 2003) and so the stock can recover quickly, as long as the environment is suitable. However, given a recent rapid increase in the number of bag light seine vessels (commonly known as the "triangle tiger" purse seiners) in combination with an unfavorable ecological environment, the fishery is at risk of collapse. We suggest fishing effort should be reduced quickly to help mitigate this risk.

4.4 Mechanisms of trophic control on chub mackerel fishing grounds in the SECS

In ocean ecosystems, phytoplanktons fix carbon dioxide into organic material by photosynthesis and consume organic carbon through respiration. Net primary production is the gross photosynthetic carbon fixation minus the carbon respired to support the maintenance requirements of phytoplankton, and it is the total organic matter directly or indirectly used by heterotrophic organisms. Variability in net primary production can propagate up the food chain and affect population dynamics at all trophic levels (Hunter and Price, 1992). When the availability of food resources regulates all food-web components, the ecosystem is said to be under "bottom-up" control. If, on the other hand, predation controls the system it is termed "topdown" control and upper food-web components regulate the population dynamics of the lower components through trophic cascades (Pace et al., 1999; Frank et al., 2005). Similarly, a number of key species at intermediate trophic levels can dominate food web dynamics through "waspwaist" control (Cury et al., 2000). The type of trophic control depends on the ecosystem state, diversity and integrity (Hunter and Price, 1992; Chassot et al., 2007).

Chub mackerel feed mainly on crustaceans, primarily *Euphausia pacifica*, copepods and amphipods, followed by fish like sardines, anchovies and small squids (Zheng et al., 2003; Zhang, 2005). The value of the chub mackerel's trophic level is 3.55 relative to a value of 1.0 for phytoplankton (Zhang and Tang, 2004). Considering the position of chub mackerel in the

food web, it is difficult to presume that the increase in net primary production is caused by a reduction in the chub mackerel biomass, i.e., through top-down control. Therefore, we think it more likely that a change in the abundance of key species at intermediate trophic levels or perhaps interspecific competition is responsible for the convex parabolic relationship.

Some studies indicate predatory competition between chub mackerel and hairtail (Trichiurus haumela) in the East China Sea (Hong et al., 1997) or large jellyfish in the SECS (Jiang et al., 2010). Hairtail and chub mackerel have distinct optimal environmental windows (Cury and Roy, 1989; Hong et al., 1997). We analyzed the relationship between the spawning stock abundance of hairtail in the East China Sea (Xu et al., 2011) and the SCPUE in this study. The results show a significant negative correlation between the two species (Fig. 6, r=-0.65, P<0.05), which again provides evidence for the competitive relationship. Therefore, we hypothesize that the competition in combination with variations in net primary production might cause the convex parabolic relationship we found. Namely, when the net primary productivity on the chub mackerel fishing grounds increases but is still too low to favor hairtail or large jellyfish, the biomass of chub mackerel increases. However, with further increases in net primary production, the optimal environmental window shifts to favor hairtail and large jellyfish (Hong et al., 1997; Jiang et al., 2010) and their abundance increases, which restrains chub mackerel through competition and decreases the chub mackerel biomass (Hong et al., 1997; Jiang et al., 2010).

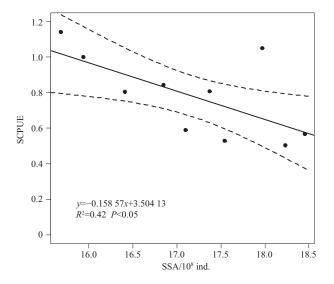


Fig.6. The relationship between standardized CPUE (SCPUE) and spawning stock abundance of hairtail (SSA). The data of spawning stock biomass of hairtail were from Xu et al. (2011). Dashed lines were 95% confidence interval for the regression line.

On the other hand, some studies show that when the abundance of phytoplankton reaches a certain level, negative feedback can operate between phytoplankton and zooplankton. For example, the relationships between the number of copepods and the abundance of diatoms or the dinoflagellate both indicate that feedback inhibition exists in the East China Sea (Xu et al., 2003; Xu, 2006). The negative feedback makes the abundance of zooplankton decrease with further increase of net primary productivity, subsequently reducing the abundance of pelagic fishes such as chub mackerel (Chen and Xu, 1990). At the same time, zooplankton is also expected to control the abundance of phytoplankton through a top-down interaction (Xu, 2006) and the abundance of chub mackerel through a bottom-up interaction (Chen and Xu, 1990). If so, the ecosystem is under waspwaist control and can result in the convex parabolic relationship. Because few studies have focused on long-term changes in the abundance and formation mechanisms of species composition of zooplankton in the SECS, it is difficult to further describe the impact of zooplankton on fluctuations of the biomass of chub mackerel. In addition, the relationship between net primary productivity and algae blooms may be worth examining, because algal blooms may directly affect the ecosystem of chub mackerel fishing grounds in the SECS (Wang, 2010).

Based on the available research, it is difficult to draw conclusions on which mechanism of trophic control plays the largest role on the chub mackerel fishing grounds. However, the results of this study indicate that it is non-linear and complex, judging by the relationship between net primary production and standardized CPUE.

5 Conclusions

The spatial and temporal fluctuations in ocean primary productivity can cause sizable bias in the estimation of the abundance of fish stocks by using in-situ ocean primary production that are typically sparse in time and space. However, satelliteacquired ocean primary production provides more suitable spatial and temporal scales to support such research.

When fish biomass and potential yields are estimated based on ocean primary production, a positive relationship between ocean primary production and the abundance of fish is always implicit (Ning et al., 1995; Lu et al., 2000; Li and Lu, 2008; Huang et al., 2010). However because mechanisms of trophic control in ocean ecosystems are complicated (Hunter and Price, 1992; Chassot et al., 2007), the relationships may be non-positive, such as we found here. As such, before evaluating fish stocks based on ocean primary production, fishery scientists should take into account the mechanisms of trophic interactions.

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