

Benthic fluxes of nitrogen and phosphorus at southern bluefin tuna *Thunnus maccoyii* sea-cages

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ABSTRACT: To assess the effects of southern bluefin tuna farming on benthic nutrient cycling, we measured sedimentation rates, porewater nutrients, sedimentary total nitrogen (N) and phosphorus (P) content, and benthic fluxes at 2 tuna sea-cages and associated control (non-farm) sites in South Australia over the course of a farming season. Sedimentation rates exceeded 40 g dry weight m⁻² d⁻¹ only at the sea-cage sites, and porewater concentrations of ammonium and phosphate were up to 10 and 100 times that measured at control sites, respectively. The highest ammonium and phosphate fluxes from the sediments into the water column were recorded at sea-cage sites (9962 and 2177 μmol m⁻² h⁻¹, respectively) towards the end of the season, and these were in excess of 10 times those recorded at control sites in any month. The annual average of the sediment fluxes associated with southern bluefin tuna farming produced over 7 and 40 times the daily requirements of N and P, respectively, for calculated primary productivity. The high sedimentation rates, porewater concentrations and benthic flux rates recorded at sea-cages at the end of the farming season were not observed 4 mo after the southern bluefin tuna were harvested. These data show that sedimentation rates and sediment geochemistry respond rapidly to farming activities. The risks associated with farming southern bluefin tuna include enrichment of pelagic nutrients from benthic fluxes that can lead to increased primary production. Thus continuation of site following on an annual basis is strongly recommended. Sustainability of the coastal ecosystem supporting southern bluefin tuna farming must consider the regional consequences from these inputs of N and P, occurring not only through increased sedimentation but also direct nutrient availability in the water column.

KEY WORDS: Aquaculture environments · Nutrients · Sedimentation · Sea-cage farming · South Australia

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INTRODUCTION

Australia has the world's largest quota of southern bluefin tuna (SBT) *Thunnus maccoyii* at 5265 t (CCSBT 2007). More than 90% of the Australian quota is currently farmed after capture, with this industry contributing to more than 20% of Australia's gross value of aquaculture production in 2004–2005 (Newton et al.

2006) worth AU\$138 M in direct sales in 2006–2007 (Econsearch 2008). SBT are caught in the Great Australian Bight off Southern Australia between December and March and then towed back to the waters off Port Lincoln, South Australia, for fattening over 6 to 9 mo in a 172 km² farming zone. Approximately 280 000 SBT are fed 50 000 to 60 000 t of baitfish, predominantly Australian sardine *Sardinops neopilchar-*

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dus, to produce an additional 4380 t per year between 2000 and 2003 (Jeffries 2004). SBT farms are situated in open coastal waters where tidal flows reach 20 cm s^{-1} , with a weak residual current ($\sim 1 \text{ cm s}^{-1}$) to the north–northeast during both summer and winter (Herzfeld et al. 2008). The seafloor under these farms consists mostly of poorly sorted silts and fine sands, with finer calcareous sediments in the south and coarser organic-poor sediments in the north (Fernandes et al. 2006) and few visible epiflora or fauna. A preliminary model of nitrogen (N) loads suggests that the industry discharges between 1137 and 2200 t of N per year into the marine environment, with soluble excretion products accounting for 59 to 64% of daily feed inputs (Fernandes et al. 2007a). Previous seafloor video footage and infaunal sampling completed as per the South Australian state government-legislated tuna environmental monitoring program has found waste food within 50 m of the sea-cages and polychaetes at an elevated abundance within 5 m of the sea-cages (Clarke et al. 2000).

In the present study, we investigated the environmental effects of SBT farming in light of the effects of sea-cage farming, such as increased organic load to the sediments, documented for various finfish species elsewhere (Holby & Hall 1991, Hargrave et al. 1993, Karakassis et al. 2000, McGhie et al. 2000, Aguado-Gimenez & Garcia-Garcia 2004, Vita et al. 2004). We were particularly interested in how SBT aquaculture affects sedimentation rates, organic matter accumulation and cycling in the sediments, and the potential impacts and risks to sustainability of coastal resources.

SBT are farmed in shallow coastal waters (<25 m deep), where benthic–pelagic coupling may exert a strong influence over the nutrient availability in the water column (Fisher et al. 1982, Sundback et al. 1991, Vidal et al. 1997, Hopkinson et al. 1999). In coastal areas, the recycling of organic material by the sediments may substantially contribute to the N (up to 190%) and phosphorus (P) (up to 21%) requirements of phytoplankton (Blackburn & Henriksen 1983, Hopkinson et al. 1999). Benthic nutrient fluxes are greatly influenced by the rate of sedimentation and the rate at which nutrients move from the sediment to the overlying seawater via diffusion, bioturbation by infauna or advection (Goldhaber et al. 1977, Boucher & Boucher-Rodoni 1988, Huettel & Rusch 2000). These fluxes respond to changes in organic loading to the sediments, but the response of each element may be different (Blackburn & Blackburn 1992, Howarth et al. 1995, Giblin et al. 1997, Heggie et al. 1999) and at temperate latitudes they are subject to strong seasonal fluctuations (Jorgensen & Sorensen 1985, Jensen et al. 1990). Here we investigate whether sedimentation rates, sediment nutrient concentrations and benthic fluxes mea-

sured adjacent to SBT sea-cages are different from control sites 1 km away, and whether these variables show significant seasonal variation.

MATERIALS AND METHODS

Study sites. Two commercially operated sea-cages (P1 and P2) and 2 control sites (C1 and C2) were studied. Sites P1 ($34^{\circ} 38.654' \text{ S}$, $136^{\circ} 00.423' \text{ E}$) and C1 ($34^{\circ} 38.541' \text{ S}$, $135^{\circ} 59.038' \text{ E}$) were located in the northern part of the farming region, whereas P2 ($34^{\circ} 42.544' \text{ S}$, $135^{\circ} 59.164' \text{ E}$) and C2 ($34^{\circ} 41.837' \text{ S}$, $136^{\circ} 00.119' \text{ E}$) were in the southern area. The sedimentary characteristics and depositional regime of the area are described in Fernandes et al. (2006). A detailed description of farm management practices for P1 and P2 is given in Fernandes et al. (2007a). Briefly, both P1 and P2 were approximately 40 m diameter sea-cages with a 10 m net drop, situated in 22 and 20 m water depths, respectively. SBT in P1 and P2 were fed baitfish (consisting mainly of *Sardinops* spp.), with an average of 11.1% dry weight (DW) N and 2.1% DW P (Fernandes et al. 2007b). The biomass in P1 started at 30 t and 56 t were harvested 160 d later, with stock fed an average of 2890 kg d^{-1} . The biomass in P2 started at 39 t and 74 t were harvested 135 d later, with stock fed an average of 2514 kg d^{-1} . C1 and C2 were located at least 1 km from any stocked sea-cage. The water depth at C1 and C2 was 18 m. Sampling was conducted throughout 2004, in February–March, May, July and November; fish were stocked in P1 from February to July and in P2 from April to August. Sediment samples from P1 and P2 were taken at the edge of the sea-cages. The ambient seawater temperature was highest in March (22°C) and lowest in July (14.5°C), with approximately equal temperatures in May and November (16.5°C).

Sedimentation. Sedimentation rates were measured at each site during each month with sediment traps, comprising paired PVC barrels (height 400 mm, diameter 85 mm) attached to a rope via freely rotating stainless steel frames. Sedimentation rates were measured in duplicate 1 m above the seafloor at 0, 30 and 60 m from the edge of the sea-cage or the control site. Sediment traps were orientated in a southeast, south or southwest direction away from the edge of the sea-cages. Although the prevailing/residual current is north–northeast (Herzfeld et al. 2008), the placement of the sediment trap ropes had to avoid the anchor ropes of the sea-cages and allow the vessel to maintain steerage during deployment. The PVC barrels were lead-weighted (40 g) at the bottom to ensure correct vertical orientation. Each series of sediment traps was deployed for a period of at least 48 h but no more than 96 h. Nine out of 96 sediment traps were lost during the deploy-

ment period. At the end of the deployment period, sediment traps were retrieved and the contents were immediately spiked with HgCl_2 to a final concentration of 10 mg l^{-1} . Within 4 h, the contents were sieved (1 mm mesh) to remove non-sedimentary matter (e.g. live zooplankton) that was not part of the passive material flux. The contents were then vacuum-filtered through pre-combusted (450°C overnight) and pre-weighed glass-fibre filters ($0.7 \mu\text{m}$). The filters were then placed in pre-combusted glass petri dishes (450°C overnight) to dry at 50°C for at least 16 h. The mass of material on the filter papers was corrected for salt that impregnates the filters, and the results expressed in units of $\text{g DW m}^{-2} \text{ d}^{-1}$ (i.e. total sedimentation rate).

To determine the sedimentation rate of nutrients, the material collected on the filter papers was removed with a spatula, homogenised with a mortar and pestle and analysed as for the sediments (see 'N and P content of sediments'). The N or P content of the sedimentary material was then used to determine the nutrient flux to the sediments by multiplying the percentage of N or P by the total sedimentation rate measured for that sample. The distance of the sediment trap from the sampling location was not taken into account for the processing of N or P content, where samples with sufficient material for analysis of both N and P were randomly assigned for analysis of each element.

Nutrient fluxes. Measurements of ammonium, nitrate plus nitrite and phosphate fluxes were made at each site for each month, using a manually operated shipboard incubation system. The target of 6 acceptable sediment core samples, suitable for incubation, could not always be collected at all sites due to surface resuspension of sediments or gaining an inadequate volume of overlying water. The variation in sample numbers per site ($n = 3$ to 6 per site per month) was random. Due to unforeseeable logistical constraints, C2 was not sampled in November. Sediments were sampled using a HAPS corer (Kannevorff & Nicolaisen 1973) deployed from a 17 m motor vessel. Sediment core samples for nutrient fluxes, porewater and N and P content were collected from the edge of the sea-cages, in an area of approximately 9 m^2 , on the south-eastern to southwestern side of the sea-cage where the prevailing current is to the northeast. Access to the sea-cages was limited by the position of anchor lines. At control sites, sediment core samples for nutrient fluxes, porewater and N and P content were collected within an area of approximately 40 m^2 due to the movement of the vessel under anchor. Removable opaque PVC barrels (length 300 mm, internal diameter [i.d.] 105 mm) were fitted to the corer and used to collect and house the sediments and ambient overlying water (minimum volume 800 ml). Sediment cores with a visibly undisturbed sediment surface, clear overlying

seawater and containing at least a 10 cm depth of sediment were used in the incubations. These cores were capped (with opaque PVC lids) at both ends immediately after collection. The bottom seal had double O-rings and the lid a single O-ring around the edge of the barrel. The lid also had a stainless steel stirrer penetrating through it with a magnetic couple that drove a brass propeller (width 10 mm, length 4 mm), sealed by an O-ring. The rotation of the blade (7 rps) generated a shear stress of approximately 0.08 to 0.1 N m^{-2} at the sediment surface, assuming a mean grain size of $150 \mu\text{m}$ and a logarithmic velocity profile for the change in velocity with depth of overlying water (Gill 1982, Nielsen 1992). Temperatures were maintained within $\pm 0.8^\circ\text{C}$ of the ambient water temperature during the experimental period. Nutrient fluxes were determined from the change between initial and final concentrations of nutrients dissolved in the overlying seawater (Hargrave et al. 1993). Incubations were run for 2 to 4 h to reduce problems with non-linear nutrient changes (Nicholson & Longmore 1999). Duplicate samples of the overlying seawater were taken at the start and end of each incubation using a clean 20 ml plastic syringe, filtered ($0.45 \mu\text{m}$) and then stored at -20°C until analysis. Samples were analysed for nitrate plus nitrite ($\text{NO}_x\text{-N}$), ammonium ($\text{NH}_4^+\text{-N}$) and phosphate ($\text{PO}_4^{3-}\text{-P}$), using a QuickChem 8000 Automated Ion Analyser. Nutrient concentrations of duplicate samples were averaged. The change in nutrient concentration between the start and end of the incubation was then adjusted to account for the sediment surface area, duration of incubation and volume of overlying seawater to determine the rate of nutrient release or uptake (Nicholson & Longmore 1999). Positive measurements represented a flux out of the sediments into the overlying water.

Porewater. To measure concentrations of ammonium and phosphate in sedimentary porewater, sediment cores ($n = 2$ per site per month) were collected using the HAPS corer and stainless steel barrels (67 mm i.d.). The top 2 cm of sediment was sectioned, transferred into a plastic centrifuge tube and refrigerated for up to 4 h before porewater extraction via centrifugation ($3000 \times g$, 10 min). The supernatant was withdrawn with a clean syringe then treated and analysed as above for ammonium and phosphate. There was insufficient supernatant to analyse for nitrate plus nitrite concentrations.

N and P content of sediments. To determine total N and P contents in sediments, sediment cores ($n = 4$ per site per month) were collected using the HAPS corer and stainless steel barrels (67 mm i.d.) at each site each month. The top 1 cm of sediment was immediately sectioned from the core upon retrieval and these core sections were frozen at -20°C until laboratory analysis.

Note that only 1 cm depth of sediment was required for analysis of elemental content, whereas 2 cm was required for porewater samples to gain enough water to analyse. Samples were freeze-dried, sieved through 500 μm to remove large shell fragments and homogenised with a mortar and pestle. N was analysed by continuous flow-isotope ratio mass spectrometry (CF-IRMS) using a Europa Scientific ANCA-SL elemental analyser coupled to a Geo 20-20 mass spectrometer. P was determined in a Varian Vista Axial ICP-AES after digestion of samples with aqua regia (1:3 HNO_3 :HCl mixture) (Standards Australia 1997).

Modelling phytoplankton requirements. To estimate the importance of benthic nutrient fluxes in sustaining pelagic primary productivity, we compared N and P fluxes to algal demand using stoichiometric conversions assuming Redfield molar ratios for algae of C:N:P = 106:16:1 (Hopkinson et al. 1999). Primary productivity ($\text{mg C m}^{-2} \text{d}^{-1}$) was modelled using the vertically generalised production model of Behrenfeld & Falkowski (1997) from measured chlorophyll *a* ($\text{chl } a$; $\mu\text{g l}^{-1}$) (Lauer 2005), water temperature, irradiance ($\text{MJ m}^{-2} \text{d}^{-1}$) and day length (h). Irradiance data for Port Lincoln were obtained from the Australian Bureau of Meteorology, and day length was obtained from Geoscience Australia.

Data analysis. SPSS (v. 12) was used for all data analyses. Two-way ANOVAs were used to assess the null hypotheses that there were no significant differences in (1) nutrient fluxes, (2) porewater concentrations, (3) total N/P and (4) ratio of total N to P between sites or months, or from their interaction. Site and month were considered as fixed factors. The analyses were carried out by comparing P1 and C1, and P2 and C2 separately. Separate analyses are justified by the difference in production periods at P1 and P2, where farming at P2 started 2 mo after P1, as well as the difference in sediment type between the northern and southern locations where sampling occurred. Type IV sums of squares were used to account for the missing nutrient flux data from C2 in November. Type III sums of squares were used for the remaining variables. *Post hoc* analysis (main effects with Tukey's Honestly Significant Difference test for factor of month, interaction effects with univariate and pairwise comparisons using Fisher's least significant difference test) was conducted for any significant factors. To meet the assumptions of normality and homoscedasticity, data on ammonium and phosphate fluxes, porewater concentrations, total N and total P were \log_{10} -transformed prior to analysis and checked by graphical inspection of residuals. As 3 nitrate plus nitrite fluxes were zero or negative, a log-transform was not possible, thus a conservative α of 0.01 was used for this variable, compared to 0.05 for all other variables.

RESULTS

Sedimentation

Although there was a great deal of temporal variability, sedimentation rate only exceeded 40 $\text{g DW m}^{-2} \text{d}^{-1}$ at the sea-cage sites, and only while they were stocked (Fig. 1). P1 had the highest sedimentation rates during March and July (above 79 and 50 $\text{g DW m}^{-2} \text{d}^{-1}$, respectively), 4 to 10 times those measured at any other site during the same month. Sedimentation rates were greatest at P2 during May (31 to 49 $\text{g DW m}^{-2} \text{d}^{-1}$), although these were only slightly higher than at C2.

The patterns in the sedimentation rates of N and P over the 4 months were similar to the dry-matter sedimentation rates (Fig. 2). For N, P1 had the highest values during March and July (566 and 638 $\mu\text{mol N m}^{-2} \text{h}^{-1}$, respectively), while P2 recorded the highest during May (420 $\mu\text{mol N m}^{-2} \text{h}^{-1}$). Similarly, P1 had the highest P values during March and July (56 and 64 $\mu\text{mol P m}^{-2} \text{h}^{-1}$, respectively), while P2 recorded the highest during May (20 $\mu\text{mol P m}^{-2} \text{h}^{-1}$). The sedimentation rates of N and P at sea-cage sites exceeded those at control sites only on a few occasions during the farming season.

Nutrient fluxes

The ammonium and phosphate fluxes increased from March to July at both sea-cages (Fig. 3); surprisingly, fluxes at control sites increased in colder months of the year (July–November), particularly at C1. The highest fluxes of ammonium and phosphate were recorded at P1 (9962 and 2177 $\mu\text{mol m}^{-2} \text{h}^{-1}$, respectively) and P2 (644 and 1476 $\mu\text{mol m}^{-2} \text{h}^{-1}$, respectively) during July, and these were in excess of 10 times those recorded at either control site in any month. The high rates recorded at sea-cages during July were not observed in November, some months after farming for the season had finished. Ammonium fluxes were significantly higher at sea-cage sites than control sites (Table 1a). Significant differences among months were also found (Table 1a), with ammonium fluxes in July significantly higher than in May at P1 over C1 ($p = 0.031$), and where P2 was higher than C2 ($p = 0.035$). There was a significant interaction of site and month for the phosphate flux (Table 1a) with sea-cage sites having higher fluxes than control sites only when they were stocked. P1 had higher phosphate fluxes than C1 for March, May and July (all $p < 0.001$), and P2 was higher than C2 for May and July (both $p < 0.001$).

The nitrate plus nitrite fluxes exhibited patterns that differed from the ammonium and phosphate fluxes. Fluxes at control sites increased from March to July,

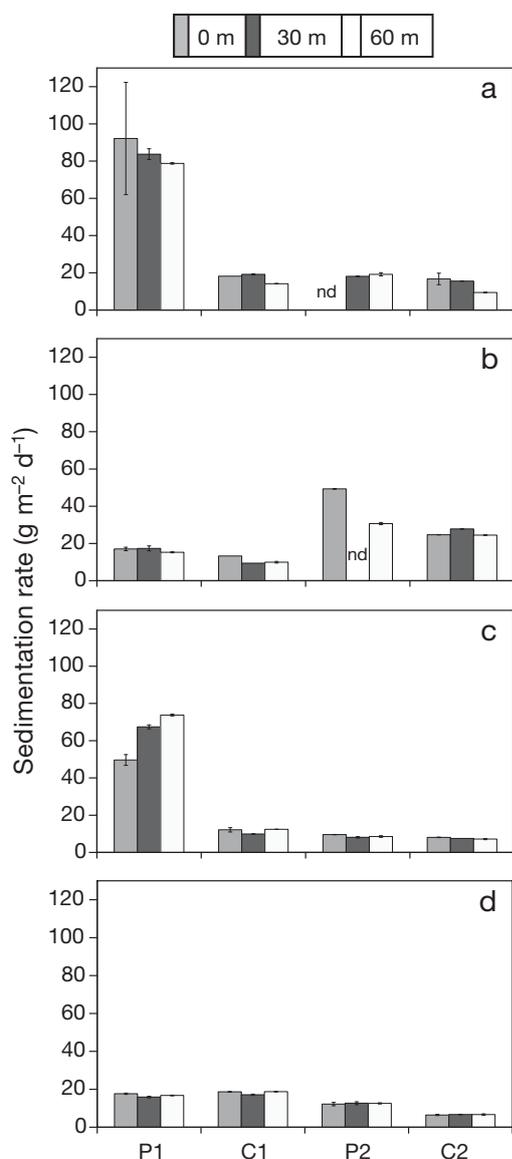


Fig. 1. Sedimentation rates 1 m above the seafloor at distances of 0, 30 and 60 m from the sea-cage (P1, P2) and control (C1, C2) sites during (a) March, (b) May, (c) July and (d) November. Bars indicate means ($n = 1$ or 2 traps, $\pm \text{SE}$). nd: no data due to trap loss.

whilst at the sea-cage sites they were more variable. The highest nitrate plus nitrite flux was observed at P1 during November ($122 \mu\text{mol m}^{-2} \text{h}^{-1}$), almost double any other measurement, as opposed to peaks in July for P2 and both control sites. There was a significant interaction of site and month for nitrate plus nitrite flux (Table 1a), with no readily apparent pattern among sites. C1 had higher fluxes than P1 in July ($p = 0.001$), and the reverse occurred in November ($p < 0.001$), and C2 had higher fluxes than P2 in May ($p = 0.029$). Overall, inorganic N fluxes averaged across months were dominated by ammonium, with mean ratios of ammo-

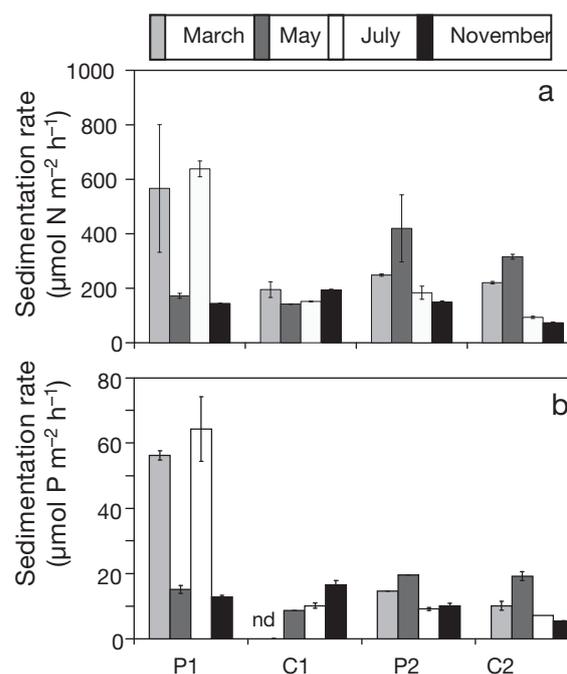


Fig. 2. Sedimentation rates of (a) N and (b) P measured 1 m from the bottom at sea-cage (P1, P2) and control (C1, C2) sites for each month sampled during 2004. Bars indicate means ($n = 1$ or 2 traps, $\pm \text{SE}$). nd: no data for that site/month

nium:nitrate plus nitrite of 9 and 97 at sea-cages (P2, P1 respectively) in comparison to only 1.2 and 1.7 at the control sites (C2, C1 respectively).

Porewater concentrations

P1 showed the greatest increase in the concentration of ammonium in the porewater between March and July (156 to $617 \mu\text{M}$) and these concentrations exceeded the range measured at C1 and C2 by a factor of 10 (Fig. 4). The concentration then halved (to $306 \mu\text{M}$) between July and November. Concentrations were much lower at P2 and showed a slight increase of about 20% between March and November, whereas control sites had maxima in July. Porewater concentrations of ammonium were significantly greater at P1 than C1 (Table 1b), with concentrations in July and March significantly different from one another ($p = 0.049$). There was a significant interaction of site and month for P2 and C2 (Table 1b): P2 had higher concentrations than C2 for March ($p = 0.016$), May ($p < 0.001$) and November ($p < 0.001$).

The patterns in the concentration of phosphate in the porewater were similar to those for ammonium. Again, the concentrations at P1 (27 to $195 \mu\text{M}$) exceeded those very low concentrations measured at the control sites, this time by a factor of up to 100. Both sea-cage sites

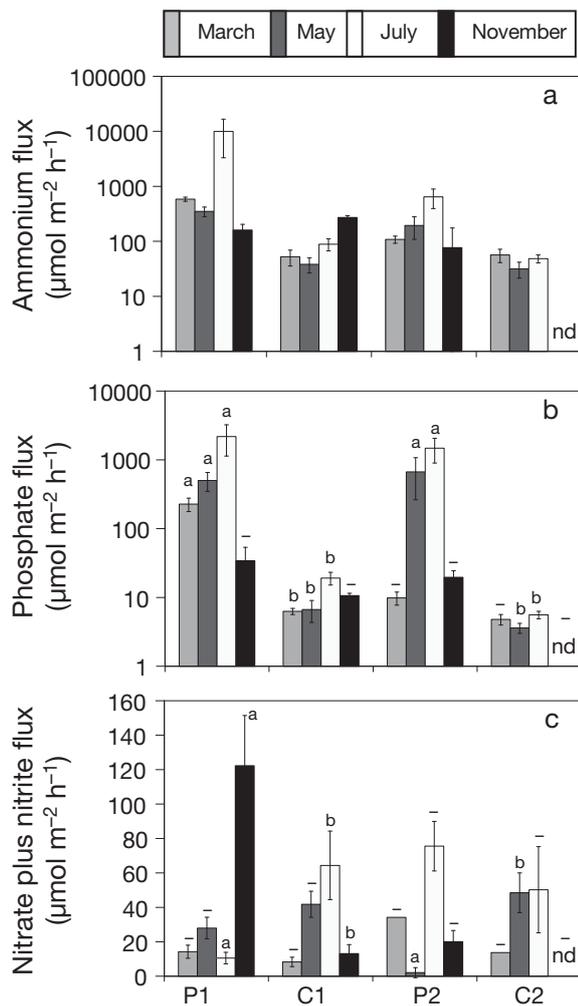


Fig. 3. Nutrient fluxes of (a) ammonium, (b) phosphate and (c) nitrate plus nitrite recorded during 2004 at sea-cage (P1, P2) and control (C1, C2) sites. Bars indicate means ($n = 4$ to 6 cores, \pm SE). nd: no data for that site/month. Different letters above panels denote significantly different sites from pairwise comparisons of P1 and C1 or P2 and C2 for each month separately. Dashes denote no significant difference between sites

experienced maximum concentrations of phosphate in the porewater during July, with a pronounced increase between March and July (by a factor of 4 at P1 and 15 at P2). There was then a sharp decrease to November. At P1 and C1, concentrations varied as a result of the interaction of site and month (Table 1b), with concentrations at P1 higher than C1 for all months ($p < 0.001$). Porewater concentrations of phosphate were significantly greater at P2 than C2 (Table 1b).

N and P content of sediments

The N content of sediments was lowest at C1 (0.06 to 0.08%) and highest at P2 (0.12 to 0.20%) (Fig. 5). P2

and C2 showed decreased N content in May, relative to March, before increasing in July. P1 and C1 showed increased N content from March to July. N content decreased in November at control sites and increased at sea-cage sites. There was a significant interaction of site and month at P1 and C1, as well as P2 and C2 (Table 1c). P1 had higher N content than C1 for July ($p = 0.006$) and November ($p < 0.001$), and P2 had a higher N content than C2 for March ($p = 0.045$), July ($p = 0.002$) and November ($p < 0.001$).

The P content of sediments was consistently lowest among sites at C2 (0.03 to 0.04%) and highest among sites at C1 (0.05 to 0.07%), although the highest values were found at the sea-cage sites in July. For sea-cage sites, the pattern of change among months was the same, where P content increased from March to July, before decreasing in November. C2 was invariant among months but C1 was variable. The lowest and highest P contents of sediments were measured at P2 (0.03 and 0.10%, respectively). There was a significant interaction of site and month on the P content at P1 and C1 as well as P2 and C2 (Table 1c). C1 had higher P content than P1 for March ($p = 0.004$), and P2 had a higher P content than C2 for July ($p < 0.001$) and November ($p = 0.001$).

Molar ratios of N:P

The molar N:P ratio of the sediments was lowest at C1 (1.9 to 2.4), highest at C2 (6.9 to 8.1) and P2 (5 to 8.5) and in the middle of the observed range at P1 (2.8 to 5.6) (Fig. 5). At sea-cage sites, the ratio decreased from March to July and increased from July to November. For C1 and C2 there was no temporal pattern. There was a significant interaction of site and month on the N:P ratio at all sites (Table 1c). P1 had higher ratios than C1 for March ($p < 0.001$) and November ($p < 0.001$), and C2 had higher ratios than P2 for July ($p < 0.001$).

The molar ratio of N:P of the sinking sediment matter collected in the sediment traps at the northern sites ($P1 = 10.7 \pm 0.4$ [mean \pm SE], $n = 8$; $C1 = 13.9 \pm 1$, $n = 5$) was lower than the southern sites ($P2 = 15.9 \pm 0.6$, $n = 5$; $C2 = 16.3 \pm 1.5$, $n = 8$). The ratio of N:P for porewater concentrations was lower at sea-cage sites ($P1 = 4.3 \pm 1.6$, $n = 8$; $P2 = 6 \pm 1.9$, $n = 8$) than at control sites ($C1 = 14.6 \pm 1.5$, $n = 8$; $C2 = 13.8 \pm 2.4$, $n = 8$). The ratio for sediments was lower at the northern sites ($P1 = 3.9 \pm 0.3$, $n = 16$; $C1 = 2.2 \pm 0.1$, $n = 16$) than the southern sites ($P2 = 6.8 \pm 0.4$, $n = 16$; $C2 = 7.3 \pm 0.2$, $n = 16$). The ratio of the nutrient fluxes for the sea-cage sites ($P1 = 7.3 \pm 2.8$, $n = 21$; $P2 = 5 \pm 1.5$, $n = 20$) was lower than for the control sites ($C1 = 9.3 \pm 1.1$, $n = 20$; $C2 = 17.7 \pm 2$, $n = 16$).

Table 1. Two-way ANOVA outputs for (a) the fluxes of ammonium, phosphate and nitrate plus nitrite, (b) porewater concentrations of ammonium and phosphate and (c) sedimentary content (%) of N, P and the N:P ratio at sea-cage (P1, P2) and control (C1, C2) sites. Significant sources of variation are shown in **bold**

	Source of variation	P1, C1				P2, C2			
		df	MS	F	p	df	MS	F	p
(a) Fluxes									
Log ₁₀ ammonium	Site	1	9.10	55.7	<0.001	1	3.91	30.1	<0.001
	Month	3	0.63	3.9	0.018	3	0.58	4.5	0.011
	Site × Month	3	0.28	1.7	0.188	2	0.34	2.6	0.093
	Error	32	0.16			29	0.13		
Log ₁₀ phosphate	Site	1	13.8	169.9	<0.001	1	18.75	167.1	<0.001
	Month	3	1.6	19.5	<0.001	3	4.61	41.1	<0.001
	Site × Month	3	1.7	20.9	<0.001	2	2.98	26.5	<0.001
	Error	32	0.08			29	0.11		
Nitrate plus nitrite	Site	1	1319	2.1	0.159	1	0.32	0.0	0.987
	Month	3	4202	6.6	0.001	3	5677	5.1	0.006
	Site × Month	3	9057	14.3	<0.001	2	4419	4.0	0.030
	Error	32	635			29	1108		
(b) Porewater concentrations									
Log ₁₀ ammonium	Site	1	4.23	156.7	<0.001	1	0.38	286.7	<0.001
	Month	3	0.12	4.4	0.043	3	0.08	62.1	<0.001
	Site × Month	3	0.06	2.4	0.147	3	0.14	104.3	<0.001
	Error	8	0.03			8	0.001		
Log ₁₀ phosphate	Site	1	12.0	366.1	<0.001	1	2.42	47.1	<0.001
	Month	3	0.23	7.1	0.012	3	0.19	3.7	0.060
	Site × Month	3	0.19	5.7	0.022	3	0.19	3.8	0.059
	Error	8	0.03			8	0.05		
(c) % content of sediment									
Log ₁₀ N	Site	1	0.23	48.6	<0.001	1	0.15	39.2	<0.001
	Month	3	0.03	5.95	0.003	3	0.04	11.1	<0.001
	Site × Month	3	0.03	6.32	0.003	3	0.02	3.9	0.021
	Error	24	0.005			24	0.004		
Log ₁₀ P	Site	1	0.03	2.49	0.128	1	0.26	26.6	<0.001
	Month	3	0.05	4.95	0.008	3	0.08	8.1	0.001
	Site × Month	3	0.03	3.12	0.045	3	0.06	6.4	0.002
	Error	24	0.01			24	0.01		
N:P	Site	1	23.5	53.4	<0.001	1	1.8	1.6	0.211
	Month	3	3.3	7.5	0.001	3	1.9	1.8	0.177
	Site × Month	3	3.3	7.4	0.001	3	7.3	6.7	0.002
	Error	24	0.44			24	1.1		

Phytoplankton primary productivity

We found no appreciable difference in calculated phytoplankton primary productivity between sea-cages and control sites (Table 2), except in July when sea-cages exceeded control sites by 30%. This result was driven by higher chl *a* concentrations at sea-cage sites (1.36 µg l⁻¹) compared to controls (0.98 µg l⁻¹) (Lauer 2005). The highest calculated primary productivity occurred in February, driven by higher temperatures, longer day lengths and higher surface irradiances. The lowest calculated primary productivity occurred in November, primarily as a result of lower chl *a* concentrations (Lauer 2005). At the control sites, benthic fluxes supplied between 7 and 25% of the N requirements

and between 9 and 85% of the P requirements for calculated primary production. At the sea-cage sites, benthic fluxes supplied between 40 and 752% of the N requirements and between 107 and 4109% of the P requirements for the calculated primary production.

DISCUSSION

Sedimentation rates above 40 g DW m⁻² d⁻¹ were found only during the farming season and were only observed at sea-cage sites, demonstrating the increased input of particulate material associated with SBT farming. The sedimentation rates at control sites ranged from 7 to 28 g DW m⁻² d⁻¹, whereas at sea-cage

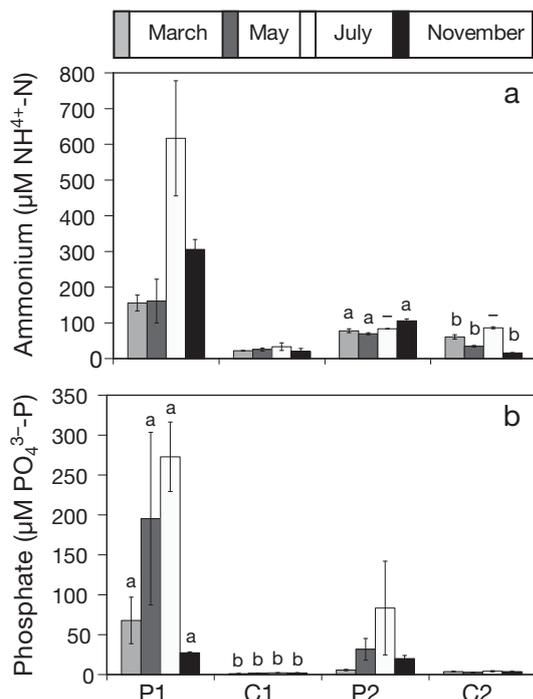


Fig. 4. Concentrations of (a) ammonium and (b) phosphate in the porewater of the sediments at sea-cage (P1, P2) and control (C1, C2) sites. Bars indicate means ($n = 2$ cores, \pm SE). Different letters above panels denote significantly different sites from pairwise comparisons of P1 and C1 or P2 and C2 for each month separately. Dashes denote no significant difference between sites

sites the range was 8 to 92 g DW $\text{m}^{-2} \text{d}^{-1}$. The latter rates are lower than for other species cultured in more protected waters, such as salmon (58 to 68 g DW $\text{m}^{-2} \text{d}^{-1}$) (Findlay et al. 1995), seabream and seabass (25 to 1870 g DW $\text{m}^{-2} \text{d}^{-1}$) (Mac Dougall & Black 1999). However, rates for experimental northern bluefin tuna sea-cages in the Mediterranean are even lower (4 to 8 g DW $\text{m}^{-2} \text{d}^{-1}$) (Vita et al. 2004) as a consequence of the smaller tonnage (1 to 4 t) compared to commercial SBT sea-cages (40 to 60 t). Although large pieces of uneaten feed were not observed in the sediment trap material, uneaten pieces were on occasion observed on the seafloor adjacent to sea-cage sites (P. Lauer & M. Fernandes unpubl. data). Fernandes et al. (2007a) reported that approximately 3% of feed given to SBT is uneaten. The measured sedimentation rates therefore potentially underestimate the total particulate flux to the seafloor adjacent to SBT sea-cage sites. The increased sedimentation at sea-cage sites in comparison to control sites is likely to derive from faecal material.

The SBT in sea-cages monitored in the present study received approximately 88 to 100 kg N d^{-1} in feed during the period of deployment of sediment traps. Assuming that the footprint of sedimentation of faecal material from the sea-cages extends to 100 m from the

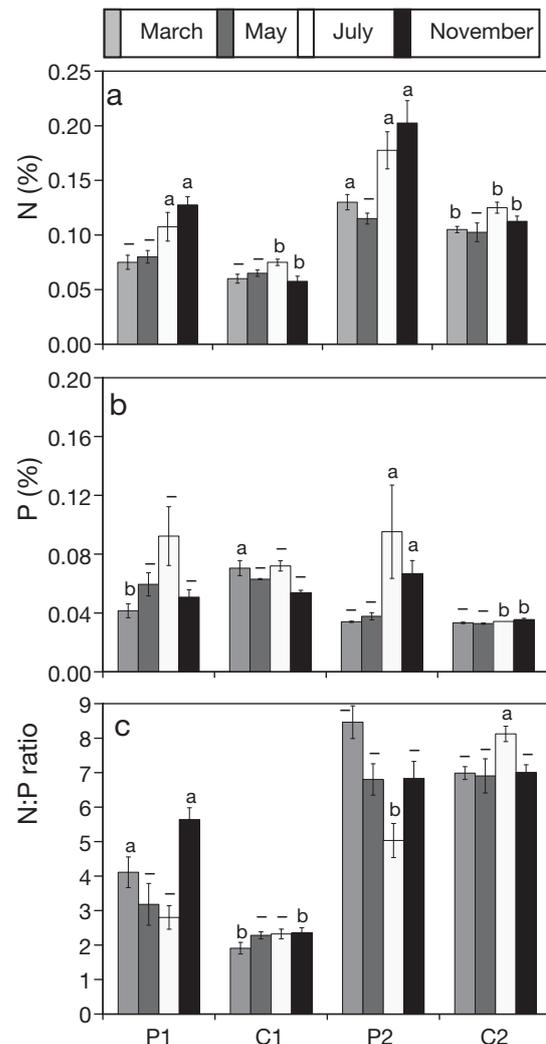


Fig. 5. (a) N content, (b) P content and (c) molar N:P ratio of the sediments throughout 2004 at sea-cage (P1, P2) and control (C1, C2) sites. Bars indicate means ($n = 4$ cores, \pm SE). Different letters above panels denote significantly different sites from pairwise comparisons of P1 and C1 or P2 and C2 for each month separately. Dashes denote no significant difference between sites

edge, 12% of daily N inputs are retained by SBT for growth, 3% is uneaten and up to 64% is excreted as soluble wastes (Fernandes et al. 2007a), this feed input to the receiving seafloor area translates into 0.41 to 0.46 g N $\text{m}^{-2} \text{d}^{-1}$. The average sedimentation rate at sea-cage sites for the days of sampling was 0.1 to 0.15 g N $\text{m}^{-2} \text{d}^{-1}$, suggesting that 24 to 32% of N inputs sinks to the seafloor within 100 m of the edge of the sea-cages (Fig. 6). Similarly, for P (assuming identical values as for N for retention, uneaten feed and soluble excretions of feed-derived P), the input from the bait-fish fed to stock was approximately 17 to 19 kg P d^{-1} , or 0.08 to 0.09 g P $\text{m}^{-2} \text{d}^{-1}$. The average sedimentation

Table 2. Modelled rates of primary production, N and P demand to sustain primary production, benthic fluxes and fraction of demand met by benthic fluxes

Site	Month	Production (mg C m ⁻² d ⁻¹)	Demand (mmol m ⁻² d ⁻¹)		Benthic fluxes (mmol m ⁻² d ⁻¹)		Fraction of demand (%)	
			N	P	N	P	N	P
Sea-cages								
	February	1850	23.3	1.5	9.4	3.1	40	212
	March	1312	16.5	1.0	6.9	14.0	42	1360
	July	1357	17.1	1.1	128.3	43.8	752	4109
	November	641	8.1	0.5	6.9	0.5	86	107
Controls								
	February	1882	23.7	1.5	1.6	0.1	7	9
	March	1211	15.2	1.0	1.9	0.1	13	13
	July	1073	13.5	0.8	3.0	0.3	22	35
	November	701	8.8	0.6	2.2	0.5	25	85

rate at sea-cage sites was 0.01 to 0.034 g P m⁻² d⁻¹, suggesting 13 to 39% of P inputs sinks to the seafloor within 100 m from the edge of the sea-cages. These percentages suggest that >60% of the N and P in faecal material from SBT farms does not reach the seafloor within 100 m from the edge of SBT sea-cages.

The high sedimentation rates in the vicinity of the pens were associated with a dominance of ammonium in inorganic N fluxes from the sediments. The ratio of ammonium to nitrate plus nitrite fluxes was 7 to 55 times higher at the sea-cage sites than at the respective control sites. Increased organic loading increases the ammonium fluxes relative to nitrification and denitrification (Blackburn & Blackburn 1992, Heggie et al. 1999). Ammonium fluxes at sea-cage sites measured

throughout the farming season significantly exceeded the natural variation at control sites. The maximal ammonium flux found adjacent to sea-cage P1 (9962 μmol m⁻² h⁻¹ in July) exceeded, by at least a factor of 6, those reported elsewhere for finfish farming, whereas the maximal flux at P2 (644 μmol m⁻² h⁻¹) was similar to previous reports (Hall et al. 1992, Hargrave et al. 1993, Christensen et al. 2000). The difference in nutrient fluxes between sea-cage sites suggests that management practices adopted by different operators can have a significant effect on benthic deposition and remineralisation. The difference potentially reflects the higher feeding rate and longer duration of farming at P1 than at P2. The background biogeochemical and hydrodynamic conditions at sea-cage sites could also contribute to the observed differences. The impact of SBT farming on benthic fluxes of phosphate was even more marked than for inorganic N. Phosphate fluxes at SBT sea-cage sites were 2 to >7 times those recorded in trout farms in Scandinavia (Holby & Hall 1991, Christensen et al. 2000). These very high values suggest comparatively minor binding to carbonate or iron in the sediments, perhaps as a consequence of saturation of the substrate, the presence of organic complexes (Koch et al. 2001) and patchy anaerobic conditions (Caraco et al. 1989).

The average of inorganic N fluxes (ammonium and nitrate plus nitrite) at sea-cage sites was 337 to 3185 μmol N m⁻² h⁻¹ (P2 and P1, respectively) whereas the value for phosphate fluxes was 651 to 831 μmol P m⁻² h⁻¹ (P2 and P1, respectively). Benthic fluxes of N were on average 1 to 7 times higher than measured sedimentation rates, whereas values for P were 18 to 48 times sedimentation rates, indicating that the system recycles labile wastes reaching the seafloor, with any accumulation being transient (Fig. 6). The higher fluxes than measured sedimentation rates are likely to be a result of the remineralisation of the material not

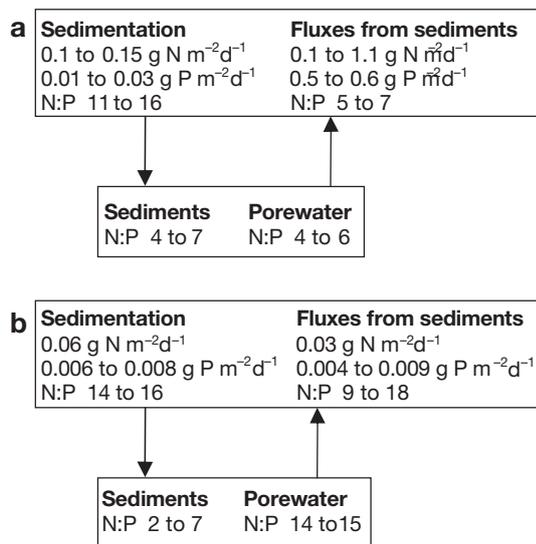


Fig. 6. N and P sedimentation rates, benthic fluxes and N:P ratios averaged for (a) southern bluefin tuna sea-cage sites when stock was fed and (b) over the sampling period at control (non-farm) sites

caught in the sediment traps, such as uneaten feed. Indeed, the highest benthic flux measurements were associated with uneaten pieces of feed on the sediment surface of incubated cores. Another cause for this apparent discrepancy is the fact that benthic fluxes integrate inputs over time. However, the balance between sedimentation and remineralisation at the seafloor is achieved over the period of several months when integrated over the season (Fernandes et al. 2007a). In the case of control sites, benthic nutrient fluxes accounted for approximately 47 to 55% and 44 to 150% of measured sedimentation rates for N and P, respectively (Fig. 6). Calculated primary productivity data suggested a greater deficit in N supply from the sediments than P. Smith & Veeh (1989) concluded that about 90% of primary production in Spencer Gulf was sustained by internal recycling of nutrients. Although results from our control sites suggest lower values of ~50%, sediments under the sea-cage sites release a large excess of nutrients to the water column that are then exported into the surrounding environment, particularly during the period near the end of the farming season.

Despite the high rate of benthic turnover, N content in the sediment at sea-cage sites increased by up to 63% from March to November, whereas the annual variation at control sites was less than 30%. We also observed a general increase in N content of sediments at control sites from March to July, before dropping in November. The increase in N during the farming season and the decrease after the season suggests that the whole farming zone might be mildly affected by the dispersal and resuspension of fine waste material.

Although P content at control sites did not show any consistent trends throughout the year, it also varied by up to 30% among months. Unlike N content, P content decreased at sea-cage sites from July to November. The increase in P content between March and July was higher at the southern site (P2 = 279% increase) than at the northern site (P1 = 219%), whereas at control sites the equivalent change was <3% at either site. Higher carbonate content in the southern area sediments (95 versus 47% in the north, Fernandes et al. 2006) suggests higher sequestration of P by these calcareous sediments (Koch et al. 2001). Increased pore-water P concentrations may further strengthen the role of sediments as a P sink by promoting the formation of fluorapatite (Howarth et al. 1995).

Low N:P ratios (i.e. 11 to 14) of sedimentary material sinking through the water column at the northern sites provide another line of evidence of dispersal of wastes throughout the whole farming area, including our so-called control sites. These values are lower than N:P ratios of marine plankton (N:P = 16) (Redfield et al. 1963) and might result from mixing with uneaten bait-

fish detritus (N:P = 12) and, particularly, P-enriched SBT faeces (N:P = 2) (Fernandes et al. 2007b). The southern sites had sedimentary ratios that approximated marine plankton, suggesting a smaller contribution from dispersing wastes, perhaps a result of the location of these sites, upcurrent from the prevailing northern current.

Differences in N:P ratios of sediments between sea-cages and controls were driven by higher N content in the south, and relatively low P content at C2. Interestingly, all values were <7, again suggesting that the dispersal of SBT farm wastes occurs over much of the farming area. Furthermore, the decrease in N:P ratios of the sediments for both sea-cages as the season progressed clearly indicates an accumulation of P. The build-up of P under the sea-cages driven by high sedimentation rates was accompanied by significantly lower N:P ratios in porewater and benthic fluxes, with ratios approaching the ratio for SBT faeces (Fig. 6). This suggests that faeces represents the bulk of labile organic matter reaching the seafloor at sea-cage sites, and this material is quickly metabolised and recycled to the water column. Although it is likely that some sedimentary material from sea-cages reaches control sites, as evidenced by N:P ratios of sedimentary material, the sedimentation rates are lower and the material is likely to be less labile (at least for P), in part due to leaching of nutrients (Fernandes et al. 2007a) and remineralization as particles travel through the water column.

There were approximately 130 sea-cages in the 172 km² SBT farming area (Lauer 2005). Fernandes et al. (2007a) calculated that for the same experimental conditions as those studied here, uneaten feed would settle up to 25 m from the edge of sea-cages. Therefore, it is likely that elevated fluxes measured in the present study occur within this radius around SBT sea-cages. Assuming that the annual mean benthic fluxes remained elevated 25 m from the edge of the sea-cages over a farming season (115 d at P2, 151 d at P1), between 11 to 134 t N is remineralised. The remainder of the farming zone releases on average 555 to 860 t N over the same period. Similarly, for P, sea-cage affected sediment remineralises 46 to 77 t P with the remainder of the farming zone releasing on average 69 to 235 t P. Other anthropogenic sources of N and P into the coastal region over 1 yr include Port Lincoln's wastewater treatment plant (9 and 8 t of N and P, respectively, SA Water 2003) and fish processors (24 and 1 t of N and PO₄³⁻-P, respectively, Dearman et al. 2001). The annual inputs of N and P into the coastal waters off Port Lincoln from benthic fluxes, from within 25 m from the edge of sea-cages and particularly from the remaining farming area, far exceed those inputs from other anthropogenic activities.

The combined daily input of inorganic N from benthic fluxes in the farming area corresponds to 8 to 11 % of the standing stock of inorganic N in the water column (58 t N, considering an average water depth of 20 m and background concentration of $0.017 \text{ mg N l}^{-1}$, Lauer 2005). The combined daily inputs of P from benthic fluxes are 10 to 21 % of the total standing stock in the water column (10 t P, using a background phosphate concentration of 0.003 mg l^{-1} , Lauer 2005). These estimates suggest that benthic fluxes have a greater impact on the supply of P to the water column than on N. Rates of primary production in the farming area are thus more likely to be limited by N supply, or some other element. Assuming high benthic fluxes up to 25 m from the edge of the sea-cages, sediments in the footprint of the sea-cages can supply enough N to support 1 to 6 t C d^{-1} through primary production, whereas inputs from the remaining area would support approximately 32 to 37 t C d^{-1} . If there were other sources of N to the water column (e.g. fish metabolic excreta) and the system was not N-limited, then the input of P from benthic fluxes under the sea-cages could generate 42 to 54 t C d^{-1} , whereas the remaining area could support 64 to 165 t C d^{-1} . These values are based on the assumptions that all nutrients supplied from the sediments are turned into phytoplankton C mass with no net export from the farming area, and therefore represent an overestimate of actual rates of primary production as a result of benthic fluxes. C production estimates using the calculated primary productivity data suggest that approximately 1 t C d^{-1} is produced within the water column extending 25 m from the edge of the sea-cages, and 120 to 322 t C d^{-1} from the remaining area. Interestingly, the total primary productivity (i.e. sea-cage and remaining area) of the farming area using the calculated primary productivity data is higher than that predicted from the sediment fluxes alone, suggesting benthic fluxes are not sufficient to support primary productivity in the farming area. It is likely that dissolved nutrients in the form of soluble excretions from SBT (Fernandes et al. 2007a), and those imported from the Southern Ocean, contribute to the discrepancy in primary production.

Although monitoring of chl *a* within the SBT farming area did not find a significant difference among sea-cage and control sites (Clarke et al. 2000), Andersen et al. (2006) suggested that measurements of primary production should be mandatory for monitoring the ecological status of coastal waters because this is a more representative indicator than chlorophyll of the biological processes occurring in the pelagic system. It is likely that nutrients from SBT farming lead to increased primary productivity during the SBT farming season and perhaps changes in phytoplankton species diversity, with subsequent predictable responses

to increased primary production by higher trophic levels. The potential for SBT-derived wastes to reach the seafloor throughout much of the farming area has consequences for the placement of the industry's environmental monitoring control sites that are currently located throughout the SBT farming area.

CONCLUSIONS

As a consequence of SBT farming, sediments under the sea-cages act as a reservoir and source of nutrients to the pelagic system, supplying N and P in excess of phytoplankton growth requirements. The decrease in ammonium and phosphate fluxes at sea-cage sites at the cessation of the farming season suggests that the impact of SBT farming is reversible, given sufficient time for recovery. Following—the removal of sea-cages from sites after a season of production to allow sediment processes to return to background conditions over a time period of at least 1 yr—is currently a state-government requirement for SBT farming within South Australia. The results from the present study offer support for continuation of these following practices to allow for sediment recovery after SBT farming activities. Coastal sustainability of the ecosystem supporting SBT farming requires further consideration of the regional consequences from the inputs of N and P through increased sedimentation, nutrient availability and, potentially, primary production.

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