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Assessing marine plankton community structure from long-term monitoring data with multivariate autoregressive (MAR) models: a comparison of fixed station versus spatially distributed sampling data

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Abstract

We examined how marine plankton interaction networks, as inferred by multivariate autoregressive (MAR) analysis of time-series, differ based on data collected at a fixed sampling location (L4 station in the Western English Channel) and four similar time-series prepared by averaging Continuous Plankton Recorder (CPR) datapoints in the region surrounding the fixed station. None of the plankton community structures suggested by the MAR models generated from the CPR datasets were well correlated with the MAR model for L4, but of the four CPR models, the one most closely resembling the L4 model was that for the CPR region nearest to L4. We infer that observation error and spatial variation in plankton community dynamics influenced the model performance for the CPR datasets. A modified MAR framework in which observation error and spatial variation are explicitly incorporated could allow the analysis to better handle the diverse time-series data collected in marine environments.

Long-term environmental monitoring data present unparalleled opportunities to understand ecosystem dynamics and structure in natural settings. Depending on the frequency and duration of sampling, biomass or count data collected over time can allow for the characterization of seasonal and inter-annual variability in abundance patterns, the detection of changes in community dynamics and composition, and the modeling of system processes. Time-series data are also valuable as a basis for determining species interactions within communities (Ives et al. 2003; Wootton and Emmerson 2005). Estimates of ecosystem function and stability are commonly generated by assembling and examining the structure of food webs, but in addition to knowing the pattern of species interactions within an ecosystem, it is important to know the strengths of those interactions (e.g., May 1972; Ives et al. 1999; Ings et al. 2009). Estimates of the interaction strengths between species within a community can, for example, be used to infer and understand the direct and cascading effects of system drivers on that community (e.g., Hampton et al. 2008). For marine plankton communities, the construction of such weighted interaction networks can give us valuable insights into how stressors such as climate change and eutrophication affect the trophic base of pelagic marine systems.

Multivariate autoregressive (MAR) models have been successfully applied to long-term plankton abundance datasets from freshwater systems to define the positions and strengths of interactions within those communities (e.g., Ives et al. 2003; Hampton et al. 2006; Hampton et al. 2008). However, the high-resolution, multi-decadal plankton time-series required for MAR analyses are relatively uncommon for

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marine systems. Also, MAR models have primarily been used with fixed point sampling data, which may be more variable in marine environments due to the influences of spatially dynamic factors such as tides and currents, and much of the multi-decadal marine plankton monitoring data derive from samples taken at multiple, spatially distributed points.

The spatially scattered samples collected behind ships-of-opportunity by the Continuous Plankton Recorder (CPR) instrument represent a rich source of long-term plankton abundance data to which MAR analysis could potentially be applied. The CPR survey was initiated by Alister Hardy in the 1930s following his development of the towable collection instrument, and the methods have remained consistent since 1948 for zooplankton and 1958 for phytoplankton (Warner and Hays 1994; Richardson et al. 2006). Over the past 80 years, the CPR survey has collected samples along the routes of ships-of-opportunity throughout the North Atlantic and North Sea, making it the longest and most geographically wide-spread marine plankton data source currently in existence. The long temporal and large geographic range of the dataset make it a valuable resource, but questions regarding the sampling methodology of the CPR have arisen over the years (Hays and Warner 1993; Hays 1994; Clark et al. 2001; John et al. 2001).

These concerns have prompted researchers to assess the comparability of CPR data to data collected at fixed stations with common vertical net haul methods. For example, Clark et al. (2001) compared plankton data taken at the Dove Marine Laboratory sampling station to CPR data taken from the surrounding area in the central-western North Sea. They found that fluctuations in year-to-year relative abundances of dominant taxa as well as community composition shifts were well-correlated between the two datasets. However, their comparison of absolute abundances between the two data-series revealed that the CPR captured roughly 15 times fewer individuals than the net samples at Dove, with some taxon-specific variability. They suggested that most of the abundance discrepancies might be attributed to passive avoidance and some species having more effective escape responses against the small CPR entrance aperture relative to larger sampling nets. Similarly, John et al. (2001) compared plankton time-series taken at the Western Channel Observatory (WCO) L4 station to CPR data taken in the surrounding area in the English Channel. They focused on comparing abundance patterns of locally common copepods between the two datasets. Although absolute copepod abundances were notably lower in the CPR dataset by a factor varying by species from 2 to 35, they found good agreement between seasonal patterns of copepod abundance in the two datasets. There is therefore good evidence that, despite the tendency of the CPR instrument to under-sample absolute zooplankton abundances, the relative seasonal and inter-annual abundance trends determined from CPR samples are reliable (Batten et al. 2003; Richardson et al. 2006).

Since fixed point marine data may be heavily influenced by patchiness, and spatially distributed data like those collected by the CPR represent an enormous resource for the study and management of marine systems, we would like to better understand how MAR models behave with these types of data. Here we compare the plankton community properties that can be inferred from MAR analysis on fixed point data to those from spatially distributed points in the surrounding area. We selected the plankton time-series dataset collected at the WCO L4 station to represent fixed point data and used CPR sampling points from the surrounding area in the English Channel to represent spatially distributed data. The L4 and CPR datasets were selected for MAR analysis due to their high taxonomic and temporal resolution, relative longevity, consistent collection methodologies, and inclusion of phytoplankton abundance data. We did not expect the lower estimations of absolute plankton abundances from the CPR relative to net samples to significantly influence the MAR analysis because the model uses trends in standardized abundance rather than absolute abundance to detect interactions between taxa (see below). However, we did expect that variance in the time-series caused by the dramatically different sampling schemes and by potentially high and disparate observation errors could lead to model differences between the datasets.

Materials and procedures

WCO L4 data

The Western Channel Observatory (WCO) is a marine-monitoring program based at the Plymouth Marine Laboratory, Plymouth, UK. WCO has monitored zooplankton abundance in the English Channel since 1988 and started collecting phytoplankton abundance data in 1992. Samples have been collected weekly in 55-m-deep water, 18.5 km southwest of Plymouth at the L4 station (Fig. 1). Zooplankton samples are collected by replicate vertical WP2 net (200 µm mesh size, 0.25 m^2 mouth area) hauls from 50 m to the surface and are stored in 5% formalin (Eloire et al. 2010). Within a week of collection, zooplankton are enumerated and identified to major taxonomic group under a dissecting microscope. Phytoplankton bottle samples are collected at 10 m depth and preserved in 2% Lugol's solution (Southward et al. 2005). An inverted microscope is used to identify and enumerate phytoplankton species in 10–100 mL settled subsamples. WCO L4 data are freely available at www.pml.ac.uk/L4.

CPR data

The Continuous Plankton Recorder survey has been collecting consistent monthly samples along ship tracks in the English Channel since 1957 (Southward et al. 2005). The device is towed at a speed of 15–20 knots behind ships of opportunity at approximately 6–7 m depth (Batten et al. 2003). As it is towed, water enters a 1.27 cm^2 aperture at the front of the device and passes through an exposed portion of a silk mesh strip (~270 µm mesh size). An external propeller drives a winding mechanism that exposes the mesh strip to

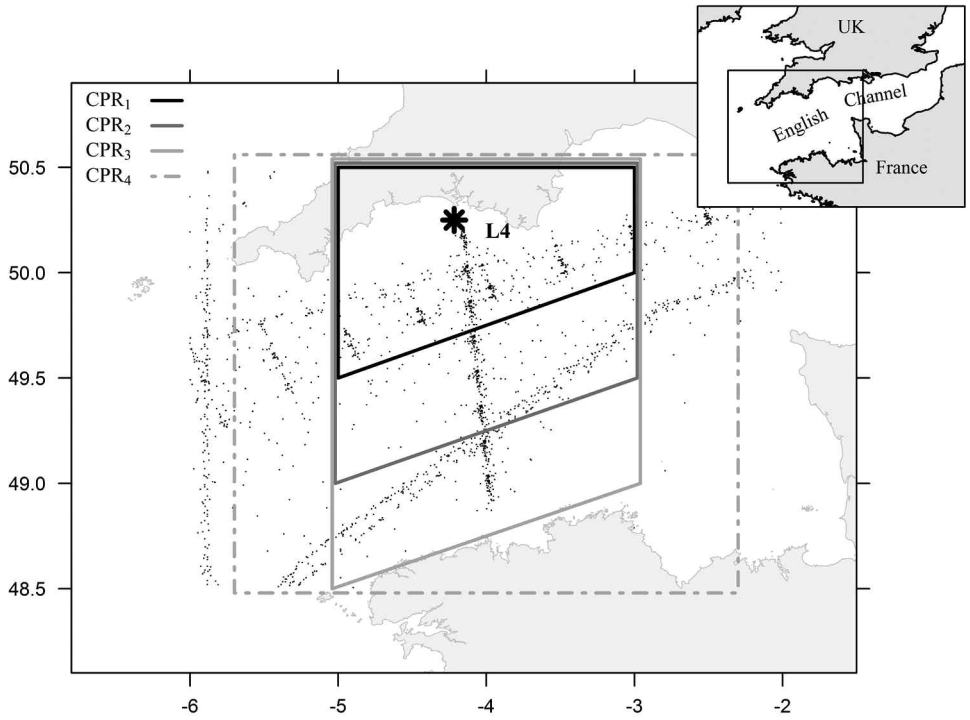

Fig. 1. Map of the L4 station location (50.25°N, –4.22°W) and the regions CPR sampling points were averaged over to create monthly time-series (CPR_1, 49.5°N/50°N to 50.5°N, –3°W to –5°W; CPR_2, 49°N/49.5°N to 50.5°N, –3°W to –5°W; CPR_3, 48.5°N/49°N to 50.5°N, –3°W to –5°W; CPR_4, 48.5°N to 50.5°N, –2.3°W to –5.7°W). Small black spots represent CPR sampling points.

the incoming water sample at a continuous rate of about 10 cm per 10 nautical miles. Another strip of silk covers the captured particles, and the sandwiched layers are wound on a spool in a tank containing ~4% buffered formalin. When the CPR is returned to the laboratory, the silk is cut into sections corresponding to 10 nautical mile samples. Zooplankton and phytoplankton in every other sample strip are identified and counted during a three-stage microscopic processing procedure, and abundance estimates are derived from the counts (Warner and Hays 1994; Batten et al. 2003).

For this study, we acquired CPR point data spanning the English Channel from the Sir Alister Hardy Foundation for Ocean Science. Four regions were selected over which to average the CPR sampling points. Three of these CPR regions expand southward from L4 (CPR_1, CPR_2, CPR_3; Fig. 1) and were selected to determine whether the proximity of the CPR samples to the fixed station affects the similarity of the model results. These regions are nested rather than adjacent because separating them would have critically reduced the number of time-steps available for our analysis. A large region, denoted CPR_4 (Fig. 1), was selected to assess whether model results can be improved by maximizing the number of spatial replicates included in the time-series.

MAR analysis

To enable direct comparisons between L4 and CPR datasets, plankton taxa were summed into groups that are ecologically or functionally similar (Table 1). We excluded groups that were counted in L4 samples but recorded only as "present or absent" in the CPR samples, that were extremely rare, and that were comprised of small-bodied species that were unlikely to have been accurately sampled by either of the methods (Eloire et al. 2010). We assembled parallel L4 and CPR abundance time-series for the plankton groups under consideration by averaging each dataset into 1-month increments and removing time steps not shared among all datasets. For each of the CPR region datasets, raw sample data were averaged by date before calculating monthly means.

To prepare the datasets for MAR analysis, the monthly plankton abundance values were $\log_{10}(x + 1)$ transformed and standardized to dimensionless units (Z-scores; e.g., Hampton et al. 2006). A Z-score for each monthly time step was calculated by first subtracting the group's corresponding multi-year mean abundance value for the month, and then dividing the difference by the multi-year standard deviation for the month. Z-scoring standardized the data such that we could directly compare model results among plankton groups and also removed average seasonal trends from the time-series. Deseasoning the abundance data should theoretically aid in the detection of interactions between plankton groups by dampening seasonal successions that relate to seasonally varying abiotic drivers. All the dataset manipulations described above were performed in R.

In the MAR model framework, both variates and covariates can be included in the analysis (Ives et al. 2003). Variates are fac-

Table 1. Summary of zooplankton aggregations applied to the L4 and CPR datasets, each group's contribution to the total plankton community, and each taxon's contribution to its group. Taxa comprising less than 1% of a group are not listed.

	Proportion of community			Proportion of group
Group	**L4**	**CPR**	**Taxa Included**	**L4 & CPR mean**
Chaetognaths	0.02	0.07	Sagitta spp.	~1.00
Pteropods	0.01	0.02	Thecosomata	>0.99
Tunicates	0.03	0.07	Appendicularians	0.99
			Doliolids	0.01
Cladocerans	0.05	0.04	Evadne spp.	0.66
			Podon spp.	0.34
Amphipods	<0.01	<0.01	Gammarid amphipods	0.94
			Hyperiid amphipods	0.03
			Isopods	0.02
			Mysid shrimp	0.01
Krill	<0.01	<0.01	Euphausiids	~1.00
Copepods				
Large calanoids	0.03	0.08	Calanus spp.	0.95
			Metridia spp.	0.03
			Candacia spp.	0.01
			Eucalanus spp.	0.01
Small calanoids	0.38	0.45	Pseudocalanus spp.	0.33
			Acartia spp.	0.28
			Temora spp.	0.15
			Paracalanus spp.	0.12
			Centropages spp.	0.06
			Clausocalanus spp.	0.02
			Ctenocalanus spp.	0.01
Cyclopoids	0.12	0.02	Oithona spp.	~1.00
Poecilostomatoids	0.19	0.01	Corycaeus spp.	0.51
			Oncaea spp.	0.49
Harpacticoids	0.01	<0.01	Euterpina spp.	0.70
			Clytemnestra spp.	0.23
			Microsetella spp.	0.05
			Alteutha spp.	0.01
Meroplankton				
Cirripedia	0.08	0.01	Cirripede larvae	1.00
Mero. Grazers (miscellaneous)	0.06	0.23	Echinoderm larvae	0.66
			Bivalve larvae	0.19
			Cyphonaute larvae	0.05
			Polychaete larvae	0.05
			Gastropod larvae	0.04
Decapod larvae	0.01	0.01	Crab & shrimp larvae	1.00

tors expected to affect their own dynamics and the dynamics of other variates (e.g., species abundances are typically treated as variates). Covariates may affect the dynamics of the variates but are unlikely to be correspondingly influenced by them (e.g., temperature or salinity would be treated as covariates). With the exception of meroplankton, we considered each plankton group as a variate in the model. Meroplankton groups were considered covariates since their abundance can be strongly influenced by benthic, rather than pelagic, processes.

The MAR framework (Ives et al. 2003) can be thought of as a series of regression equations which compare the abundance time-series of each plankton group to the t-1 lagged time-series of all other groups and any included covariates. In matrix notation, the MAR formula we used is

$$X_t = A + BX_{t-1} + CU_{t-1} + E \quad (1)$$

where, for p interacting groups and q covariates, X_t is a $p \times 1$

vector of the groups' Z-scored abundance values at time t, A is a $p \times 1$ vector of intrinsic productivities (all equal to zero here because we are using Z-scored values), B is a $p \times p$ matrix of interaction coefficients, X_{t-1} is a $p \times 1$ vector of the biomass for each group at time t-1, C is a $p \times q$ matrix of effects of covariates on variates, U_{t-1} is a $q \times 1$ vector of covariates at time t-1, and E is a $p \times 1$ vector of process errors with mean 0 and variance-covariance matrix Q. The diagonal elements of B contain the density-dependent interaction terms of each variate on itself; the off-diagonal elements are the effects of the plankton groups on one another.

Following Ives et al. (1999), we used Akaike's Information Criterion (AIC) to evaluate the fit of a suite of potential models that could be constructed from each dataset. To find the "best-fit" model structure for each dataset, we randomly constructed 100 model structures by including or excluding coefficients of B and C with equal probability, and chose the resulting model with the lowest AIC. The process was repeated 100 times (Ives et al. 1999), resulting in a single model structure with the lowest AIC of 10,000 random models. Coefficients that were retained in less than 15% of the models were dropped (Ives et al. 1999). We then used bootstrapping (n = 500) of the best-fit model to obtain 95% confidence intervals for the coefficients. Coefficients with confidence intervals that overlapped zero were eliminated, resulting in the final "bootstrapped" model (Hampton and Schindler 2006; Hampton et al. 2006). The fitting and selection of MAR models was implemented in Matlab.

MAR model comparisons

When analyzing the L4 and CPR datasets with MAR, we found that, due to the random search used to determine the best-fit (lowest AIC) model, the same dataset could generate slightly different models if the analysis was repeated. Due to this variability, rather than compare single models generated from each of the five datasets, we generated 10 replicate MAR models for each dataset. We compared the best-fit and bootstrapped B and C interaction matrices between the L4 and CPR datasets with Kendall's rank correlation (τ) in R. The 10 replicate models for each dataset resulted in 100 pairwise tests being done for each L4 to CPR comparison, so we used the mean τ- value (± the 95% confidence interval; bootstrap n = 500) from each set of tests as a measure of model similarity.

Time-series comparisons

We evaluated similarities and differences between the untransformed L4 and CPR abundance time-series for reference during comparisons of the final MAR models. To compare absolute abundances between the datasets, the single, overall mean abundance of each plankton group in each time-series was calculated. These means were compared as ratios of L4:CPR abundance for each plankton group, such that ratios greater than 1 would be indicative of more individuals being sampled in the L4 time-series. We also looked for correlations in relative abundance trends between the untransformed L4 and CPR monthly time-series. Trend similarities for each plankton group between the L4 and CPR time-series were estimated with Kendall's rank correlation as the Poisson distribution of the count values did not satisfy assumptions of parametric correlation estimates. All time-series comparison calculations were done in R.

Assessment and discussion

MAR results comparisons

The plankton community structures implied by the MAR analyses of the five data sets differ dramatically. The best-fit MAR model B-matrix (species interactions) and C-matrix (covariate effects) for each of the five datasets are plotted in Fig. 2, and the corresponding bootstrapped matrices are plotted in Fig. 3. Of 238 total potential interactions, the bootstrapped matrices retain 28 of the 66 non-zero interactions in the best-fit L4 model, 21 of the 48 non-zero CPR_1 interactions, 29 of 60 CPR_2 interactions, 29 of 67 CPR_3 interactions, and 25 of 63 CPR_4 interactions. All other interaction coefficients in the models were 0. Comparisons of the model results, both before (Fig. 2) and after (Fig. 3) bootstrapping, show that very few (3–15) non-zero interactions are shared among the models generated from the L4 and CPR time-series (Table 2). The correlation coefficients between the bootstrapped L4 model and CPR models, in which less certain interaction estimations were eliminated, are all low, with the highest correlation being between the L4 and CPR_1 region models ($\bar{\tau}$ = 0.142 ± 0.006; Table 2).

Although applying the bootstrap to the best-fit models should theoretically help narrow the non-zero model coefficients to those representing stronger, ecologically plausible interactions—thereby creating better agreement between models—no patterns of agreement emerged. For example, in the bootstrapped model results (Fig. 3), 9 out of 14 variate groups in the L4 data were diagnosed as having significant density dependence (coefficients along the B-matrix diagonal), but this within-group autocorrelation was only detected for 6 of the 14 groups in the CPR models. Only 4 of these density-dependent interactions occurred in both the L4 and the majority of CPR bootstrapped models (large and small calanoids, tunicates, and the poecilostomatoids). All of the bootstrapped models generated include unlikely interactions between plankton groups (e.g., positive effects of grazers on phytoplankton). Such implausible interactions could result from a variety of factors, including indirect biotic interactions, temporally staggered responses of taxa to a shared driver, or the successive sampling of different water masses with distinct communities. However, the L4 model contains fewer of these unlikely interactions and more non-zero values for density dependence along the B-matrix diagonal (Fig. 3), so in this case, it appears MAR results are better aligned with our ecological expectations when using the fixed point data collected at L4 versus the spatially distributed data collected by the CPR.

Time-series comparisons

CPR under-sampling is apparent for several of the plankton groups when mean abundances from the CPR datasets are

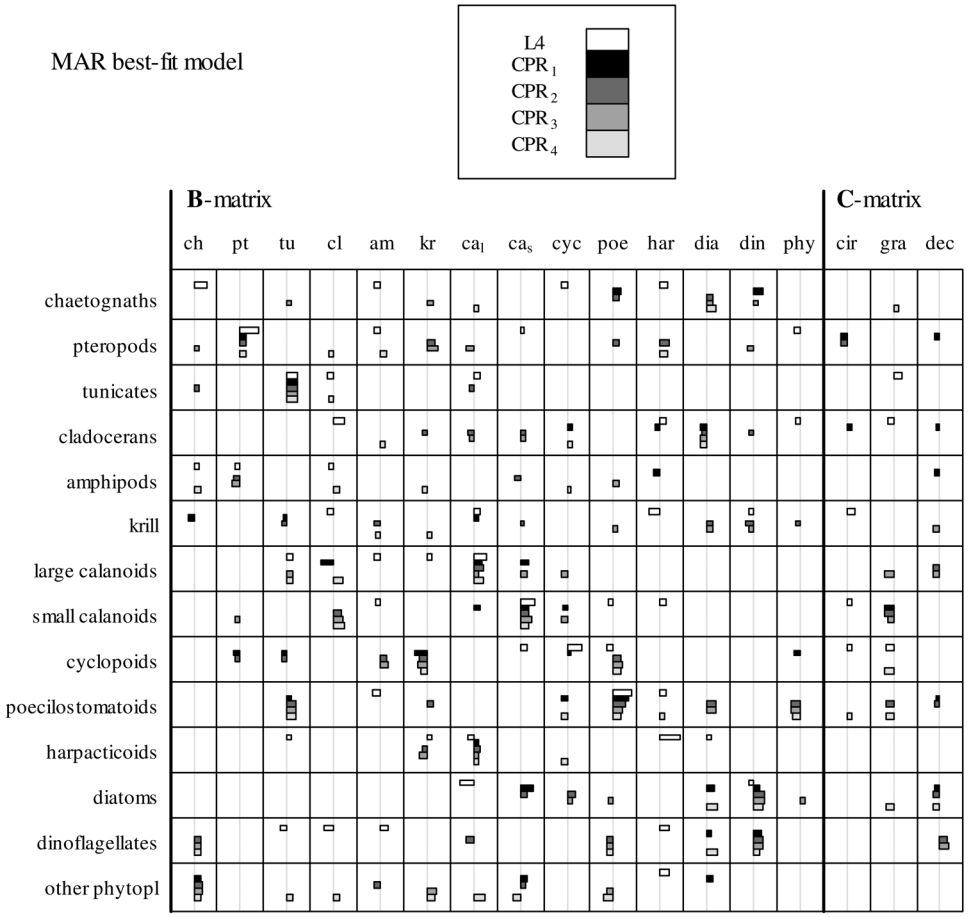

Fig. 2. Best-fit B- and C-matrices for the L4, CPR_1, CPR_2, CPR_3, and CPR_4 datasets. Each bar represents an interaction coefficient estimate, where a positive (negative) coefficient indicates a positive (negative) effect of the corresponding column group on the corresponding row group. The B-matrix column group abbreviations correspond, in order, to the row group names, and the C-matrix columns represent the cirripedia, meroplanktonic grazer, and decapod larvae groups. The x-axis range is –0.7 to 0.7, with origin 0. Only interactions included in all 10 replicate best-fit models of each dataset are shown.

compared with L4 mean abundances (Fig. 4). Comparisons of the abundance ratios reveal that this sampling effect varied by group. The lowest ratios (<5) are seen for zooplankton groups containing species of relatively large body size (>2 mm length). Very large ratios (>10) for harpacticoid, cyclopoid, and poecilostomatoid copepods indicate that dramatically more individuals from these small-bodied groups (<1 mm body length) were captured by the vertical net hauls at L4. For some groups, there appear to be increasing (e.g., pteropods) or decreasing (e.g., harpacticoids) CPR abundance trends with increasing region distance from L4 (Fig. 4). The large abundance ratios for the phytoplankton groups are not surprising since small phytoplankton were captured by the L4 bottle samples but were able to pass through the 270 µm mesh used by the CPR.

Temporal abundance trends between the L4 and CPR datasets are significantly correlated for most of the zooplankton and phytoplankton groups ($P < 0.01$; Table 3). Abundance trend correlations are strongest for the cladoceran, dinoflagellate, chaetognath, and meroplanktonic grazer groups ($\tau > 0.40$). The weakest correlations are associated with the pteropod, harpacticoid copepod, amphipod, krill, cirripedia, and poecilostomatoid groups ($\tau < 0.20$).

Why do MAR results differ among datasets?

Reasons for the differences between the L4 and CPR MAR models are suggested by comparisons of the L4 and CPR plankton abundance time-series and by examining the model B- and C-matrix results for each of the datasets. Differences between sampling equipment, sampling design, and the spatial scale over which samples were collected are all likely to have contributed to discrepancies among the L4 and CPR data-series which led to differing MAR models. Since the CPR data are best averaged over coarser temporal and spatial scales than we used in this study (Richardson et al. 2006), it is possible that spatially distributed plankton data collected under different sampling regimes could be used to construct informative MAR models if sources of variance at different spatial and temporal scales were carefully considered.

Sampling device effects

A comparison of the L4 and CPR datasets revealed that the CPR abundance estimates for several plankton groups are

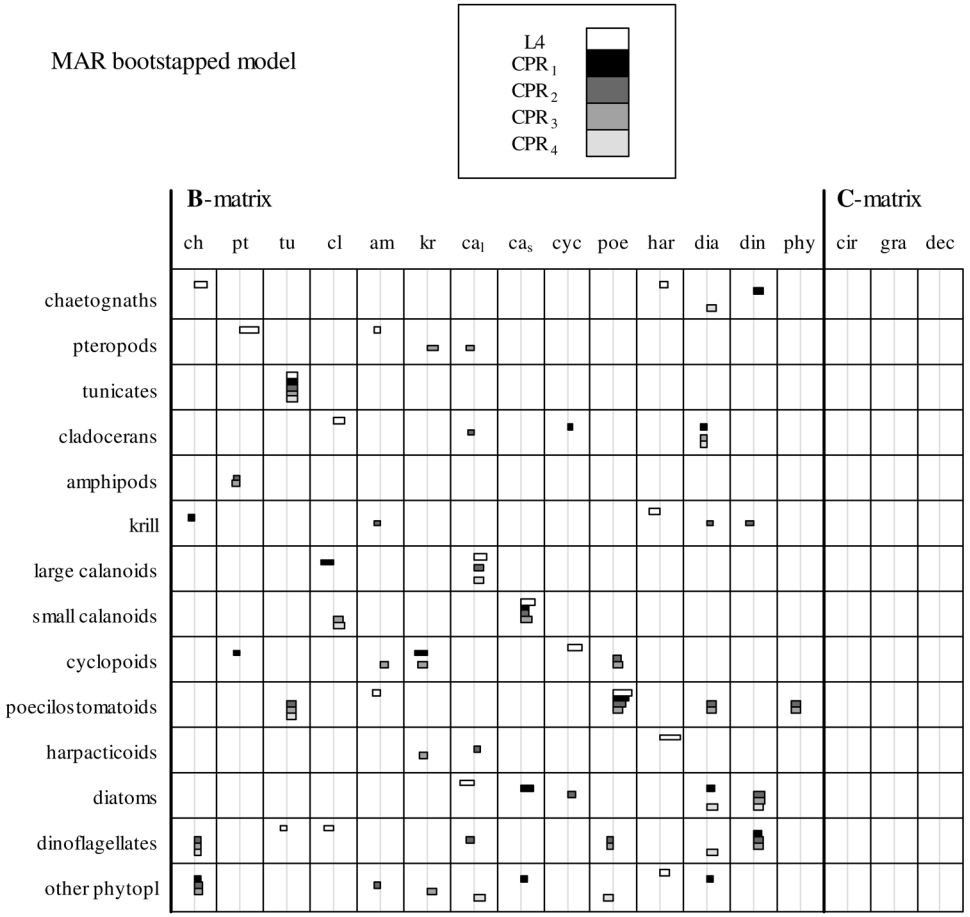

Fig. 3. Bootstrapped B- and C-matrices for the L4, CPR_1, CPR_2, CPR_3, and CPR_4 datasets. Each bar represents an interaction coefficient estimate, where a positive (negative) coefficient indicates a positive (negative) effect of the corresponding column group on the corresponding row group. The B-matrix column group abbreviations correspond, in order, to the row group names, and the C-matrix columns represent the cirripedia, meroplanktonic grazer, and decapod larvae groups. The x-axis range is –0.7 to 0.7, with origin 0. Only interactions included in all 10 replicate bootstrapped models of each dataset are shown.

Table 2. Numbers of shared interactions and correlations (±95% confidence interval) of the L4 best-fit and bootstrapped models with each of the corresponding CPR_1, CPR_2, CPR_3, and CPR_4 models.

	Best-fit models			Bootstrapped models		
Dataset comparison	Total coefficients shared	Non-zero interactions shared	Correlation $\bar{\tau}$ (±95% CI)	Total coefficients shared	Non-zero interactions shared	Correlation $\bar{\tau}$ (±95% CI)
L4 versus CPR_1	147	9	0.103 (±0.004)	198	4	0.142 (±0.006)
L4 versus CPR_2	142	11	0.067 (±0.003)	191	4	0.109 (±0.006)
L4 versus CPR_3	140	15	0.111 (±0.004)	190	3	0.069 (±0.007)
L4 versus CPR_4	142	13	0.079 (±0.003)	195	4	0.125 (±0.008)

much lower than abundances estimated from L4 samples (Fig. 4). These findings are in agreement with Clark et al. (2001) and John et al. (2001), who found that the CPR appeared to undersample certain taxa and species in comparison to samples collected with vertical net hauls at fixed stations. This phenomenon could be caused by a variety of factors, such as mesh size differences, interspecific variability in sampling device avoidance (Clark et al. 2001), and different sampling depths relative to species depth distributions (John et al. 2001).

In our analysis, the comparatively low abundance of small-bodied organisms in CPR data are likely related to the larger mesh size. Even so, because the MAR model relies on trends in standardized abundance values rather than absolute abundance values, it is unlikely the abundance differences between

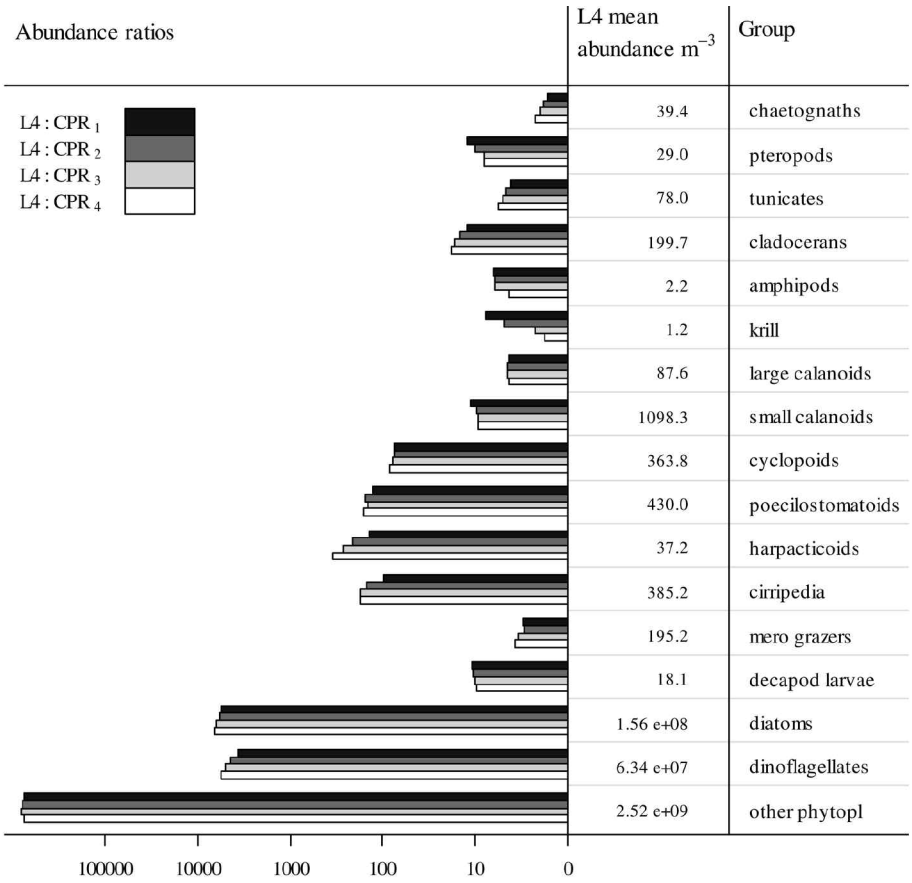

Fig. 4. Ratios of mean L4 plankton abundances to mean CPR_1, CPR_2, CPR_3, and CPR_4 plankton abundances. Bars extending left of the origin represent increasingly low plankton abundances in the CPR datasets relative to the L4 mean abundances. The x-axis is on a log scale.

Table 3. Kendall's rank correlation τ-values for plankton group abundance trends between the L4, CPR_1, CPR_2, CPR_3, and CPR_4 data-series. All relationships are significant ($P < 0.01$) unless otherwise noted.

Group	L4 versus CPR_1 τ	L4 versus CPR_2 τ	L4 versus CPR_3 τ	L4 versus CPR_4 τ
Cladoceran	0.55	0.58	0.58	0.60
Dinoflagellate	0.51	0.54	0.54	0.51
Chaetognath	0.48	0.44	0.46	0.47
Mero.grazers	0.41	0.41	0.41	0.42
Diatom	0.38	0.40	0.40	0.40
Tunicate	0.35	0.37	0.39	0.40
Malacostraca.mero	0.37	0.38	0.36	0.37
Copepod.calanoid.small	0.35	0.34	0.37	0.36
Copepod.calanoid.large	0.26	0.33	0.33	0.35
Copepod.cyclopoid	0.25	0.29	0.27	0.26
Other phytoplankton	0.22	0.22	0.21	0.23
Copepod.poecilostomatoid	0.19	0.16 ($P = 0.02$)	0.15 ($P = 0.02$)	0.21
Cirripedia	0.15 ($P = 0.05$)	0.17 ($P = 0.02$)	0.17 ($P = 0.02$)	0.19
Malacostraca.pelagic	0.12 ($P = 0.12$)	0.19 ($P = 0.01$)	0.17 ($P = 0.02$)	0.16 ($P = 0.04$)
Malacostraca.benthic	0.12 ($P = 0.08$)	0.13 ($P = 0.06$)	0.17	0.17
Copepod.harpacticoid	0.10 ($P = 0.17$)	0.13 ($P = 0.08$)	0.13 ($P = 0.07$)	0.10 ($P = 0.17$)
Mollusca.pelagic	0.04 ($P = 0.58$)	0.09 ($P = 0.18$)	0.05 ($P = 0.43$)	0.15 ($P = 0.02$)
Mean ± SE	0.29 ± 0.04	0.30 ± 0.04	0.31 ± 0.04	0.31 ± 0.03

the datasets would have directly led to the poor model agreement we observed. It is, however, possible that error associated with sampling low numbers of individuals affected the MAR results. Accurately sampling plankton abundance becomes less likely with increasing species patchiness or rarity (Wiebe 1971). Abundance estimates for less common plankton groups can therefore be expected to include more error, which could have led to discordant abundance trends between the L4 and CPR datasets and consequently differing MAR results. This hypothesis is supported by our comparison of relative plankton abundance trends between the L4 and CPR datasets (Table 3), which revealed that correlations tended to be weakest for groups less common in the plankton communities (Table 1).

Sampling design effects

The dissimilarity of sampling schemes between the L4 and CPR monitoring programs is also likely to have contributed to disagreements in plankton abundance trends and MAR results between the datasets. The vertical-only sampling scheme employed at the L4 station and the horizontal-only sampling scheme of the CPR could have produced different abundance trend estimations even if the sampling equipment, location, and times had been identical. As a fixed station, L4 could experience sudden changes in plankton abundance and community structure due to the horizontal movement of water masses by tides, winds, and circulation patterns (Irigoien and Harris 2003; Eloire et al. 2010). For example, L4 is known to be influenced periodically by riverine inputs from the Tamar estuary (Smyth et al. 2010). The MAR model may be susceptible to erroneously interpreting community changes associated with such water mass movements as plankton group interactions, thereby producing misleading results from fixed point sampling data (Francis et al. unpublished).

The horizontal CPR sampling scheme would better account for changes in plankton abundance between moving water masses, but it does not capture the strong vertical heterogeneity that can occur in plankton distributions (John et al. 2001). Many zooplankton species will position themselves in the water column in relation to horizontal features such as chlorophyll maxima or pycnoclines (e.g., Fernández de Puelles et al. 1996). Shifts in the depth distributions of these features could cause misleading peaks and declines in the CPR plankton abundance data, and taxon-specific responses to the presence of horizontal features could confound the abundance relationships MAR uses to calculate interaction strengths. Many taxa also perform diel vertical migrations that can cause their mean depth distributions to change dramatically between light and dark hours. Although the CPR does sample during both day and night, the depths to which species migrate are not always fixed and may change according to factors such as season, lunar cycle, water clarity, and food availability (see Marcus and Scheef 2010 for review). Variability in the CPR data introduced by the changing depth distributions of species may be smoothed when averaging data points over coarse time scales to determine mean seasonal or inter-annual trends in species abundance (Richardson et al. 2006), but we averaged the data into one-month increments to generate the time steps we used in the MAR model. More variability caused by inconsistent plankton distributions at fine temporal scales may have been maintained in the CPR time-series we used and affected the model results.

Spatial scale effects

In the five datasets that we examined, the spatial scale of sampling increases from L4 (smallest) to CPR_4 (largest; Fig. 1). Although averaging data collected over larger areas may buffer variance due to spatial patchiness, if marine plankton community dynamics (i.e., the process) vary by location, MAR analysis on averaged data from large areas may not reflect specific interactions among plankton. It is also possible that spatial-temporal interactions, such as the drifting of patches, could have affected the MAR results for the different CPR regions. The division of the CPR data into multiple, increasingly large regions was an attempt to explore the interaction between temporal components of variance (isolated at the L4 sampling location) and the increasing influence of spatial components of variance (Kratz et al. 1995; Larsen et al. 2001).

Our comparisons of the L4:CPR mean abundance ratios indicate some plankton groups tended to be either more or less abundant closer to L4 (Fig. 4). If we assume that the interactions among groups change across space as well, one could expect correlations between the CPR and L4 models to increase as the area considered converges on the L4 footprint. The decreasing similarities of the increasingly large CPR_1, CPR_2, and CPR_3 regions' models to the L4 model (Table 2) appear to support the expectation that the larger CPR_2 and CPR_3 regions were more likely to span multiple distinct plankton communities that exhibited different localized dynamics across the Channel. Unfortunately, data sparseness limited the choice of smallest CPR region, and all of the correlations were weak at best (Table 2).

Although the similarities of the CPR models to the L4 model decrease with increasing region size from CPR_1 to CPR_3, the model generated by the largest CPR region, CPR_4, was approximately as well correlated with the L4 model as the one for the smallest CPR region was. This pattern may reflect the potential tradeoff between incorporating location-specific environmental variability (minimizing inclusion of disparate process errors) and accounting for spatial variability (reducing observation error) in the data-series (Richardson et al. 2006). While more sources of spatial variance may be encompassed by averaging CPR data over larger areas, more observations are also captured. The mean CPR_4 sampling point distance to L4 was nearly twice that of CPR_1 (93 km and 48 km, respectively), but CPR_4 also included nearly three times as many sampling points as CPR_1 (1652 points and 575 points, respectively). Spatial coverage and environmental heterogeneity therefore appear to be important factors to jointly consider when averaging spatially scattered data points for MAR analysis.

Comments and recommendations

Fixed point and spatially distributed sampling designs pose different advantages and limitations for using either type of data to characterize plankton community interactions and properties from MAR models. In this study, the MAR interaction matrices generated from the fixed point L4 and the spatially distributed CPR data-series differed greatly. More work is currently underway to understand the behavior of MAR with different marine plankton datasets and to improve the performance of MAR over a variety of data types. Modifications to the model may help yield more consistent and reliable results from the highly variable data collected in dynamic marine environments. For example, a state-space version of the MAR model (MARSS) that explicitly accounts for observation error has recently been developed (Holmes et al. 2010). If observation error was a principal factor affecting the L4 and CPR MAR results in this study, as we suggest, such modifications to the MAR framework may better enable us to construct accurate plankton interaction networks from data collected with a wide range of different sampling techniques.

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