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Apparent Dominance of Regenerated Primary Production in the Yellow Sea

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The Yellow Sea is known to be a very productive region in terms of fisheries. However, its trophic status seems to be highly variable, ranging from oligotrophic to eutrophic, based on new production (NP) values. The NP and regenerated production (RP) values estimated from ^{15}N-labelled nitrate and ammonium uptake in spring (April 1996) and winter (February 1997) during this study ranged from 0.05 to 19.8 mg N m^{-2} d^{-1} and from 0.1 to 22.8 mg N m^{-2} d^{-1}, respectively. Our measurements and earlier observations suggested that NP in the Yellow Sea varied over the four orders of magnitude (range 0.05-180.9 mg N m^{-2} d^{-1}) temporally and spatially, and that RP (range 0.1-507.5 mg N m^{-2} d^{-1}) based on ammonium predominated during most period of the year, except in winter when both productions were low. The significant nitrogen uptake by phytoplankton below the euphotic zone and episodic entrainment of phytoplankton from below the euphotic zone into the euphotic zone, and nitrite excretion and dissolved organic nitrogen release during nitrate uptake might explain the apparent dominance of RP in the Yellow Sea.

Key words: Regenerated Production, New Production, Yellow Sea

INTRODUCTION

The introduction of the concept of new and regenerated production and its subsequent elaboration (Dugdale and Goering, 1967; Eppley and Peterson, 1979; Platt *et al.*, 1992; Bronk *et al.*, 1994) enable us to understand the potential role of phytoplankton production in marine biogeochemical cycles in a given oceanic area. Further, phytoplankton NP could be related to an exploitable production such as fisheries (Horne *et al.*, 1989; Iverson, 1990; Nielsen and Richardson, 1996).

The Yellow Sea is a semi-enclosed continental shelf area between the Korean Peninsula and China with a surface area of 487×10^9 m^2 and mean depth of 44 m (Hahn, 1993). The Yellow Sea is connected to the Bohai Sea on the northwest and the East China Sea on the south. The Yellow Sea is highly productive and important for traditional fisheries in Korea and China (Liu and Chen, 1998). Nonetheless, there are growing reports that the trophic status of the Yellow Sea is highly variable, ranging from oligotrophic to eutrophic, based on NP measurements (Yang *et al.*, 1994; Shim *et al.*, 1996; Cho *et al.*, 2001; Park *et al.*, 2002). For example, Cho *et al.* (2001) reported that NP varied over three orders of magnitude (range 0.1-155.7 mg N m^{-2} d^{-1}) during May and June in the mid-eastern part of the Yellow Sea. Together with the studies mentioned above, the results from this study suggest that the Yellow Sea is apparently dominated by RP rather than NP throughout the most seasons of the year. Possible causes for the observed apparent dominance of RP in the Yellow Sea are discussed.

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MATERIALS AND METHODS

Sampling and environmental variables

Nineteen stations were occupied during spring (April 1996) and winter (February 1997) in the Yellow Sea. The locations of the stations during each cruise are shown in Fig. 1. Water temperature and

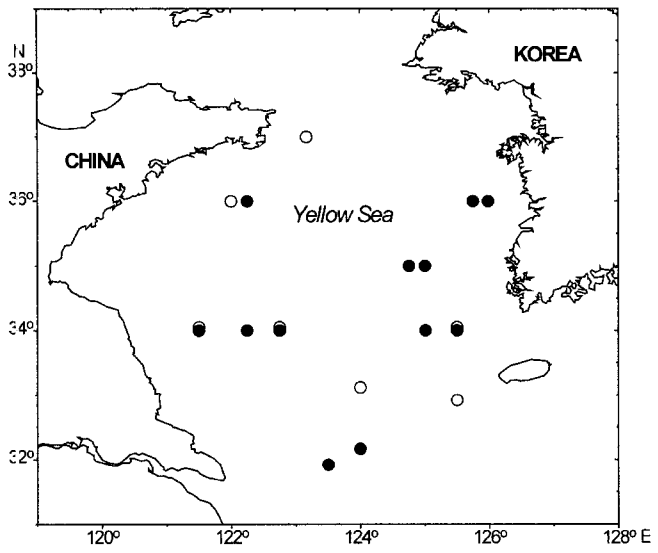

Fig. 1. Map of study area and sampling stations. Stations were sampled in April 1996 (●) and February 1997 (○).

salinity were measured with a CTD (SBE-911) mounted on a rosette sampler. For measurements of ^{15}N-isotopes based productivity and environmental variables, seawater samples were collected at 4 to 6 depths within the euphotic zone with 10 l Niskin bottles mounted on a rosette sampler. The euphotic depth (Z_e) was determined by multiplying the Secchi disc depth by 2.7. The depth of the upper mixed layer (Z_m) was arbitrarily defined as the depth where the difference of density (sigma-*t*) against the surface was less than 0.05. For analysis of chlorophyll *a* (chl *a*) concentration, aliquots (~ 1 L) of seawater samples were filtered (pressure < 100 mm Hg) through Whatman GF/F filters and the filters were used for the measurements of chl *a* concentration by a spectrophotometric method (Parsons *et al.*, 1984) after extraction with 90% acetone. The filtrates were stored frozen (-20°C) on board for nutrient analyses and subsequently analyzed using a Technicon II AutoAnalyzer and Bran+Luebbe AutoAnalyzer (Model TRAACS 2000) by the methods of Parsons *et al.* (1984). Hydrography and distributions of inorganic nutrients and chl *a* during this study were described in detail in Lee (1998) and Kim *et al.* (2000).

New and regenerated production

Uptake rates of nitrate (NP) and ammonium (RP) were measured using the stable isotope ^{15}N as a tracer (Dugdale and Wilkerson, 1986). Seawater samples were transferred into 250 ml polycarbonate bottles wrapped with perforated nickel screens (Stork Veco, Bedford, MA, USA) to simulate *in situ* light intensity at which the samples were collected, and inoculated with either $^{15}NH_4Cl$ or $K^{15}NO_3$ (all 99.3 atom%; Cambridge Isotope Lab., Woburn, MA, USA) for ammonium and nitrate uptake measurements, respectively, to bring the final tracer additions to 0.2 and 1 μM, respectively. These enrichments were not always true tracer additions (usually defined as ≤ 10% of ambient concentrations). During this study, the isotope additions led to enrichments ranging from 7.8% to >100% of ambient concentration in nitrate uptake experiments and from 11.6% to >100% of ambient concentration in ammonium uptake experiments. After isotope additions, samples were incubated for 4 h in an on-deck incubator cooled with continuously flowing surface seawater. This incubation time was employed to minimize problems related to both the effect of isotope dilution during incubation and the effect of initial surge uptake (Dugdale and Wilkerson, 1986). After the incubation, samples were filtered (<100 mm Hg) onto pre-combusted (4 h at 450°C) Whatman GF/F filters (diameter 25 mm) and stored dry at 60°C until analysis of $^{15}N/^{14}N$ ratio with an Europa Roboprep-Tracermass GC-MS (Owens, 1988). Absolute uptake rates were calculated according to Dugdale and Wilkerson (1986). The absolute uptake rates in the present study are in fact considered net nitrogen uptake rates or net nitrogen transport rates, as we did not account for nitrogen regeneration (e.g., Glibert *et al.*, 1982) or the loss of ^{15}N to the dissolved organic nitrogen pool (e.g., Slawyk *et al.*, 1998, 2000; Bronk and Ward, 2000). The effects of adding excess ^{15}N-tracers to some samples on calculating uptake rates were considered and corrected according to Eppley *et al.* (1977). Further, the effects of temperature were corrected according to Cho *et al.* (2001). Since samples for measurements of ^{15}N uptake were incubated in an on-deck incubator cooled with surface seawater, temperature differences between sea surface and sampled depths might influence uptake rates observed in samples from the deeper parts of stratified waters in April 1996. Assuming a Q_{10} of 2.3 for photosynthesis, growth, and ^{15}N uptake (Eppley, 1972; Raven and Geider, 1988), our uptake rates were corrected for the effect of the temperature difference according to the equation $\log Q_{10}=10/(t_1-t_2)$ x $\log (k_1/k_2)$, where t_1=higher temperature (°C), t_2=lower temperature (°C), k_1=uptake rate at the higher temperature, and k_2=uptake rate at the lower temperature. The Q_{10} value used for N uptake in this study was within the range (1.4 to 3.2) reported by previous

studies (Glibert *et al.*, 1982; Paasche and Kristiansen, 1982; Smith and Harrison, 1991). In this study, depth-integrated nitrogen uptake and environmental variables over the euphotic zone are presented unless otherwise stated.

RESULTS

Environmental and phytoplankton variables

Environmental and phytoplankton variables during this study are summarized in Table 1. The depth of the euphotic zone in the study area was shallow, ranging from 0.8 to 25 m, due probably to high concentrations of suspended materials and/or dissolved substances. The depth of the upper mixed layer varied from 7 to 37 m. Surface chl *a* concentrations showed two orders of magnitude variation during this study, with maximum and minimum values of 4.46 mg m^{-3} during spring bloom (April 1996) and 0.06 mg m^{-3} in the winter (February 1997), respectively. Depth-integrated chl *a* concentrations over the euphotic zone varied from 0.08 to 76.79 mg m^{-2}. Surface nitrate and ammonium concentrations ranged from 0.05 to 12.81 M and from undetectable levels to 1.73 M, respectively. Depth-integrated nitrate and ammonium concentrations over the euphotic zone ranged from 0.2 to 69.3 mg-at. N m^{-2} and from 0.1 to 23.5 mg-at. N m^{-2}, respectively.

New and regenerated production

NP integrated over the euphotic zone varied over three orders of magnitude temporally and spatially, with the minimum and maximum values of 0.05 (in April 1996) and 19.8 mg N m^{-2} d^{-1} (in April 1996), respectively, and both were found in April (Fig. 2a), indicating that the magnitude of the NP was highly variable spatially even within a study period. RP integrated over the euphotic zone was also highly variable, ranging from 0.1 (in February 1997) to 22.8 mg N m^{-2} d^{-1} (in April 1996). The euphotic zone-inte-

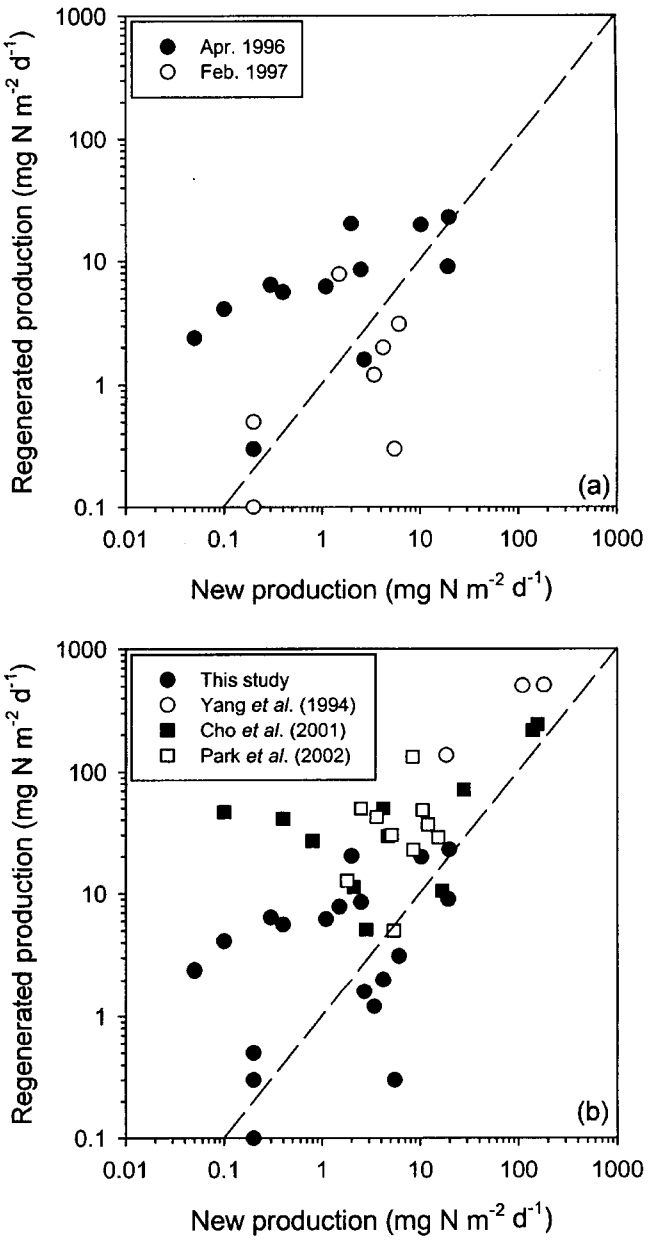

Fig. 2. Scatter-plots of depth-integrated regenerated production versus depth-integrated new production over the euphotic zone during this study (a). In (b), data from this study (●) were plotted together with those reported by the previous studies in the Yellow Sea; Yang *et al.*, 1994 (○), Cho *et al.*, 2001 (■), Park *et al.*, 2002 (□). In both plots, the dashed lines represent the 1:1 correspondence.

Table 1. Summary of environmental and phytoplankton variables during this study. Z_e, Z_m: the depth of the euphotic zone and the depth of the upper mixed layer, respectively. nd: not detectable

Date	Number of station	Z_e (m)	Z_m (m)	Chlorophyll *a*		Nitrate		Ammonium	
				Surface (mg m^{-3})	Euphotic (mg m^{-2})	Surface (μM)	Euphotic (mg-at. N m^{-2})	Surface (μM)	Euphotic (mg-at. N m^{-2})
Apr. 1996	12	0.8-20	8-36	0.32-4.46	1.18-76.79	0.05-12.81	0.2-68.7	nd-1.73	0.3-4.5
Feb. 1997	7	0.8-25	7-37	0.06-0.70	0.08-5.00	2.01-8.42	1.6-69.3	nd-0.81	0.1-23.5

grated RP was greater (range 1.2-50.5 fold) than the euphotic zone-integrated NP at 12 of 19 stations during this study (Fig. 2a). The opposite was found mostly in winter (February 1997).

DISCUSSION

Earlier measurements on NP and RP in the Yellow Sea (Yang *et al.*, 1994; Cho *et al.*, 2001; Park *et al.*, 2002) were plotted together with our data (Figure 2b); Cho *et al.* (2001) and Yang *et al.* (1994) reported the magnitudes of NP and RP observed during May and June at a tidal frontal region in the mid-eastern part and in late April in the southern part of the Yellow Sea, respectively. Park *et al.* (2002) measured them in May and November from the same area of the Yellow Sea. The NP values in the present study were within the lower range of those (10.6-51.5 mg N m^{-2} d^{-1}) reported by Chen *et al.* (1999) in May in the continental shelf of the East China Sea, which is connected to the Yellow Sea on the north. Considering the pooled data mentioned above, however, NP values in the Yellow Sea exhibit the large variations in time and space, ranging from 0.1 to 180.9 mg N m^{-2} d^{-1}. Thus, trophic status appears to be highly variable from oligotrophic to eutrophic based on NP values (Dugdale and Wilkerson, 1992). More interestingly, RP predominated in the Yellow Sea during most period of the year, except in winter; RP was greater than NP in 34 out of total 43 observations covering four seasons in the Yellow Sea, and of 9 observations in which NP was greater than RP, more than half of them were observed in winter (Fig. 2b). Given that NP is eventually related to fisheries (Horne *et al.*, 1989; Iverson, 1990; Nielsen and Richardson, 1996), the overall predominance of RP in the study area seems contradictory to the traditional view that the Yellow Sea is a highly productive region in terms of fisheries (Liu and Chen 1998).

The overall dominance of RP in the Yellow Sea might be resulted from the consistent preference for ammonium by phytoplankton, similar to the earlier observations made in other coastal and estuarine areas (e.g. McCarthy *et al.*, 1977; Cochlan, 1986; Underwood and Kromkamp, 1999; Middelburg and Nieuwenhuize, 2000). However, the phenomenal or methodological problems such as isotope dilution (Glibert *et al.*, 1982), diel periodicity of nitrogen uptake (Cochlan *et al.*, 1991; Park *et al.*, 1997), dissolved organic nitrogen (DON) release (Bronk *et al.*, 1994; Bronk and Ward, 1999; Diaz and Raimbault, 2000), and nitrite excretion during nitrate uptake (Collos, 1998) might contribute to the apparent dominance of RP in the Yellow Sea. The effect of isotope dilution seemed to be minor in this and the previous studies (Yang *et al.*, 1994; Cho *et al.*, 2001; Park *et al.*, 2002; Fig. 2b) as all employed the incubation time of 4 h to minimize the problem during incubation (Dugdale and Wilkerson, 1986), and such a correction, if applied, would only have resulted in an even higher dominance of RP. Although nighttime N uptake by the Yellow Sea phytoplankton is known to be substantial, accounting for up to 33% for ammonium and 41% for nitrate of the daily uptake (Park *et al.*, 1997), its consideration also does not significantly influence our observation. While both nitrite excretion and DON release during nitrate uptake would be potential sources for the apparent dominance of RP in the Yellow Sea, their directions of error into over- and/or-underestimates could not be accurately assessed in the present study because the release could either depend on N source or not (Bronk and Glibert, 1991; Diaz and Raimbault, 2000).

Another plausible explanations for the apparent dominance of RP in the Yellow Sea still remain. Recently, Park *et al.* (2002) reported that nitrogen uptake rates by phytoplankton below the euphotic zone in the Yellow Sea is considerable, and that the uptake below the euphotic zone accounted for 13.0 -86.2% for nitrate and 13.8-67.8% for ammonium of whole water column uptake. Since the maximum depth of the Yellow Sea is shallow by less than 100 m (Hahn, 1993), it is likely that phytoplankton below the euphotic zone could be easily again entrained into the euphotic zone by a certain physical forcing such as turbulent mixing and/or the vertical movement of thermocline. If it is true in the Yellow Sea, a portion of RP estimated from ^{15}N-ammonium uptake should be included in NP estimates. Alternatively, the considerable N production (based on either nitrate or ammonium) below the euphotic zone itself could be an exploitable production which could be passed through the aphotic zone food webs into higher trophic levels. To explain the apparent dominance of RP in the Yellow Sea, the issues for nitrite excretion, DON release, and the aphotic zone nitrogen uptake need to be addressed in the future.

CONCLUSION

The trophic status in the Yellow Sea appears to be highly variable, ranging from oligotrophic to eutrophic,

based on new production values. Our measurements and earlier observations suggested that new production, estimated using the ^{15}N-labelled stable isotope method, in the Yellow Sea varied over the four orders of magnitude (range 0.05-180.9 mg N m^{-2} d^{-1}) temporally and spatially, and that regenerated production (range 0.1-507.5 mg N m^{-2} d^{-1}) based on ammonium predominated during most period of the year, except in winter when both productions were low. The significant nitrogen uptake by phytoplankton below the euphotic zone and episodic entrainment of phytoplankton from below the euphotic zone into the euphotic zone, and nitrite excretion and dissolved organic nitrogen release during nitrate uptake might explain the apparent dominance of regenerated production in the Yellow Sea.

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