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Does the poleward boundary current off Western Australia exert a dominant influence on coastal chaetognaths and siphonophores?

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A B S T R A C T

A transect that extended 40 km offshore across the continental shelf off Perth, Western Australia, was sampled monthly during 1997 and 1998. Zooplankton was sampled at 5 km intervals with a 300 micron-mesh bongo net deployed vertically to within 3 m of the bottom, or to a maximum depth of 70 m. Numbers of species of chaetognaths and siphonores were quantified, as were abundances of the common species from these groups and of the hydromedusae *Auglaura hemistoma*. The potential influences of four environmental variables (sea-level, sea surface temperature, salinity and chlorophyll concentration) on variability in diversity and abundance were assessed using generalized additive modeling. A combination of factors were found to influence the seasonal and spatial biological variability and, of these factors, non-linear relationships always contributed to the best fitting models. In all but one case, each of the environmental variables was included in the final model. The seasonally variable Leeuwin Current, whose strength is measured as variations in local sea-level, is the dominant mesoscale oceanographic feature in the study region but was not found to have an overriding influence on the shelf zooplankton. This contrasts a previous hypothesis that subjectively attributed seasonal variability of the same taxa examined in this study to seasonal variations in the Leeuwin Current. There remains a poor understanding of shelf zooplankton off Western Australia and, in particular, of the processes that influence seasonal and spatial variability. A more complete understanding of potential causative influences of the Leeuwin Current on the shelf plankton community of south-western Australia must be cognizant of a range of biophysical factors operating at both the broader mesoscale and at smaller scales within the shelf pelagic ecosystem.

1. Introduction

The tropical, poleward-flowing Leeuwin Current, whose main body flows along the shelf break off the Western Australian (WA) west and south coasts (Ridgway and Condie, 2004), exhibits considerable seasonal and interannual variability in both strength and degree of inshore flow, which results in variable but poorly understood impacts on shelf waters (Feng et al., 2003; Pearce et al., 2006). The Leeuwin Current influences recruitment to some exploited teleosts and invertebrates (e.g. Phillips, 1981; Caputi et al., 1996, 2001), but the mechanisms of this influence largely remain unresolved. Similarly, the influence of the Leeuwin Current on the broader zooplankton community, of which larval stages of the many teleost and invertebrate species form a part, has not been investigated.

Little is known about the zooplankton community across the continental shelf of south-western Australia. Zooplankton has been sampled in inshore waters off the lower west coast of Western Australia (WA) but this has been sporadic and largely designed to support studies specifically related to coastal management. Particular interest has focused on the coastal embayments of Cockburn and Warnbro Sounds (25 km south of Cockburn Sound) (Fig. 1), just south of Fremantle, and adjacent marine waters (Environmental Resources of Australia; Department of Environmental Protection; Helleren and John, unpublished reports). Factors affecting the seasonal patterns of zooplankton in these inshore waters were not investigated.

Gaughan and Fletcher (1997) described the seasonal patterns of shelf macrozooplankton off the southern WA coast but, similar to the inshore plankton studies near Perth, this work was descriptive, with seasonal and cross-shelf variability in abundance and species composition being subjectively attributed to the seasonal changes

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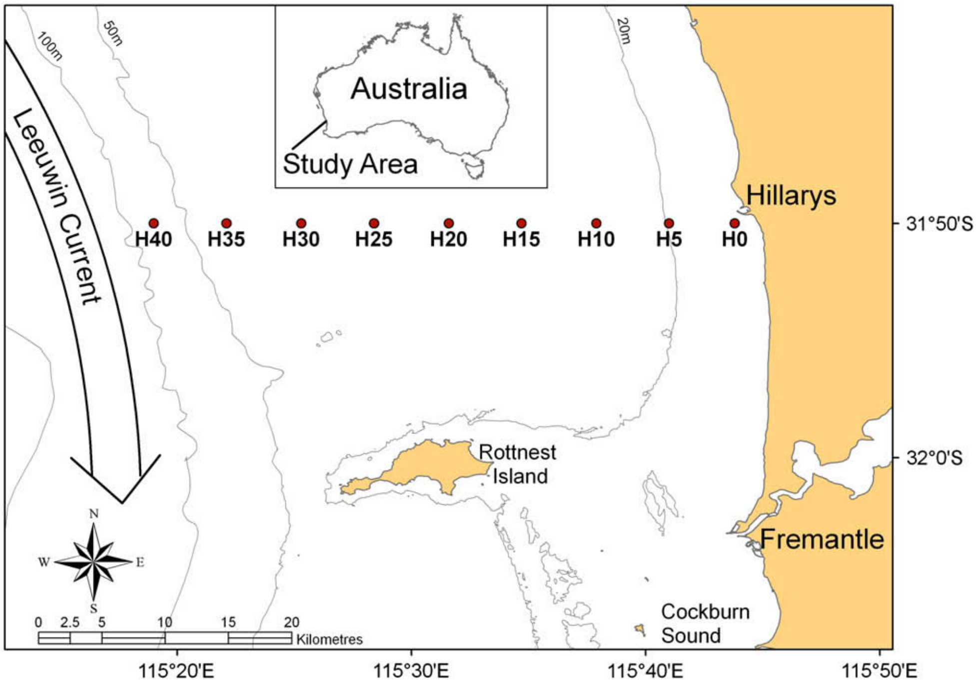

Fig. 1. The continental shelf region off Perth, Western Australia, showing the location of the study transect and sampling stations H0 to H40 (station H0 not sampled). A depiction of the Leeuwin Current is shown. The Capes Current (not shown) flows northward inshore of the Leeuwin Current.

in the strength and degree of coastal impingement of the Leeuwin Current. More recently, Strzelecki and Koslow (2006) examined mesoplankton along a cross-shelf transect that started about 40 km north of Hillarys (see Fig. 1); that study provided a detailed description of the mesoplankton, but as with Gaughan and Fletcher (1997) the hypothesized influence of the Leeuwin Current on the observed spatial–temporal patterns was not objectively assessed.

The aim of this study was to investigate the influence the strength of the Leeuwin Current, sea surface temperature (SST), salinity, chlorophyll concentration and shelf-location (i.e. distance-offshore) on zooplankton. This study focuses on chaetognaths and siphonophores because (1) it was these taxa that were hypothesized to be influenced by the Leeuwin Current on the southern WA coast (Gaughan and Fletcher, 1997) and (2) data for these groups were available as by-product of an ichthyoplankton survey undertaken during a multi-disciplinary research program. This study provides the first objective multivariate analysis of what factors are influencing the abundance of shelf zooplankton, so we aim to provide a significant improvement in the understanding of what may also be influencing recruitment variability of those exploited fish resources whose eggs and larvae co-occur in the pelagic environment with zooplankton.

2. Material and methods

2.1. Sample collection

Zooplankton was sampled each month from January 1997 to December 1998. The sampling cruise started at approximately 0900 h, taking about five hours to complete. Each station was thus sampled at a similar time each month, with variations due to influence of sea conditions on both vessel speed and operation of sampling activities. All samples were taken with vertical tows from the surface to 70 m depth or to within 3 m of the bottom in shallower water. Sampling was undertaken at eight stations spaced 5 km apart along a transect, perpendicular to the coast, from 5 km to 40 km offshore (stations H5 to H40, Fig. 1). No samples were taken at station H0, close to shore, because there was insufficient depth to allow an adequate vertical sample (see below) of zooplankton. The sample design thus consisted of 2 years $\times$ 12 months $\times$ 8 stations; some months/stations were not sampled due to poor weather, resulting a total of 175 of a possible 192 samples collected.

A CalVET net (Smith et al., 1985) fitted with a flowmeter was employed to sample plankton; this is a bongo arrangement, each net with a 27 cm diameter opening and 300 μm mesh. The nets have a sufficiently long cylindrical mid-section tapering gradually to the cod-ends to ensure that filtering efficiency is not compromised. From January to June 1997 the net was deployed so that it sampled during retrieval. Due to winch limitations, sampling from July 1997 occurred during deployment with weights added so that the net consistently sampled at approximately 1 m s^{-1}. The mouth of the net closed at the end of the drop, locking the flowmeter impeller and preventing further sampling, before retrieval to the surface. Because in both cases the net sampled vertically at 1 m s^{-1} we have assumed that there was minimal bias introduced by changing the sampling direction. At the end of each tow the plankton nets were washed with a deck-hose and the cod-end contents preserved in borax-buffered 5% formalin.

2.2. Environmental variables

SST, salinity and chlorophyll concentration were measured at each sampling station as described in Pearce et al. (2006) and Fearns et al. (2007). Monthly sea-level adjacent to Fremantle, an indicator of Leeuwin Current strength (Pearce and Phillips, 1994), was obtained from the National Tidal Facility at Flinders University (South Australia).

2.3. Sample processing

Siphonophores and chaetognaths were identified and enumerated under a dissecting microscope in the laboratory. No attempt was made to identify juvenile stages of either of these taxa.

Siphonophores typically break apart when collected in plankton nets. Physonect siphonophores were counted only when the pneumatophore and colony stem could be found, rather than relying on dislodged nectophores. Counts of calycophoran siphonophores refer only to anterior nectophores since the posterior nectophores were often dislodged. The common hydromedusa *Auglaura hemistoma* was also counted. All counts were standardized to numbers m^{-3} using the sample volumes, which ranged from 0.7 to 8 m^{-3}. As the number of species of siphonophores and chaetognaths changed significantly between summer and winter off the southern WA coast (Gaughan and Fletcher, 1997), these simple measures of diversity were also recorded.

2.4. Data analysis

Generalized additive models (GAMs) (Hastie and Tibshirani, 1990) were used to investigate which combination of sea-level, SST, salinity and chlorophyll concentration best accounted for the variability in the abundance of the dominant zooplankton and in numbers of siphonophore and chaetognath species. A stepwise procedure for sequentially fitting all possible combinations of linear and non-linear (smoothed) predictor variables was undertaken using the *S-plus* software (Version 8.0, 2002, Mathsoft Inc. Seattle): the best fitting model for each response variable was chosen through examination of residual deviances using the Akaike information criterion (AIC, Chambers and Hastie, 1992). The abundance of each taxon and numbers of species of siphonophore and chaetognath were the response variables investigated.

Initial modeling indicated that four data points appeared to have an unduly large influence on the variance and these were therefore removed from further analyses, leaving a final sample size of 171 observations. Examination of residuals showed unacceptable influence of zero values. To account for this, a binary presence/absence term was added to the above four covariates. Because presence/absence fits on only two values (i.e. 0 or 1) and taxa were often not found in samples, this term was invariably part of the chosen model but is not further discussed. Fitted GAMs are illustrated as partial regression plots that show the shape of the relationship between response and predictor variables.

3. Results

3.1. Environmental variables

Pearce et al. (2006) provide detailed descriptions of the environmental characteristics along the study transect, including plots of SST, salinity and chlorophyll concentration along the transect for 1997 and 1998, and an SST-salinity biplot. Besides using these provided data in the GAMs, some of the data from Pearce et al. are replotted here to show the spatial and seasonal differences in the predictor covariates to assist with interpretation of the results from the GAMs.

Sea-level peaked in each year during May and June (late autumn–early winter) and then declined till October (mid-spring) before again starting to increase. Sea-level was higher in January and February (summer) of 1997 than in 1998, but in this second year was higher in the eight consecutive months from May to December (Fig. 2a). SST gradually increased by 2.5–4 °C across the shelf during autumn (April) to spring (October–November) (Fig. 2b). During summer the cross-shelf pattern in SST was less predictable, with differences of 1.0–1.5 °C (Fig. 2b). Monthly mean SST was comparatively lower in January to February and September to October of 1998 than in the same months for 1997. Salinity followed a similar seasonal trend to SST, decreasing through autumn and winter following summer maxima (Fig. 2c). Salinity was considerably higher at site H5 from January to February 1997 than at the more offshore sites. Salinity was also a little higher from September to December in 1997 than in 1998 but, except for the more variable sites H5 and H10, was otherwise similar. A spike in chlorophyll (cross-shelf mean of ~0.9 mg l^{-1}) occurred during February 1997, mainly as a result of a value of 2.25 mg l^{-1} (the highest recorded in the study) at site H25 (Fig. 2d). In 1998 chlorophyll peaked over winter (cross-shelf mean of ~1 mg l^{-1}); chlorophyll increased at the three inner stations (H5–H15) from April to June, while H20–H30 had a strong peak in chlorophyll concentration in June only, which was mirrored but with lower concentrations at H35 and H40.

3.2. Composition

Eight species of chaetognaths were recorded, with *Flaccisagitta enflata* and *Mesosagitta minima* dominant. Siphonophores were less abundant than chaetognaths but more diverse; 26 siphonophore species were recorded, with members of the genus *Lensia* being the most common and *Chelophyes appendiculata* being the most abundant. All the chaetognaths and siphonophore species identified are tropical to sub-tropical species, with no cold-water types found (e.g. Alvariño, 1965; Mackie et al., 1987). *Auglaura hemistoma*, the most commonly encountered Hydromedusae, is also a widespread warm-water species.

3.3. Spatio-temporal variability

Numbers of siphonophores and chaetognath species and abundance of each dominant taxon exhibited considerable variation among seasons and locations across the shelf (Fig. 3). Numbers of siphonophores were usually around 0.1–1.0 m^{-3}, with an overall average of 0.3 species m^{-3}. Chaetognaths were more diverse, with an overall average of 0.7 species m^{-3}. The numbers of chaetognath and siphonophore species reached maxima in autumn/winter of both years (Fig. 3a and b). For both groups, the diversity was greater in 1998 than in 1997, and for each there was a spike in diversity inshore in May 1998.

Flacosagitta enflata was the most abundant species recorded, reaching densities of 30–50 individuals m^{-3} in May 1997, and 10–30 individuals m^{-3} in May 1998 (Fig. 3c). *Mesosagitta minima* reached densities of 5–20 individuals m^{-3} in early 1998 (Fig. 3d), in contrast to the remaining species that typically occurred at densities less than 10 individuals m^{-3} (Fig. 3e–h). Abundances of *M. minima*, *Aidanosagitta regularis*, *Pterosagitta draco*, *Chelophyes appendiculata*, and *Auglaura hemistoma* were higher in 1998 than in 1997, whereas no such difference was observed for *F. enflata*. The abundances of the chaetognaths *F. enflata* and *A. regularis* peaked in autumn/winter (Fig. 3c, e), whereas *M. minima* reached a maximum density in summer and autumn (Fig. 3d). *Pterosagitta draco* was most abundant in autumn. In 1998, relatively large numbers of *C. appendiculata* were caught at the mid-shelf stations H20 to H30 in summer/autumn but were otherwise in low abundance (Fig. 3f). The hydromedusa *A. hemistoma* was most abundant in autumn/winter of 1998 at inner sites H5 and H10 and at the outer shelf.

All the analysed species showed a marked increase in abundance at station H5 in May 1998 and there were also substantially more species of both siphonophores and chaetognaths (this feature is masked by averaging of the two inshore sites in Fig. 3). The concentrations of *Chelophyes appendiculata*, *Aidanosagitta regularis*, *Pterosagitta draco* and *Auglaura hemistoma* were the highest recorded during the entire 2-year survey period. At this time densities were also relatively high at stations H10 and H15. The environmental data examined here were not sufficient to explain the high diversity and abundance recorded at the inshore stations

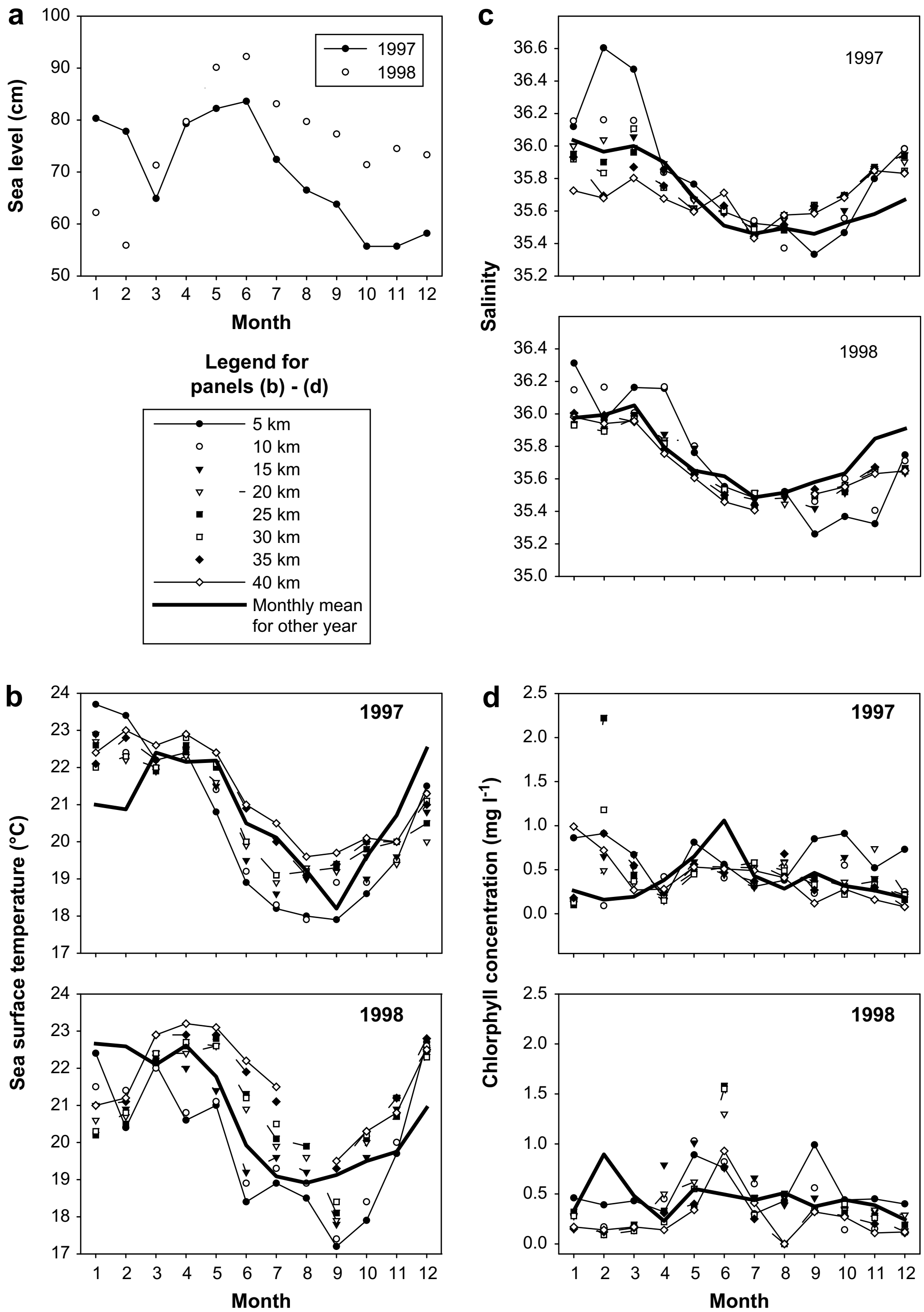

Fig. 2. Monthly (a) sea-level, (b) sea surface temperature (SST), (c) salinity and (d) chlorophyll concentration off Perth in 1997 and 1998. The latter three variables were measured along a transect across the shelf that sampled monthly at 5 km intervals from 5 to 40 km offshore. For the within-year plots of SST, salinity and chlorophyll, the monthly means for the alternate year are provided to show the main differences. Error bars are not included to improve readability of the plots.

in May 1998 (see Section 3.3) so some alternative influential factors are discussed in Section 4.2.

3.4. Relationship with physico-chemical variables

Prior to fitting GAMs using the suite of four target predictor covariates (i.e. sea-level, SST, salinity and chlorophyll concentration), GAMs for each response variable were fitted to these covariates along with the additional covariates month and distance-offshore because these latter two covariates might be expected to encompass the explanatory power of the temporal and spatial variation of the other variables. These additional analyses confirmed the considerable temporal and spatial variability observed in Fig. 2 with month and distance-offshore contributing to the models for 8 and 7 of the 8 response variables respectively (Table 1). In no case were month and distance-offshore able to account for sufficient variability to negate inclusion of several of the target covariates in the fitted models. Nonetheless, inclusion of

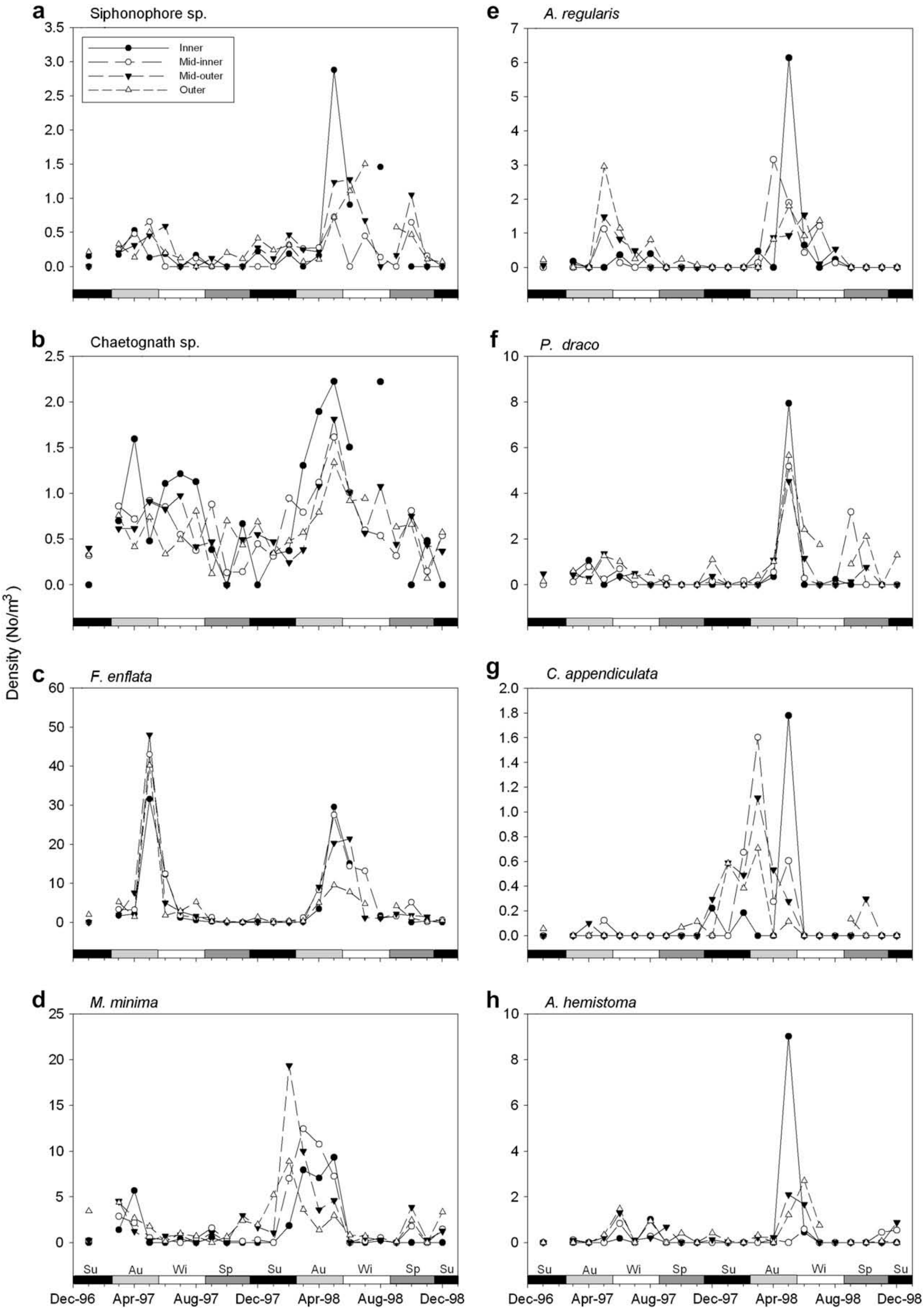

Fig. 3. The numbers of species of siphonophores and chaetognaths, and concentrations of four chaetognaths, one siphonophore, and one Hydromedusae off Perth between January 1997 and December 1998. To facilitate visual interpretation of the plots, the data for adjacent sampling stations were averaged. The use of average values is for descriptive purpose only and was not used in the analyses. Error bars are not included to improve readability of the plots. The sampling stations are shown in Fig. 1 and refer to distance-offshore (i.e. H5 is 5 km from port, etc). Inner shelf – H5 and H10; Mid-inner shelf – H15 and H20; Mid-outer shelf – H25 and H30, Outer shelf – H35 and H40. Su – summer; Au – autumn; Wi – winter; Sp – spring.

Table 1
Analysis of residual deviance table for generalized additive models (GAMs) of zooplankton data against the predictor covariates sea-level (sl), sea surface temperature (sst), salinity (sal) and chlorophyll concentration (chl). Month and distance-offshore were included in an initial series of GAMs to determine if these covariates encompassed the explanatory power of the target covariates, and then excluded to allow the target variables, which vary spatially and temporally, to explain the data. When "s" precedes a covariate in the model, this notation indicates that a smoothing factor was applied to achieve the best fit, indicating a non-linear relationship with the predictor variable. Each null model started with predictor covariates as for (a); all possible combinations of linear and smoothed covariates were then iteratively assessed, with the Akaike information criterion (AIC) used to choose the best fit.

Predictor variables	Model	Including month and distance-offshore	AIC	Excluding month and distance-offshore	AIC
(a) Number of chaetognaths	Null	s(dos) + s(month) + s(sl) + s(sst) + s(chl) + s(sal)	18.46	s(sl) + s(sst) + s(chl) + s(sal)	32.24
	Final	s(dos) + s(month) + s(sl) + sst		Null model accepted	
(b) Number of siphonophores	Final	s(dos) + s(month) + s(sl) + s(sst) + s(chl)	15.11	Null model accepted	21.61
(c) *Flaccisagitta enflata*	Final	Null model accepted	370.64	Null model accepted	454.95
(d) *Mesosagitta minima*	Final	s(month) + s(sl) + sst + s(sal) + s(chl)	237.93	s(sl) + s(sal) + s(chl)	322.94
(e) *Aidanosagitta regularis*	Final	Null model accepted	11.12	Null model accepted	19.16
(f) *Pterosagitta draco*	Final	Null model accepted	31.38	Null model accepted	44.47
(g) *Chelophyes appendiculata*	Final	Null model accepted	1.25	Null model accepted	4.35
(h) *Auglaura hemistoma*	Final	Null model accepted	14.79	Null model accepted	21.95

month and distance-offshore provided additional explanatory power, with AIC scores invariably indicating a stronger fit when these two covariates were included.

GAMs that used only the target covariates indicated that there were no linear responses and that for all but one of the predictor variables the null model was accepted, with each of sea-level, SST, salinity and chlorophyll concentration contributing to the best fits (Table 1, Fig. 4). The variability of *Mesosagitta minima*, the exception, was best explained by a model that included three of the four target variables (sea-level, salinity and chlorophyll concentration). Given that any correlative relationships between the predictor variables are accounted for in the statistical modelling, the inclusion of three or four of the predictor variables in the fitted models indicates that changes in abundance are influenced by a suite of factors.

Partial correlations of the response variables versus the predictor covariates selected by each GAM did not indicate a consistent relationship across taxa for any one predictor covariate, although there was a tendency for dome-shaped relationships between the zooplankton and both salinity and chlorophyll concentration (Fig. 4). Sea-levels up to 80 cm had a weak positive effect on numbers of species of both chaetognaths and siphonophores, and then a strong positive effect between 80 and 90 cm (Fig. 4). For both *Flacosagitta enflata* and *Aidanosagitta regularis* sea-level had a positive effect up to 80 cm, thereafter a negative effect. Sea-level also had a positive effect on *Pterosagitta draco*, but with a plateau at 70–80 cm, followed by a negative effect at 80–90 cm. *Mesosagitta minima* and *Auglaura hemistoma* exhibited a bimodal response to sea-level, while *Chelophyes appendiculata* had a domed, but not particularly strong, relationship with sea-level (Fig. 4).

4. Discussion

4.1. Spatio-temporal patterns and relationship with physico-chemical variables

The predictor and response variables examined here do not indicate that the Leeuwin Current alone exhibited a major influence on the zooplankton in shelf waters off Perth. This study confirmed that the parts of the zooplankton community examined showed strong patterns of seasonal and spatial variability; combinations of SST, salinity, chlorophyll concentration and possibly other factors influenced the zooplankton along with strength of the Leeuwin Current. Although mechanisms of influence could not be determined here, relationships between zooplankton and environmental variables have not previously been objectively evaluated for shelf waters off southern WA and warn against oversimplifying the interpretation of correlative relationships that may be observed between biological measures and single environmental variables.

The increased diversity of both chaetognaths and siphonophores off Perth when sea-level exceeded 80–90 cm indicates a positive relationship with a strong flowing Leeuwin Current. The Leeuwin Current was stronger overall during 1998 (mean sea-level = 75.89 cm) than in 1997 (mean = 70.03 cm) and for most months of 1998 was also stronger than in 1997. Positive relationships with sea-level were also found for four of the six species examined. However, statistical modeling could not confirm the subjective inferences by Gaughan and Fletcher (1997) that the Leeuwin Current has a dominant influence on seasonal dynamics of coastal zooplankton off south-western Australia. Furthermore, this study has established that the two most abundant species of macrozooplankton found in this study, *Flacosagitta enflata* and *Mesosagitta minima*, not only responded differently to sea-level, but also to salinity and chlorophyll concentration, supporting our contention that the Leeuwin Current alone is not the major driver of variability.

Although the strength of the Leeuwin Current alone cannot explain variability on shelf zooplankton, we cannot conclude that the Current does not have an important affect. We suspect that annual or monthly means of sea-level may not be the metric required to investigate cause and effect relationships of shelf zooplankton, and indeed may not be expected to given that sea-level is essentially a measure of gross current flow and not of smaller-scale flows (e.g. cross-shelf penetration). Further hypotheses relating to how biophysical factors might be affecting zooplankton are provided below.

4.2. Physical transport and cross-shelf exchange

Previous studies have demonstrated that the Leeuwin Current transports tropical species southwards. Based on observations of tropical communities at the Abrolhos Islands, 350 km north of Perth, Saville-Kent (1897) and Dakin (1919) postulated a tropical southwards flow off WA. The presence of tropical and sub-tropical zooplankton species (Markina, 1976) and some tropical benthic species (Maxwell and Cresswell, 1981) in shelf waters off southern Australia have been attributed to the Leeuwin Current. Similarly, Hutchins (1991) and Hutchins and Pearce (1994) observed that the arrival of tropical fish larvae at Rottnest Island (on the continental shelf off Perth) in autumn coincided with the seasonal strengthening of the Current. These earlier studies indicate that the Leeuwin Current exerts a direct impact on occurrence of some taxa through acting as a transport mechanism.

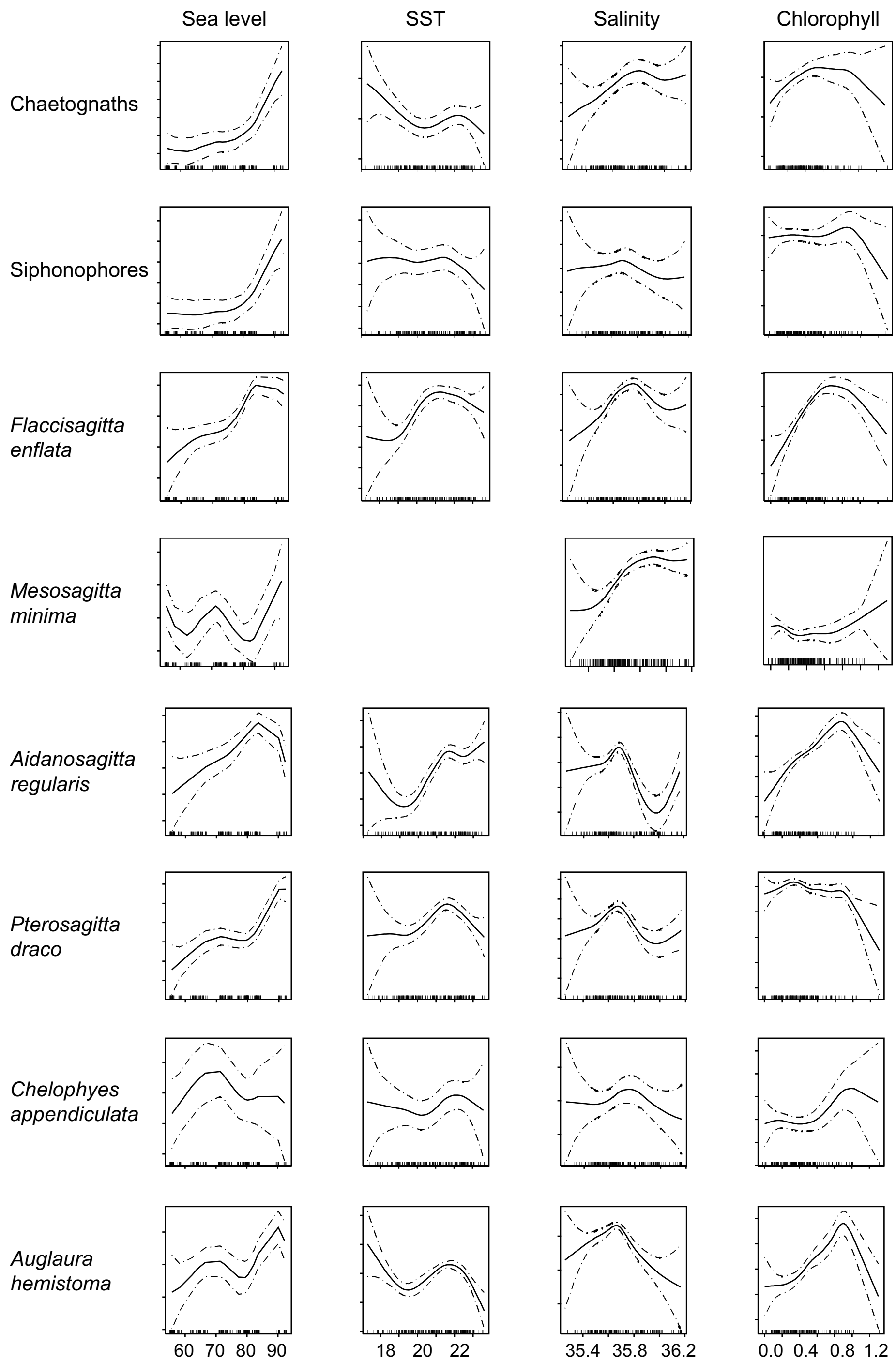

Fig. 4. Partial regression plots from the GAMs in Table 1. Predictor covariates are shown across the top of the figure (sea-level – SL, sea surface temperature – SST, salinity, and chlorophyll concentration) and response variables (diversity or abundance) down the side. The 95% confidence intervals are depicted by the dotted lines.

In the context of shelf waters inshore of the main body of the Leeuwin Current, satellite images of SST and delineation of water bodies based on physico-chemical properties clearly show penetration of Leeuwin-Current water shorewards across the continental shelf (Pearce et al., 2006), representing a potential mechanism for rapid cross-shelf transport of plankton. This penetration across the shelf varies seasonally; in 1997 and 1998 Leeuwin-Current water extended shoreward to at least the mid-shelf (Station H20) for four to six months of each year. Transport and exchange (or displacement and replacement) of zooplankton due to the Leeuwin Current is thus a regular feature of the continental shelf in this region, but lack of data on rates of exchange between Leeuwin-Current water and shelf water preclude the ability to infer rates of exchange of plankton. Nonetheless, the inclusion of sea-level as a significant predictor variable for the zooplankton provides evidence that cross-shelf exchange is at least partially responsible for the spatio-temporal variability seen for each zooplankton category considered here.

The plankton community along the study transect could also be influenced by the Capes Current, a mid-shelf counter-current which flows northward along the lower west and mid west coasts of Australia, driven by the strong northwards wind stress between about October and March (Pearce and Pattiaratchi, 1999). Pearce et al. (2006) recorded water derived from the Capes Current at transect-stations >10 km offshore during summer months. However, unlike the Leeuwin Current for which there is a proxy measure of strength (i.e. sea-level), a similar metric for the Capes Current has yet to be developed despite that this current has recently been linked to upwelling events (Gersbach et al., 1999; Hanson et al., 2005), albeit well to the south of the transect sampled in this study. Similar to the Leeuwin Current, the Capes Current also varies in strength within and between years so would be expected to exert variable influence on shelf zooplankton.

5. Conclusion

The Leeuwin Current could be a dominant factor for the shelf zooplankton but this influence is not simply via transport of plankton but perhaps also by a number of co-occurring changes that could include sporadic pulses of nutrients alongside increased temperatures. While the seasonal variability in the Leeuwin Current is a fundamental feature of the seasonal changes in ocean conditions along the WA coast, further investigation is required if the causative processes are to be better understood. The stronger explanatory power of the GAMS when month and distance-offshore were included, implies that other factors besides those examined here are influencing shelf zooplankton. Such factors may include physical (transport, exchange or lack thereof), chemical (nutrients), and biological (prey field, physiological responses) mechanisms. Further investigations of the influence of the Leeuwin Current must include consideration of non-linear responses to both Leeuwin Current strength and a range of other environmental variables. Alternative measures of Leeuwin Current strength and a measure of the strength of the Capes Current need to be investigated. In particular, estimates of rates of exchange between these currents and shelf water are urgently required.

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