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Effects of eutrophication on the planktonic food web dynamics of marine coastal ecosystems: the case study of two tropical inlets

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Abstract

We studied the plankton dynamics of two semi-enclosed marine coastal inlets of the north of Jurong Island separated by a causeway (SW Singapore; May 2012-April 2013). The west side of the causeway (west station) has residence times of ca. one year and is markedly eutrophic. The east side (east station) has residence times of one month and presents lower nutrient concentrations throughout the year. The higher nutrient concentrations at the west station did not translate into significantly higher concentrations of chlorophyll *a*, with the exception of some peaks at the end of the South West Monsoon. Microzooplankton was more abundant at the west station. The west station exhibited more variable abundances of copepods during the year than did the east station, which showed a more stable pattern and higher diversity. Despite the higher nutrient concentrations at the west station (never limiting phytoplankton growth), the instantaneous phytoplankton growth rates there were generally lower than at the east station. The phytoplankton communities at the west station were top-down controlled, largely by microzooplankton grazing, whereas those of the east station alternated between top-down and bottom-up control, with mesozooplankton being the major grazers. Overall, the trophic transfer efficiency from nutrients to mesozooplankton in the eutrophic west station was less efficient than in the east station, but this was mostly because a poor use of inorganic nutrients by phytoplankton rather than an inefficient trophic transfer of carbon. Some hypotheses explaining this result are discussed.

Key words: Eutrophication; Trophic efficiency; Phytoplankton; Zooplankton; Grazing; Growth; Food web; Singapore; Monsoon

1. Introduction

Increased inputs of nutrients over the last decades have originated eutrophication in many aquatic ecosystems around the world. The effects of these nutrient loadings are different in freshwater and in coastal marine ecosystems, although in both cases they define the relationship between the sizes of producers and grazers (Smith et al. 1999; 2006). In lakes, this relationship is unimodal (Havens 2013): in ultraoligotrophic and hypereutrophic lakes the size (either too small or too large) or the palatability of phytoplankton disrupt the flux of energy throughout the food web by inhibiting large zooplankton grazing (Elser, 1999; Havens et al., 2000; Paerl et al., 2001; Havens 2013). In mesotrophic lakes, however, short cladoceran/rotifer-based food webs efficiently transfer the energy from primary producers to fish (Havens 2013). Marine systems, on the other hand, usually display more complex planktonic food webs and less clear responses to nutrient concentrations (Oviatt et al., 1989; Anderson et al. 2002). Nevertheless, according to nutrient loads and their ratios, we can roughly classify marine systems in (1) upwelling, with high concentrations of inorganic nutrients and diatom-dominated; (2) oligotrophic oceanic systems, poor in nutrients and picoplankton-dominated; (3) mesotrophic systems, with moderate and balanced nutrient concentrations and usually subjected to seasonality; and (4) eutrophic systems, with high levels of nutrients and high N to Si ratios, and usually dominated by inedible algae (Smith et al., 1999). From a trophic transfer efficiency point of view, it is expected upwellings being more efficient than oligotrophic and eutrophic systems (Sommer et al. 2002). Mesotrophic systems should alter food web structure and its efficiency throughout the seasonal cycle (Calbet et al., 2008).

Even though anthropogenic nutrient enrichment of coastal marine systems has been linked to stimulation of some harmful phytoplankton species (mostly dinoflagellates; Anderson et al. 2002; Heisler et al, 2008), the blooming of diatoms that can be readily consumed by micro- and mesozooplankton (Suzuki et al., 2002; Aberle et al., 2007; Castellani et al., 2008) also may occur (Oviatt et al., 1989). The dominance of one group of phytoplankton over another will greatly influence the planktonic food web dynamics and the overall efficiency of the system. Therefore, the effects of eutrophication on marine coastal systems seem indeed less predictable than in freshwater ones.

Another important difference between marine and freshwater systems resides on the nature of their major planktonic herbivorous. While in lakes cladocerans highlight as major consumers of the secondary production (Edmonson and Litt, 1982; Sarnelle, 1992), in marine systems this role is undertaken by microzooplankton (Sherr and Sherr, 2002; Calbet and

Landry, 2004; Schmoker et al., 2013). Microzooplankton, with fast generation times are proven to be very efficient grazers even in very eutrophic conditions or during harmful dinoflagellate blooms (Andersen and Sørensen, 1986; Calbet et al., 2003; Schmoker et al., 2013). Microzooplankton are, at their turn, the preferred prey of copepods, the dominant crustacean grazers of the oceans (Fessenden and Cowles, 1994; Suzuki *et al.*, 1999; Broglio *et al.*, 2004; Saiz and Calbet, 2011). Under this food web scenario, it would be expected the link between phytoplankton and microzooplankton being strong under eutrophy, and, opposite to freshwaters, the trophic transfer efficiency throughout the food web not being largely diminished respect more mesotrophic conditions. Moreover, given the tight dependence of phytoplankton on nutrients and the unimodal relationship between biomass and diversity of phytoplankton and zooplankton (Irigoien et al., 2004), one would expect that more eutrophic sites, with constant anthropogenic nutrient discharges, would generally favour the settlement of stable and less diverse planktonic food webs compared to the more variable mesotrophic conditions, likely more influenced by climatological phenomena (e.g, seasonal spring blooms).

To validate these hypotheses we focused on the succession and trophic dynamics of plankton at two semi-enclosed sites (west and east station) on Singapore's coast, north of Jurong Island. This island is a reclaimed landmass linked to the mainland by a causeway, which does not allow east-west water exchange. The flushing characteristics of both sites, based upon DHI MIKE21 FM Advection Dispersion Model (www.mikepoweredbydhi.com), support that the water exchange in the west station is much lower than the water exchange in the east site. At the west station, with a narrower and longer mouth facing SW, the water exchange was < 20 % for the two-month of simulation period carried out; whereas at the east station, with a wider mouth facing SE, 80 % of the water was flushed out of the area within a month. Eutrophication models for lakes show that the rate of water renewal is key to modify the nutrient loading and the level of eutrophication of a system (Dillon and Rigler 1974; Vollenweider 1976; Shindler, 2006). Therefore, we expect the west station being more eutrophic than the east one; this was confirmed by previously preliminary data (Schmoker unpublished). The study area is influenced by the Southeast Asian Monsoon, which provides a wide variety of environmental conditions and food web scenarios. The Southeast Monsoon divides the year into four periods: two main monsoon seasons, the Northeast Monsoon from November to early March and the Southwest Monsoon from June to September, and two inter-monsoon periods (late March to May and October to November). Heavy rains and winds characterize both monsoon periods, while throughout the Inter Monsoon transitions the

rain is intermittent and winds are weak and variable (National Environment Agency, 2009; Behera et al., 2013).

Our goal was therefore twofold: On the one hand, we aimed at assessing the importance of eutrophication on planktonic succession, trophic dynamics, and food web transfer efficiency of marine planktonic food webs. On the other hand, providing a necessary frame to validate our hypotheses, we wanted to characterise the major drivers of the plankton succession of these two sites and provide an up-to-date record of the plankton dynamics and species description for inshore waters at Singapore. The plankton of these sites in the southwest sector of Singapore has never been studied before.

2. Material and methods

2.1. Sampling and basic analysis

We sampled two stations at two-week intervals, from May 2012 to May 2013, on the southwest coast of Singapore (Fig. 1; west station; 01°N17.949'N, 103°42.383'E and east station; 01°17.694'N, 103°43.340'E). We measured temperature and salinity every 25 cm using a YSI 6920 S2 multi-probe sensor calibrated before each survey, and we took samples for chlorophyll *a* (chl *a*) and small planktonic organisms <100 µm at 1 m (hereafter, "surface"), 10 m and 15-20 m (near the bottom) using a 5 L Niskin bottle. To collect mesozooplankton we pulled a 50-cm mouth, 100 µm-mesh plankton net from bottom to surface by hand. We also obtained light profiles (PAR = photosynthetically active radiation) with an Underwater Quantum Sensor (LiCor LI-192). We measured oxygen concentration using an optode system (Presens, Germany) at 1 m, 10 m and 15-20 m.

In the laboratory, we estimated chl *a* concentrations by filtering 250 to 500 ml through 10 µm screens and 150 to 250 mL through GF/F filters. Chl *a* was extracted from all the filters overnight in 90% acetone at 4ºC in the dark, and concentrations were then determined from *in vitro* fluorescence with acidification using a Turner Designs Trilogy model fluorometer (Strickland and Parsons, 1972). Inorganic nutrients (nitrate, ammonium, phosphate and silicate) were estimated following a standard protocol using a Skalar Flow Injection Analysis Autoanalyzer (APHA 4500). The minimum level of detection for all inorganic nutrients was 0.01 mg L^{-1}.

2.2. Microplankton and mesozooplankton abundance and biomass determination

Microplankton samples (250 mL of seawater) were fixed with acidic Lugol's solution (2% final concentration) and stored at room temperature in the dark. Subsamples of 10 mL were

allowed to settle for 6 h in Utermöhl chambers, and microplankton organisms were counted for the whole chamber. Their volumes were approximated by the closest geometrical shapes and they were converted to carbon using the equations of Menden-Deuer and Lessard (2000). Mesozooplankton samples were fixed with 4% formaldehyde. Around 1000 individuals were counted per sample (Omori and Ikeda, 1984) identified, when possible, to species level, and sized and converted to carbon using the equations of Uye (1982).

2.3 Primary production estimation

We determined primary production using the oxygen measurement method (light and dark bottles; Cullen, 2001). We sampled water at 1 m with a 5 L Niskin bottle, and then we homogenously distributed it into six 300 mL BOD bottles. Three bottles were kept in the light and three more were kept in the dark by covering them with aluminium foil. We measured oxygen at the beginning and at the end of the incubation with an optical oxygen probe (Presens, Germany). All bottles were incubated for ca. 24h *in situ* at the depth of water collection (1 m) to keep incident light and temperature conditions identical for all bottles. For carbon conversion we used the ratio of moles of carbon to moles of oxygen (i.e., 1 mg O_2 equals to 0.375 mg C).

2.4 Micro- and mesozooplankton grazing experiments

We used the dilution method (Landry and Hassett, 1982) to estimate phytoplankton growth rate and mortality rate from microzooplankton (< 200 µm organisms) grazing on nine dates at both sites, and used a size-fractionation approach for mesozooplankton (> 200 µm organisms). For all the experiments, filters, tubing, meshes and bottles were acid washed and then rinsed with ultrapure water prior to each use. Water was collected at 1 m with a 5 L Niskin bottle and experiments were set up within 2 h after sampling. For microzooplankton, treatments were established by diluting measured amounts of seawater, reverse-screened with 200-µm mesh to remove mesozooplankton, with 0.22 µm-filtered seawater. This diluting water was obtained by gravity filtration using a 0.22-µm filter capsule Acropak filter (Whatmann) into a clean 25 L polycarbonate carboy (Nalgene, USA). Duplicate 1.3 L polycarbonate bottles (Nalgene, USA) were prepared for 5 dilution treatments with percentages of unfiltered seawater volumes of 12, 25, 50, 78 and 100%. Nutrients (10 mL of f/2 medium with silicate per litre) were added to promote constant phytoplankton growth in the treatments. We used two bottles, filled with 200 µm screened seawater without nutrient amendment, as no-nutrient controls, and two bottles were filled to be used as initials. All

bottles were incubated for ca. 24h *in situ* in mesh bags hanging from the boat at the same depth as that of water collection (1 m). We estimated chl *a* concentration at the beginning and at the end of the incubation by filtering 150- 250 mL onto GF/F filters and processing the filters as above. For all experiments, the net phytoplankton growth rates, estimated from changes in chl *a* concentration during the incubation period, were plotted against the fraction of undiluted water, and a model I linear regression was fitted to the data to obtain the slope (*m*; grazing mortality rate, d^{-1}) (Landry and Hassett, 1982). In three out of the 18 experiments we found saturated feeding responses (Gallegos, 1989). For those the linear regression was fitted only to the highly diluted treatments to obtain the phytoplankton instantaneous growth rates with added nutrients (μ_n; d^{-1}), and the *m* (d^{-1}) values were derived from those growth rates (as per Gallegos, 1989; Calbet and Saiz, 2013). Microzooplankton impacts on standing stock (% standing stock removed d^{-1}) were calculated using the equations provided by Landry *et al.* (2000).

For mesozooplankton grazing determinations we collected water at 1 m depth with a 5 L Niskin bottle. Triplicate 2.4 L polycarbonate bottles (Nalgene, USA) were sequentially (1/3 at a time) filled with unfiltered seawater directly from the Niskin bottle; in these bottles the community of mesozooplankton was present. Nutrients (10 mL f/2 media per litre) were added to the bottles. Two additional 1.3 L bottles were filled and used as initials. We estimated grazing based on chl *a* differences between initial and final bottles using the equations of Frost (1972). Controls for these bottles were the 200-µm pre-screened and nutrient amended dilution bottles (100% treatment of the dilution series not containing mesozooplankton). As for microzooplankton grazing, all bottles were incubated for ca. 24h *in situ* at 1 m depth. At the end of the incubation, the mesozooplankton in the experimental bottles were collected by filtering the sample through a 200-µm sieve, and they were counted under the stereomicroscope. The ingestion rates per individual were obtained then, and these rates were scaled to the entire water column using the abundances the integrated plankton net hauls.

3. Results

3.1. Physico-chemical parameters

The water columns at both west and east stations were generally well mixed vertically, with temperature ranging between 28ºC and 31ºC (Fig. 2a, b) and salinity between 26 and 32 at both stations (Fig. 2c, d). In general, the water was relatively colder during the end of the winter months and warmer from April to July (Fig. 2a, b). Salinity varied concurrently with

217 the monsoons: the Southwest Monsoon period presented lower salinities (higher rainfall), and
218 the second Inter Monsoon transition of 2012 and the first Inter Monsoon transition of 2013
219 showed higher salinities (Fig. 2c, d). Some weak haloclines and thermoclines were observed
220 at a depth of about 5 m during the Inter Monsoon transitions and at the end of Southwest
221 Monsoon (Fig. 2).

222 We present only a representative plot of the light attenuation in the water column
223 (Fig. 3). On average for the period sampled, light intensity at 5 m depth was reduced to 6 and
224 10% of near-surface light at the west and east stations, respectively. Consequently, only 1 and
225 2% of the near-surface light reached 10 m at the west and east station, respectively.

226 Generally, the west station showed higher inorganic nutrient concentrations than the
227 east station during the whole year (on average three times more nitrate and ammonium and
228 two times more phosphate and silicate, $p < 0.001$, Two-way ANOVA; Fig. 4a-h). Nitrate
229 peaked during the Southwest Monsoon at both stations, the concentrations being relatively
230 lower for the rest of the year. No major dissimilarities were observed among the different
231 depths sampled, except for three occasions at the west station (in October 2012, December
232 2012, and April 2013) when the concentrations of nitrate at 1 m dropped nearly to zero.
233 Similar drops in surface nitrate concentrations were more frequent at the east station (Fig.4a,
234 b). Both stations also showed a noticeable peak of nitrate by the end of March 2013. The west
235 station showed widely variable concentrations of phosphate throughout the year, with higher
236 values during the Southwest Monsoon (Fig. 4c). After this period, there was a decoupling
237 between surface and deeper waters. The east station had very stable concentrations of
238 phosphate through the year, with the exception of three peaks, two during the Southwest
239 Monsoon and the third at the end of March 2013 (Fig. 4d). The pattern of fluctuations of
240 silicate at 1 m throughout the year was similar for both sites, although the west station
241 showed higher peaks (Fig. 4e, f). The silicate concentrations gradually decreased from the
242 first sampling, rose to a peak in August, then dropped abruptly to low levels sustained until
243 December, when they started rising again. Deeper samples generally showed higher values
244 than surface ones, with the exception of the August peak. The ammonium concentrations of
245 deeper waters were quite similar for both stations (Fig. 4g, h). However, the surface values
246 differed for the first half of the Southwest Monsoon period.

247 Our sampling for dissolved oxygen concentration only started in September 2012. As
248 expected, surface waters had more dissolved oxygen than deeper layers at both stations (Fig.
249 5a, b). Oxygen concentrations were above the normally acceptable concentrations for fish life
250 (5 mg L^{-1}) at 1 m, but were below that in the deeper waters of the west station for most of the

year. All the samples showed normoxic conditions for zooplankton (> 2 mg L^{-1}; Richmond *et al.* 2006; Roman *et al.*, 2012).

3.2. Plankton abundance

Bulk phytoplankton community biomass was represented as chlorophyll *a* (chl *a*) concentration. In general, we found higher chl *a* at surface (1 m) at both stations. The chl *a* concentration was more variable in the west station (coefficient of variation, CV of 138%), with peaks at the end of the Southwest Monsoon > 30 µg L^{-1} (Fig. 6a). The concentrations during the second half of the Northeast Monsoon were relatively low there (< 2 µg L^{-1}), but peaked again by the end of April 2013. The chl *a* of the east station was more constant (CV 88%), with rises at the beginning and second half of the Southwest Monsoon period (Fig. 6b). The phytoplankton blooms during the second half of the Southwest Monsoon were more evident in the average chl *a* of the entire water column. Overall, there were no significant differences in the chl *a* concentration at both stations (Two-way ANOVA). From August 2012 we also quantified the concentration of chl *a* in cells > 10 µm (Fig 6c, d). While in the east station the contribution of larger cells to total chl *a* oscillated some (from 60 to 100%, with only two exceptionally low values) the west station showed wide seasonal fluctuations (Fig. 6c, d). At the west station the contribution of > 10 µm cells was low by the end of August (10%) and gradually increased to 90-100% between October 2012 and January 2013. After that the contribution of large cells decreased again until March 2013 and became erratic from then on.

The seasonal patterns of diatom abundance (mostly *Skeletonema* spp., *Pseudo-nitzschia* spp., *Lauderia* sp., and *Helicotheca* sp. at both stations) were very different between stations (Fig. 7). At the west station, diatoms flourished at the end of Southwest Monsoon and declined again during the second half of the Northeast Monsoon (Fig. 7a). At the east station, on the other hand, diatoms erratically peaked without any clear seasonal pattern (Fig. 7b). Both stations showed higher counts of diatoms at the surface than in deeper layers. Overall, diatoms were more variable in their abundance at the west station than at the east station (CV=242% *vs.* 142%, respectively). Dinoflagellates (mostly *Gyrodinium* spp., *Ceratium* spp., and *Protoperidinium* spp.) and ciliates (*Strombidium*-like) showed a heterogeneous distribution throughout the year, with peaks not occurring in any specific season (Fig. 7c-f). They were much more abundant at the west station, although this difference was only significant for dinoflagellates ($p < 0.02$). Of special note, there were a drastic decrease of ciliates at the west station during September, and the absence of massive harmful algal

285 blooms. In general, the concentrations of ciliates and dinoflagellates were highest in surface
286 water. As with diatoms, dinoflagellates and ciliates were more variable during the year at the
287 west station than at the east station (Fig. 7c-f).
288 We focus on copepods to describe the seasonality of mesozooplankton, because they
289 dominated the community (> 99% of the abundance). The west station showed large
290 variations in total copepod abundance during the year (CV 108%), with peaks during the
291 Inter Monsoon periods, and lower, although still rather high, abundances the rest of the year
292 (Fig. 8a). The first peak, in November 2012, coincided with a bloom of the cyclopoid
293 *Oithona simplex*, and the second peak, in March 2013, was a combination of roughly equal
294 abundances of calanoids (mostly *Bestiolina similis*), cyclopoids (*O. simplex*) and
295 harpacticoids (*Euterpina acutifrons*; Table Annex 1). The east station exhibited overall lower
296 copepod abundance ($p < 0.01$) and a more stable pattern throughout the period studied (CV
297 55%), with only one peak in December 2012 (Fig. 8b), mostly an increase in the calanoid
298 *Temora turbinata* (Table Annex 1). At both stations, *B. similis*, *Parvocalanus crassirostris*,
299 *O. simplex*, *E. acutifrons*, and *T. turbinata* dominated the copepod community through the
300 year. On average, during the sampling period at the west station, cyclopoids and calanoids
301 showed similar abundances, and harpacticoids were less abundant (Fig. 8c). At the east
302 station, on the contrary, calanoids dominated most of the year, with the exception of the very
303 ends of the monsoon phases, when combined cyclopoid and harpacticoid abundance equalled,
304 and even surpassed, that of calanoids (Fig. 8d). Both stations showed predominance of
305 calanoids in early February 2013. The east station had higher diversity, here defined as
306 species richness. Ranges of species richness at this station were 8-21 for copepods and 11-33
307 for all mezooplankton. Those ranges at the west station were 7-14 and 12-25. Overall, the
308 copepod species richness was greater at the east station than at the west station in14 out of 19
309 samplings (average 50% higher). The Shannon-Wiener diversity index was also higher at the
310 east station (2.34) than at the west station (1.94). None of the major species/groups of
311 phytoplankton, microzooplankton and copepods at the west station were correlated with any
312 of the physical variables or with any of the prey (Spearman non-parametric correlation).
313 However, at the east station ciliates ($r = -0.46$), *P. crassirostris* ($r = 0.58$), and *O. simplex*. (r
314 $= 0.79$) were significantly correlated with temperature, and the later species was also
315 correlated with salinity ($r = 0.47$). None of the copepod species appeared to be correlated
316 with any of the prey; however, ciliate abundance was correlated with chl *a* ($r = 0.29$) and
317 dinoflagellates ($r = 0.36$).
318

319 *3.3. Primary production*

320 We conducted 7 experiments to estimate phytoplankton primary production at both stations
321 (Table 1). Overall, gross primary production was higher and less variable at the east station
322 than at the west station ($p < 0.01$, Two-way ANOVA). At the west station it ranged from 6 to
323 43 mg C m^{-3} h^{-1}, and at the east station it ranged from 35 to 55 mg C m^{-3} h^{-1}. Net primary
324 production was also more variable at the west station, at times showing negative values,
325 indicating the losses by respiration were more than the new production. At the east station the
326 net primary production was always positive.

327

328 *3.4. Phytoplankton grazing and growth rates*

329 The dilution technique allows for simultaneous estimates of phytoplankton growth rates,
330 nutrient limitation and microzooplankton grazing. Microzooplankton grazing rates rendered
331 daily impacts on the standing stock of phytoplankton of similar magnitude (from 0 to ca.
332 100%) at both stations (Table 2; $p = 0.18$). Phytoplankton growth rates were more variable at
333 the west station (from -0.5 to 1.62 d^{-1}; CV 150%) than at the east station (0.21 to 1.8 d^{-1}; CV
334 60%). Nutrients were never significantly limiting at the west station, but they limited
335 phytoplankton growth on four occasions at the east station (Table 2). Mesozooplankton
336 grazing impact was strongly variable and significant in 3 and 7 of the 9 experiments at each
337 of west and east station, respectively. Impacts ranged from 0 to > 100% of the standing stock
338 of phytoplankton being consumed daily at each station (Table 2). Grazing rates were negative
339 on many occasions at the west station.

340

341 *3.5. Overall efficiency of the system*

342 We calculated the chl *a* produced per µM of Nitrate at both sites, and the carbon of grazers
343 supported per unit of prey biomass (Table 3). In the west station, 1 µM of Nitrate sustained
344 0.82 µg chl *a*; whereas, in the east station the same amount of nutrient supported 2.1 µg ($p <$
345 0.05; t.test two-tailed for unequal variances). The biomass of grazers per unit of biomass of
346 chl *a* was also different at both stations (Table 3), these being higher at the west station.
347 However, the differences were not statistically significant. Microzooplankton biomass
348 supported similar biomasses of copepods at both sites (Table 3).

349

350

351 **4. Discussion**

352 *4.1. Population dynamics*

353 The seasonal shifts in the directions of the major currents affect the species composition of
354 Singapore waters (Gin *et al.*, 2000; 2006), and could be expected to influence our sampling
355 sites, particularly the east station that is more open, less eutrophic, and with a shorter water
356 residence time. Therefore, we anticipated greater seasonal differences in abundance of
357 organisms and species diversity at the east station than at the west station. While our data
358 confirmed our hypothesis for diversity, we found more variability in abundances at the west
359 station. The key to interpreting this result may be found in the higher and more variable
360 concentrations of inorganic nutrients (a factor fuelling the entire food web) at the west station
361 and in the interplay of primary producers with some physicochemical variables (see below).
362 The dominant phytoplankton species found in our study, and the timing of the major
363 bloom at the end of the Southwest Monsoon, do not differ from previous records in Singapore
364 waters (Tham, 1953; Gin *et al.*, 2000; 2006; Pham *et al.*, 2011; Schmoker et al., 2014). What
365 is surprising, however, was the absence of harmful algal blooms during our survey, because
366 they have been a recurrent phenomenon in harbours and coastal waters of Singapore (Holmes
367 and Teo, 2002; Gin *et al.*, 2006). The variability and unpredictability of these episodes,
368 together with the limited duration of our survey, preclude any specific hypothesis about this
369 observation.
370 Regarding microzooplankton, no earlier data are available for Singapore, except for
371 some descriptions of Tintinnida and large dinoflagellates obtained by net-collections (Tham,
372 1953; 1973). Those papers, although unique in their time, merely described the appearance of
373 some groups, without providing abundances. Yet, as occurred in our study, Tham also
374 observed a lack of seasonality among protozoans. Concerning ciliates, the drop of abundance
375 we observed in mid-September needs special mention. That could have been connected with
376 the poor condition (negative growth rates) of phytoplankton during the preceding month, but
377 it may have another explanation. A few days before our recording of low ciliate abundance,
378 on September 9, there was a moderate oil spill (< 60 metric tons) resulting from a collision of
379 two vessels in the area (*http://www.mpa.gov.sg*). Patches of oil and foam from chemical
380 dispersants were evident during that sampling day. Ciliates are more sensitive than other
381 planktonic organisms to hydrocarbons and chemical dispersants (Almeda *et al.*, 2014) and
382 could, therefore, have been negatively affected by those substances.
383 According to previous mesozooplankton studies in the Strait of Singapore and
384 southern Strait of Malacca, we expected maximum abundances of copepods around March
385 (Wickstead, 1961; Rezai *et al.*, 2004). Therefore, it is unexpected we observed that seasonal
386 pattern only at the west station, not at the east station, which in theory is more influenced by

Singapore Strait water. Despite this, at the east station copepods in particular, and plankton in general, were more dependent on the seasonal variations of temperature. Other records in the Singapore Strait have also shown distinctive seasonal patterns (Tham, 1953; 1973), which suggests there is wide inter-annual variability in the area. This underlines the need for proper description of biodiversity (monitoring) and its controls over extended periods in Singapore waters (Schmoker *et al.*, 2014).

4.2. Food web dynamics in relation to the level eutrophy

Overall, nutrient concentrations were high and would not have limited phytoplankton growth at the west station, unless rapidly taken by other competitors (i.e., prokaryotes). However, they were limiting on four occasions at the east station. With our experimental design we cannot discern whether this limitation was produced by just one of the several nutrients, but it seems plausible to assume the major restrictive nutrient at the east station was nitrogen. This element has been identified as limiting in marine waters of Singapore and in wet atmospheric depositions to the area (Gin *et al.*, 2006; He *et al.*, 2011). Moreover, the average molar N:P ratio in water for the sampling period was < 16, combining nitrate and ammonium as nitrogen sources, which also indicates possible nitrogen limitation.

Paradoxically, the phytoplankton of the west station with more available nutrients and presenting more eutrophic conditions displayed lower primary production and instantaneous growth rates (independent of grazing). Of particular note are the negative instantaneous phytoplankton growth rates and primary production estimates obtained in August and the beginning of September. It is not possible to conclude why nutrients were poorly used by the phytoplankton of the west station and why there were sudden mortality episodes, but some speculation is possible: (1) Light penetrated less (ca. factor of 0.5) at the west station and was certainly limiting below 10 m. The phytoplankton blooms at the west station mostly occurred during periods of water column stability, which would allow the algae to grow in the favourable upper column conditions, being light-limited the rest of the year. Notably, the maximum light penetration found in our study at the west station coincided with the largest phytoplankton bloom observed, in October 2012. (2) Oxygen levels were not low enough to produce phytoplankton mortality, but we cannot discard a massive mixing event re-suspending reduced toxic compounds from the sediment. (3) Unaccounted sources of mortality may have been acting at this site. These would include viruses, parasites, bacterial infections, and pollutants. Regarding this last aspect, the oil spill episode mentioned above may have had a strong impact, and the site has high concentrations of some heavy metals in

the water column and underlying sediments. The concentrations of some metals (e.g., Cd, Cu, Sn, Zn) were a full order of magnitude greater in the sediments of the west station than of the east station (Calbet *et al.*, 2016); similar concentrations to those measured in the west station water column are described as toxic for some planktonic organisms (Wilson and Freeberg, 1980; Hook and Fisher, 2001; Bielmyer *et al.*, 2006). (4) From our food web efficiency estimation we deduce that inorganic nutrients are inefficiently converted into phytoplankton biomass at the west station. This could be result of some sublethal effects, as mentioned in the previous point, or being consequence of a faster nutrient uptake by prokaryotes, fuelling an important microbial food web in this site (Kirchman *et al.*, 1994; Middelburg and Nieuwenhuize 2000). This later fact is corroborated by the higher biomass of microzooplankton per µg chl *a*, and by the lack of phytoplankton response to the ammonium peaks at the beginning of the Southwest Monsoon in the west station.

Beside natural and unknown mortality sources, it was evident that the phytoplankton was under strong grazing pressure at both sites. As hypothesized, at the west station we found rather constantly high microzooplankton grazing rates, with only one exception coinciding with the above-mentioned, unanticipated phytoplankton mortality episodes. At the east station the grazing rates of microzooplankton were also relatively high and within the range expected for similar areas (Calbet *et al.*, 2004; Schmoker *et al.*, 2013). Mesozooplankton grazing impacts on phytoplankton were, on the other hand, higher at the east station. This fact was reinforced by the greater stability of copepod abundance in the east station. Given the high abundances of ciliates and heterotrophic dinoflagellates at the west station, and its particular copepod community (high proportions of cyclopoids), it is reasonable to assume that copepods would graze preferentially on those protozoans (heterotrophic pathway). Unfortunately, we did not quantify this grazing link; but the negative mesozooplankton grazing rates obtained in ca. half of the experiments at the west station are a clear indication of this artifact (Nejstgaard *et al.*, 2001). At the east station, on the other hand, the copepod community was dominated by herbivorous/omnivorous calanoids, favouring a more classic food web. Despite that, the combined grazing impacts of both microzooplankton and mesozooplankton on phytoplankton were high compared with other very productive areas (Vargas *et al.*, 2007; Calbet, 2008; Schmoker *et al.*, 2013). Therefore, we conclude that the phytoplankton communities of the west station, showing more eutrophic conditions, were indeed top-down controlled (mostly by microzooplankton), likely fuelling an important microbial food web. The lower instantaneous growth rates of phytoplankton at the west station helped the grazers to "catch-up" with their prey there. The overall trophic transfer

efficiency of the system from nutrients upwards the food web was lower here than the east station; however, this was mostly result of an inefficient use of inorganic nutrients by phytoplankton rather than an impairment of the food web above primary producers. Trophic dynamics at the east station alternated between top-down and bottom-up controls, depending on the season. These results agree with the relationship between flushing and bottom-up effects in the estuaries of the Gulf of Mexico (Livingston *et al*., 1997), and San Francisco (Kimmerer, 2002); however, as the latter author pointed out, generalizations are difficult.

In summary, our results have confirmed the differences in the responses to eutrophication between freshwater and marine planktonic food webs, and have emphasized the role of microzooplankton as primary consumer in eutrophic coastal waters. Even if we have added new understanding of the dynamics of the plankton communities of particular sites of Singapore, and of the functioning of marine eutrophic food webs, there are still uncertainties very difficult to resolve with intermittent sampling and discrete experimentation. Thus, properly scaled monitoring programs, including routine experimentation on natural plankton communities, are needed to comprehend these ecosystems better.

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Table I. Results of the quantification of primary production by oxymetric methods. The gross primary production (GPP) and the net primary production (NPP) are shown for the two sampled stations (mg C m^{-3} h^{-1}). SD corresponds to the standard deviation of the mean.

Date	GPP west station (mg C m^{-3} h^{-1})	SD	NPP west station (mg C m^{-3} h^{-1})	GPP east station (mg C m^{-3} h^{-1})	SD	NPP east station (mg C m^{-3} h^{-1})	SD
August 7, 2012	34.9	5.41	3.76	54.7	9.96	19.57	9.96
August 23, 2012	5.6	5.82	-20.00	38.2	1.60	7.98	1.60
September 5, 2012	15.3	5.07	-2.96	44.2	10.11	17.93	10.11
September 18, 2012	11.5	3.71	0.82	44.6	9.19	31.67	9.19
October 9, 2012	13.1	10.86	-12.13	34.7	6.61	12.12	6.61
March 13, 2013	42.7	11.59	19.01	37.8	2.54	14.65	2.54
April 2, 2013	19.8	3.47	3.31	41.7	5.35	21.15	5.35

Table II. Results of the dilution and mesozooplankton grazing-rate incubation experiments at both stations (west station and east station). μ = natural instantaneous growth rate of the phytoplankton community (d^{-1}). Nut. limit. = evidence of nutrient limitation of the natural phytoplankton community was estimated by comparing undiluted bottles with and without nutrient additions (t-test; $p < 0.05$). m = grazing rate of microzooplankton or mesozooplankton (d^{-1}). The coefficient of determination (r^2) is given between parentheses for the dilution grazing experiments. %SS = the percentage of the phytoplankton standing stock consumed daily considering absence of phytoplankton growth.

		West station				East station			
Date	**Group**	**μ (d^{-1})**	**Nut. lim.**	**m (d^{-1})**	**%SS**	**μ (d^{-1})**	**Nut. lim.**	**m (d^{-1})**	**%SS**
August 7, 2012	Micro	1.62	no	0.54 (0.72)	97.2	1.80	no	0.57 (0.65)	111.7
August 7, 2012	Meso			0.52	178.0			0.18	44.3
August 23, 2012	Micro	-0.24	no	0.00 (n.d)	0.0	0.99	yes	0.46 (0.79)	61.0
August 23, 2012	Meso			0.11	84.8			0.30	146.5
September 5, 2012	Micro	-0.50	no	0.36 (0.62)	24.1	0.48	no	0.25 (0.62)	28.6
September 5, 2012	Meso			0.00	0.0			0.06	50.1
September 18, 2012	Micro	0.30	no	0.47 (0.48)	42.9	0.70	yes	0.50 (0.48)	54.9
September 18, 2012	Meso			-0.12	0.0			0.06	67.9
October 9, 2012	Micro	0.67	no	0.40 (0.40)	46.4	1.16	no	0.30 (0.31)	47.7
October 9, 2012	Meso			-0.06	0.0			0.02	10.3
March 13, 2013	Micro	1.16	no	0.47 (0.87)	68.2	0.21	yes	0.27 (0.61)	26.4
March 13, 2013	Meso			0.52	574.9			0.20	346.7
April 2, 2013	Micro	0.12	no	0.45 (0.83)	38.1	0.29	yes	0.00 (n.d.)	0.0
April 2, 2013	Meso			-0.02	0.0			-0.02	0.0
April 9, 2013	Micro	0.37	no	0.33 (0.37)	33.2	0.77	no	0.33 (0.63)	41.0
April 9, 2013	Meso			-0.02	0.0			0.79	413.9
April 23, 2013	Micro	0.38	no	0.66	57.9	1.01	no	0.87	93.71
April 23, 2013	Meso			-0.52	0.00			-0.10	0.00

n.d. not determined

667 **Table III.** The values in columns represent the year-round average of biomass sustained by
668 unit of biomass of the "Units" column. For instance, 1 µM Nitrate supports 0.82 µg Chl *a* at
669 the west station and 2.1 µg at the east station. Microz represents the combination of ciliates
670 and dinoflagellates. The values between parentheses are the SD of the mean.

Station	Units	µg Chl *a*	µg C microz	µg C copepods
West station	1 µM Nitrate	0.82 (1.1)	3.2 (2.4)	6.7 (8.6)
	1µg Chl *a*		10.0 (12.2)	18.2 (26.2)
	1 µg C microz			3.2 (4.2)
East station	1 µM Nitrate	2.1 (2.7)	10.1 (17.2)	15.0 (17.9)
	1µg Chl *a*		5.1 (4.6)	13.6 (24.3)
	1 µg C microz			2.0 (2.9)

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673

674 **Figure Legends**

675 **Figure 1.** The study area showing the position of the sampling stations.

676 **Figure 2.** Time series of the vertical profiles of temperature (a,b; ºC), and salinity (c,d) for
677 the two stations sampled, west station and east station. The dots correspond to sampling
678 events. The Southwest Monsoon (SWM) and Northeast Monsoon (NEM) are indicated as
679 solid bars above each plot.

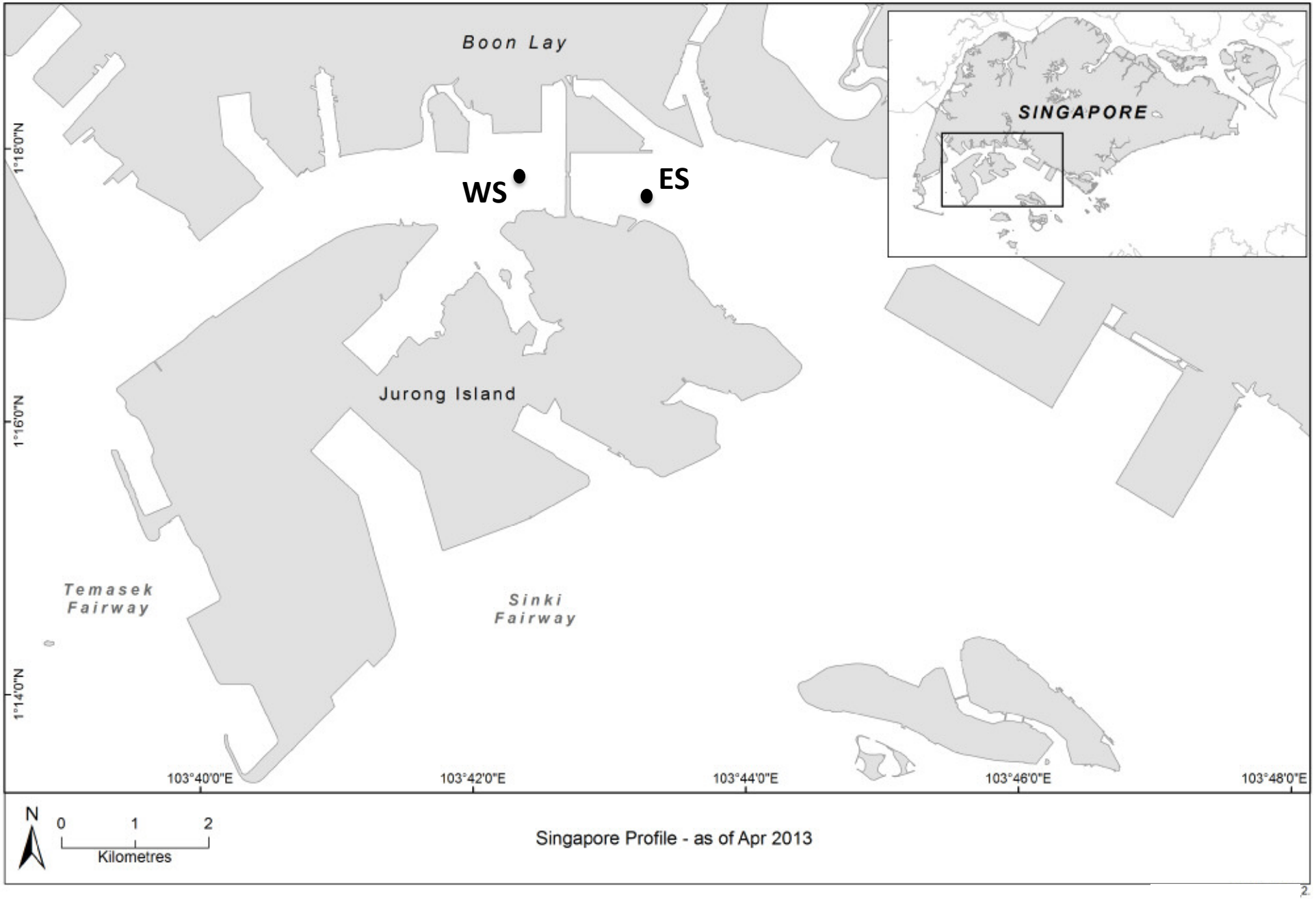
680 **Figure 3.** Representative vertical profiles of irradiance at both stations at noon (PAR; µE m^{-2}
681 s^{-1}; April 4, 2013).

682 **Figure 4.** Time series of the vertical profiles of nitrate (a,b), phosphate (c,d), silicate (e,f),
683 and ammonium (g,h) in µM for west station (left) and east station (right). The Southwest
684 Monsoon (SWM) and Northeast Monsoon (NEM) are indicated as solid bars in the upper part
685 of each plot. **Figure 5.** Time series of the vertical profiles of oxygen concentration (mg L^{-1})
686 for west station (a) and east station (b). The Southwest Monsoon (SWM) and Northeast
687 Monsoon (NEM) are indicated as solid bars in the upper part of each plot.

688 **Figure 6.** Time series of the vertical distribution of total chlorophyll *a* (chl *a*; a,b), and > 10
689 µm chl *a* (c,d) µg L^{-1} for west station (left) and east station (right). The Southwest Monsoon
690 (SWM) and Northeast Monsoon (NEM) are indicated as solid bars in the upper part of each
691 plot.

692 **Figure 7.** Time series of the vertical distribution of diatoms (a,b), dinoflagellates (c,d), and
693 ciliates (e,f) in cells L^{-1} for west station (left) and east station (right). The Southwest
694 Monsoon (SWM) and Northeast Monsoon (NEM) are indicated as solid bars in the upper part
695 of each plot.

696 **Figure 8.** Time series of the abundance of copepods in individuals L^{-1} (a,b) for west station
697 (left) and east station (right). The Southwest Monsoon (SWM) and Northeast Monsoon
698 (NEM) are indicated as solid bars in the upper part of each plot. The proportions that major
699 groups constituted of the community are shown in the lower plots (c,d).
700


Boon Lay
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1°18'0"N
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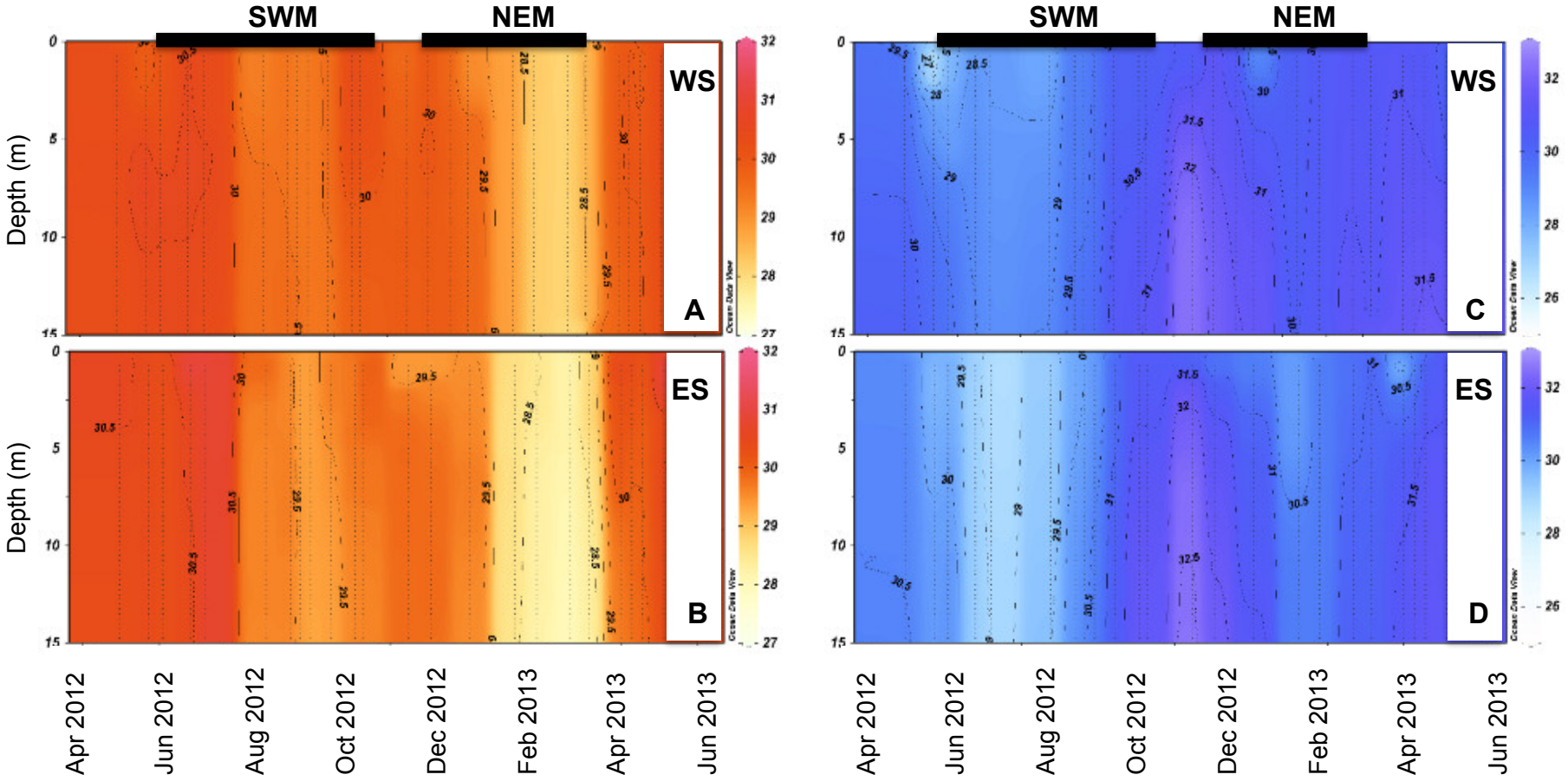
Singapore Profile - as of Apr 2013

Fig. 1


SWM
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Depth (m)
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Feb 2013
Apr 2013
Jun 2013

Fig. 2

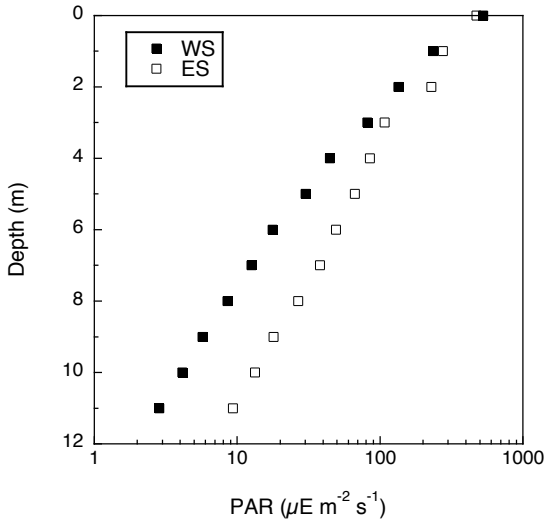

Fig. 3

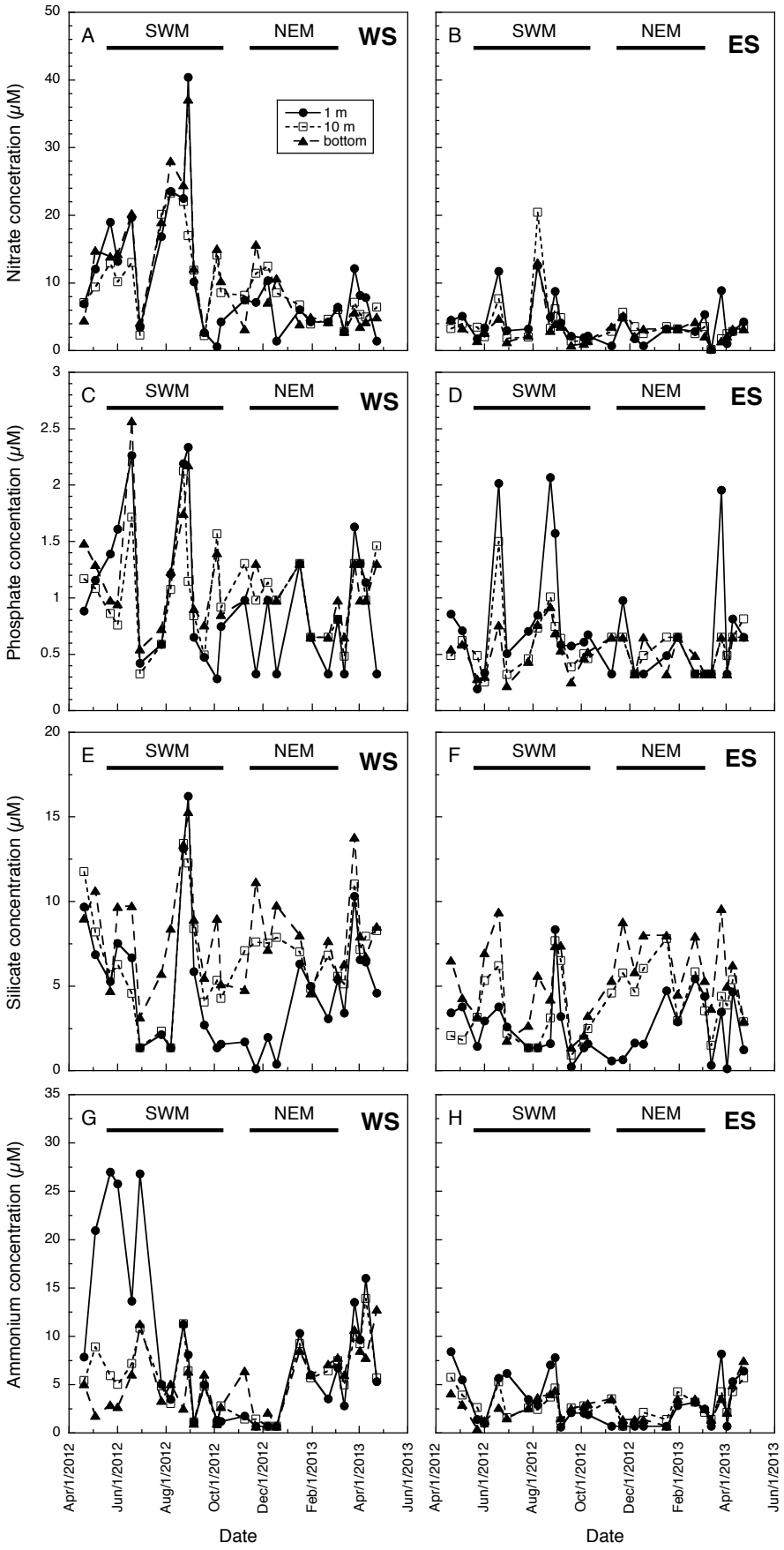
A
B
C
D
E
F
G
H
SWM
NEM
WS
ES
1 m
10 m
bottom
Nitrate concetration (μM)
Phosphate concentation (μM)
Silicate concentration (μM)
Ammonium concentration (μM)
Apr/1/2012
Jun/1/2012
Aug/1/2012
Oct/1/2012
Dec/1/2012
Feb/1/2013
Apr/1/2013
Jun/1/2013
Date

Fig. 4

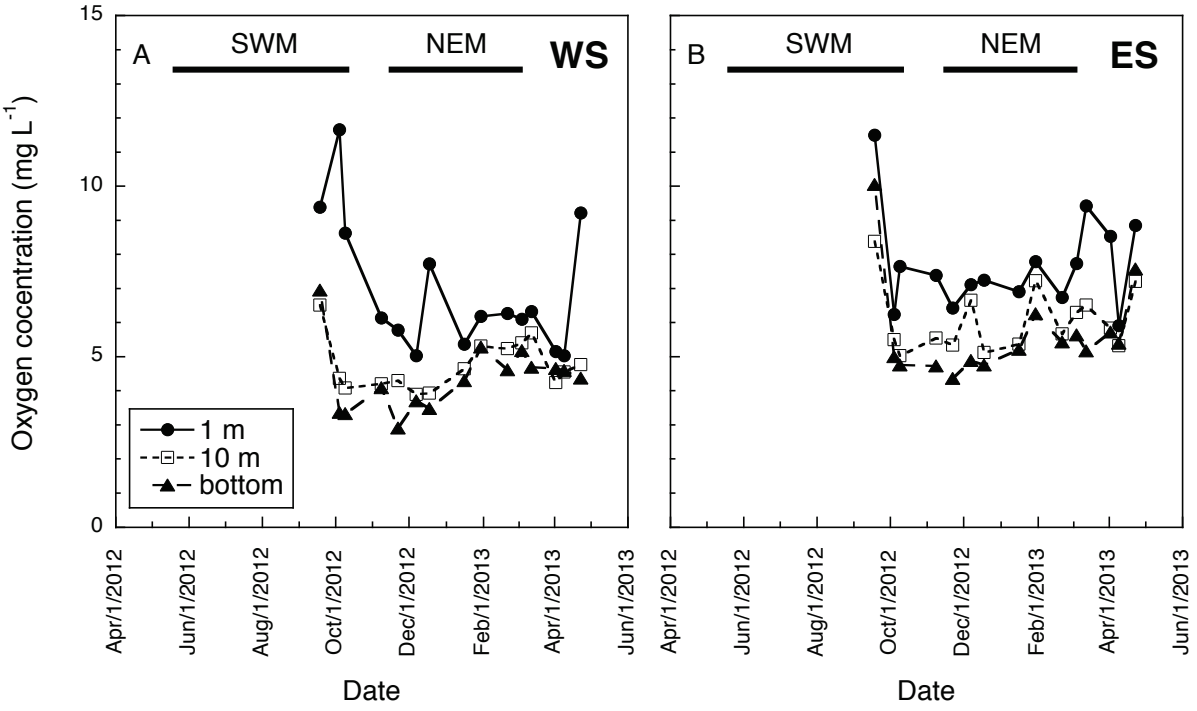
A
SWM
NEM
WS
B
SWM
NEM
ES
Oxygen cocentration (mg L-1)
15
10
5
0
1 m
10 m
bottom
Apr/1/2012
Jun/1/2012
Aug/1/2012
Oct/1/2012
Dec/1/2012
Feb/1/2013
Apr/1/2013
Jun/1/2013
Date

Fig. 5

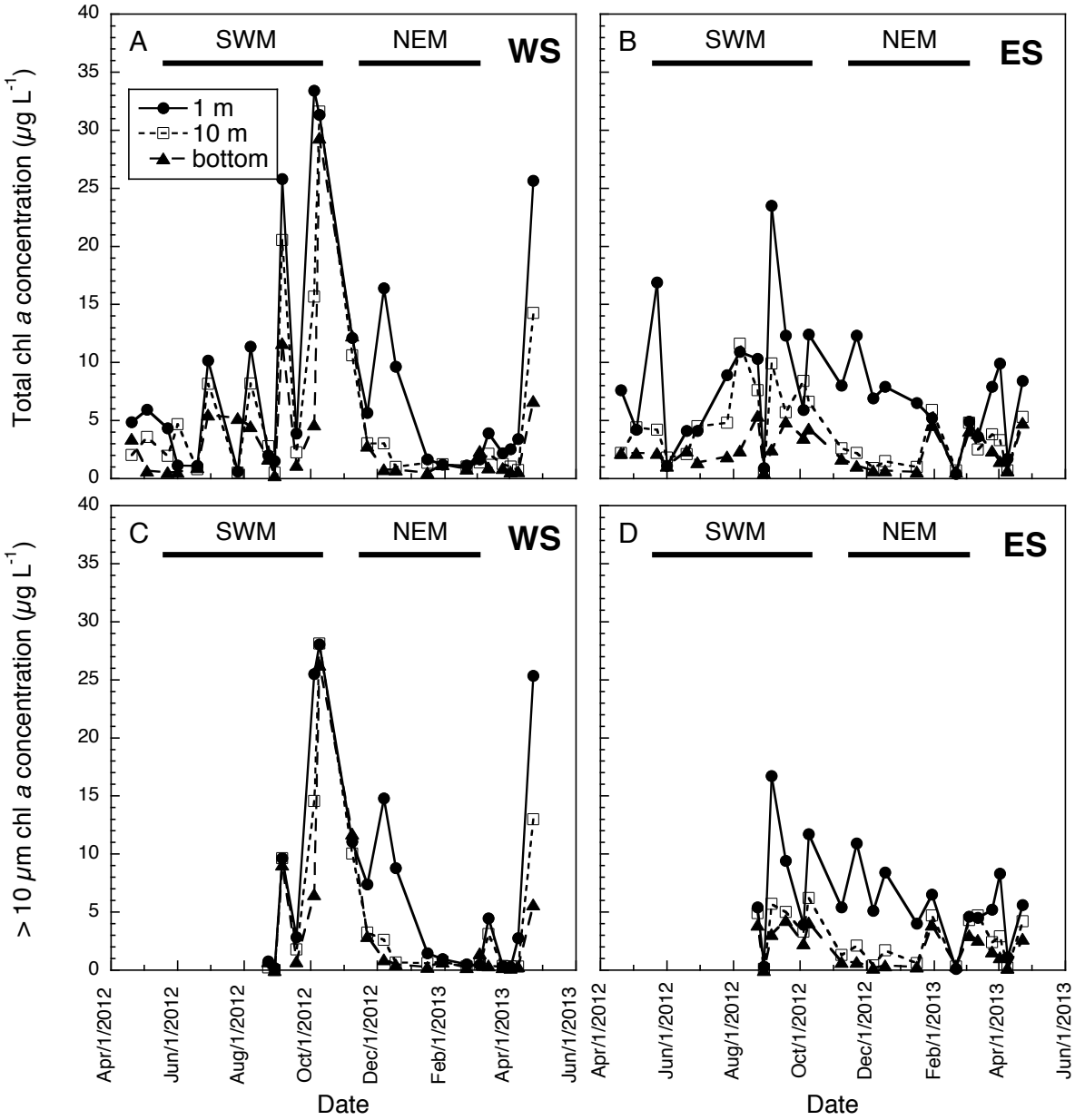
A
SWM
NEM
WS
B
SWM
NEM
ES
1 m
10 m
bottom
Total chl a concentration (μg L-1)
C
SWM
NEM
WS
D
SWM
NEM
ES
> 10 μm chl a concentration (μg L-1)
0
5
10
15
20
25
30
35
40
Apr/1/2012
Jun/1/2012
Aug/1/2012
Oct/1/2012
Dec/1/2012
Feb/1/2013
Apr/1/2013
Jun/1/2013
Date

Fig. 6

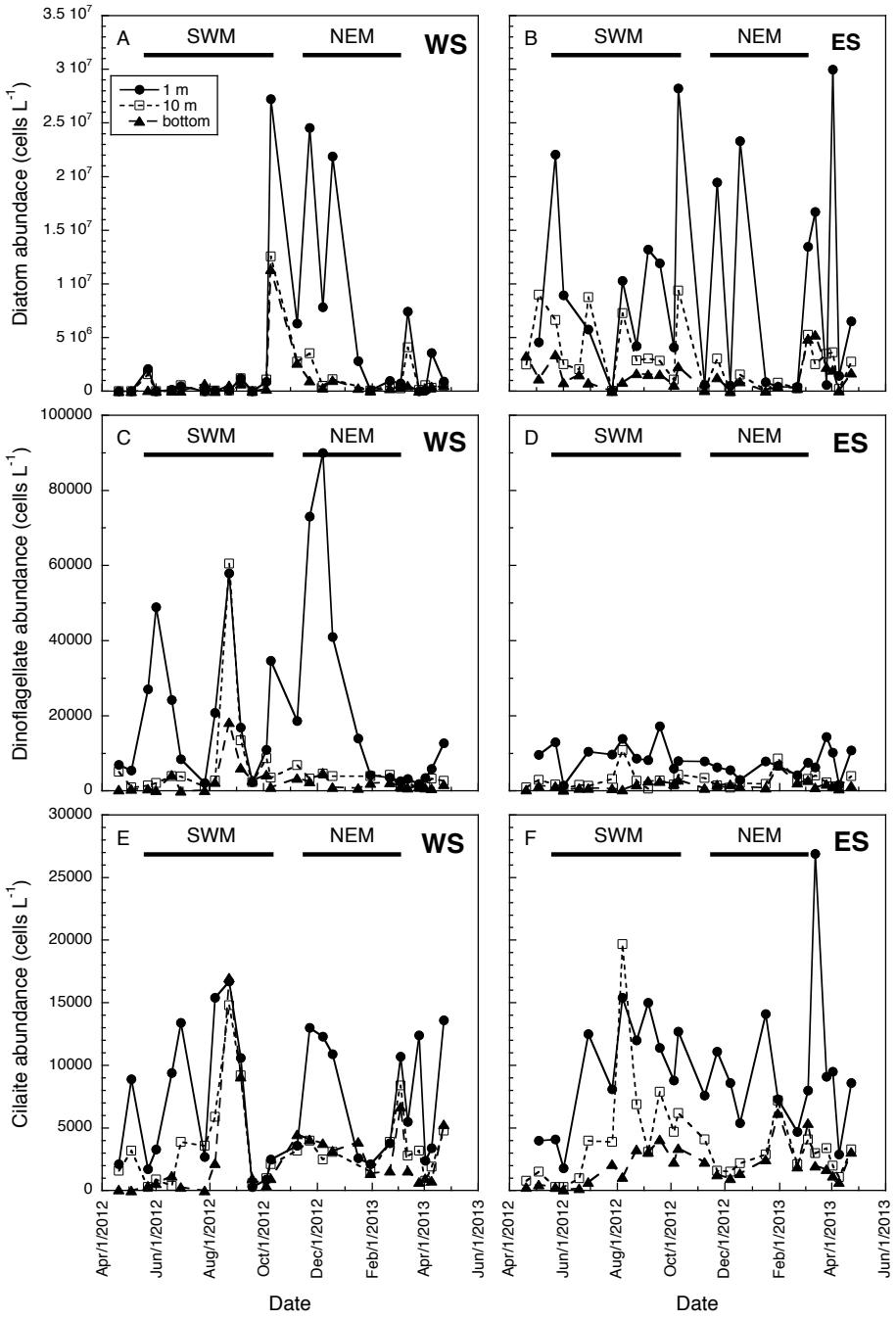
A
B
C
D
E
F
SWM
NEM
WS
ES
1 m
10 m
bottom
Diatom abundace (cells L-1)
Dinoflagellate abundance (cells L-1)
Cilaite abundance (cells L-1)
3.5 10^7
3 10^7
2.5 10^7
2 10^7
1.5 10^7
1 10^7
5 10^6
0
100000
80000
60000
40000
20000
30000
25000
15000
10000
5000
Apr/1/2012
Jun/1/2012
Aug/1/2012
Oct/1/2012
Dec/1/2012
Feb/1/2013
Apr/1/2013
Jun/1/2013
Date

Fig. 7

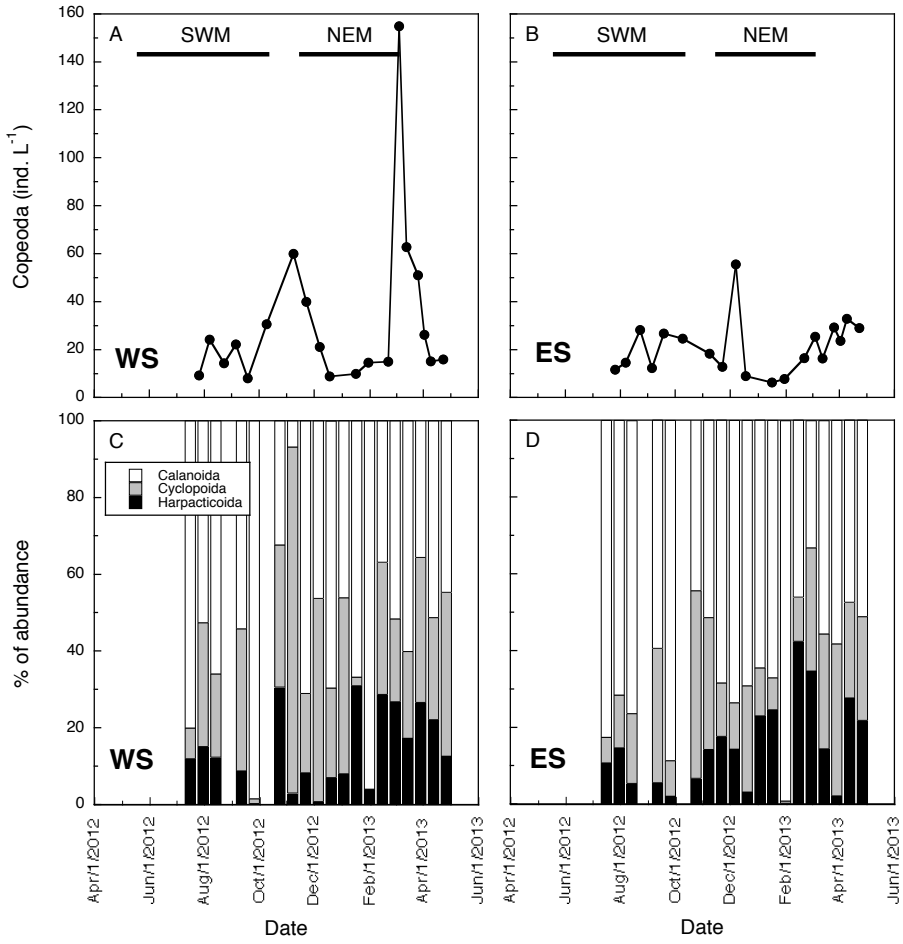
A
SWM
NEM
WS
B
SWM
NEM
ES
Copeoda (ind. L-1)
C
Calanoida
Cyclopoida
Harpacticoida
WS
D
ES
% of abundance
Apr/1/2012
Jun/1/2012
Aug/1/2012
Oct/1/2012
Dec/1/2012
Feb/1/2013
Apr/1/2013
Jun/1/2013
Date

Fig. 8