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Effects of the Leeuwin Current on the Distribution of Carnivorous Macrozooplankton in the Shelf Waters off Southern Western Australia

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Plankton samples were collected using 500-μm nets in the surface waters (up to a depth of 70 m) of the continental shelf in three regions (Albany, Bremer Bay and Esperance) off southern Western Australia in July 1992 (winter) and January 1993 (summer). The carnivorous zooplankton of these samples were characterized by low species richness and high variability in abundance. Abundances of most of the major taxa collected differed significantly between seasons and many also differed between regions. Siphonophores and chaetognaths dominated the carnivorous plankton, with lower abundances of hydromedusae and raptorial copepods. The most abundant siphonophores were *Chelophyes appendiculata* and *Eudoxoides spiralis* in summer and winter, respectively. The most abundant chaetognaths were *Sagitta minima* in summer, with *Pterosagitta draco* and *Sagitta enflata* dominant during winter. Overall, the numbers of species of both siphonophores and chaetognaths were highest during winter. At this time, there was also a trend for decreasing numbers of species in an easterly direction between Albany and Esperance, which was probably due to the presence of subtropical species entrained within the warm Leeuwin Current, which was flowing east along the continental shelf during winter. During summer, when the current was not present in this region, there was an even spread of fewer species along the coast.

Keywords: zooplankton; coastal current; continental shelf; Western Australia

Introduction

Seasonal or interannual variations in oceanographic conditions (e.g. currents and advective processes) can influence the composition and distribution of zooplankton within a region (e.g. Colebrook, 1977; Pagès & Gili, 1991). The more conspicuous carnivores in marine zooplankton include chaetognaths, siphonophores, hydromedusae and ctenophores, which apart from their potential influence on other taxa, have also been used as indicators of ocean currents or different water masses (e.g. Bieri, 1959; Pagès & Gili, 1991). Thus, their occurrence and distribution may reflect mesoscalar hydrographic events or advective processes.

The major hydrographic feature in shelf waters of southern Western Australia (WA) is the warm Leeuwin Current which consists of relatively fresh tropical water from north of WA that entrains saltier subtropical water from the eastern Indian Ocean as it flows south along the western coast of WA (e.g. Cresswell & Peterson, 1993). This surface current, the main core of which is typically 100–150 m deep, flows parallel to the coast at speeds up to 1 m s^{-1} and usually tracks along the continental shelf edge. Cresswell and Peterson (1993) have shown that an increase in surface temperature along a transect moving into the Leeuwin Current was accompanied by an increase in the strength of the current, i.e. warmer water was associated with higher current velocities. The influence of the current can extend to a depth of 300 m and thus typically extends through the entire water column when the current is on the continental shelf. The current rounds Cape Leeuwin on the south-west corner of WA (Figure 1) and then flows east. As the Leeuwin Current progresses south and then east, the temperature decreases and the salinity increases due to mixing with local waters (Cresswell & Peterson, 1993). Due to seasonal differences in wind stress along the west coast of WA, the Leeuwin Current flow is stronger in winter than in summer. Furthermore, the strength of the current and its position along the continental shelf can also vary between years.

The biological implications of the Leeuwin Current on marine ecosystems off southern WA have recently begun to receive more attention (e.g. Lenanton *et al.*,

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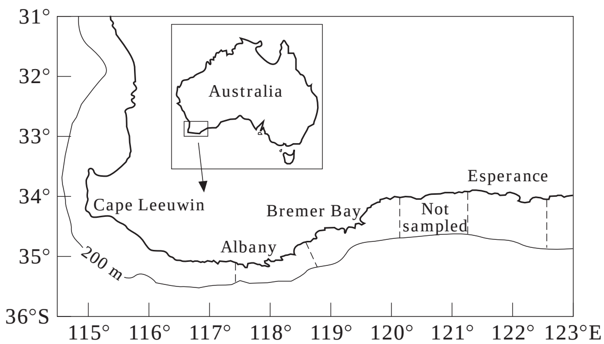

FIGURE 1. The study area off southern Western Australia. The edge of the continental shelf is indicated by the 200 m isobath in this and the following figures.

1991; Morgan & Wells, 1991). Previously, Markina (1976) found that the zooplankton fauna of the western Great Australian Bight had a strong tropical component derived from equatorial waters from the west coast of Australia. This same conclusion was found for some benthic invertebrates and a pelagic teleost, and in this case was related to the presence of the Leeuwin Current (Maxwell & Cresswell, 1981). More recently, the Leeuwin Current has also been shown to have a strong influence on the location of pilchard spawning off southern WA and the subsequent fate of their eggs and larvae (Fletcher *et al.*, 1994). However, any direct influences of this current on the macrozooplankton component of pelagic ecosystems off southern WA have not been documented.

The aim of this paper is to examine the effects of the Leeuwin Current on the composition, distribution and abundance of carnivorous macrozooplankton (i.e. those retained by 500-µm mesh) in waters of the continental shelf off southern WA.

Materials and methods

Sampling procedures

Sampling was conducted between Albany (118°E) and Esperance (122°E) on the southern coast (34–35·5°S) of WA (Figure 1). This area was divided into four regions, each of which corresponded to about 120 km of coastline. Only three of these regions, which were centred on the ports of Albany, Bremer Bay and Esperance, were sampled (Figure 1). Samples were taken between 5 and 25 km offshore in the Albany and Bremer Bay regions, and between 5 and 40 km offshore in the Esperance region, reflecting the different width of the continental shelf in these areas. Sampling was carried out in July 1992 and January 1993 (i.e. winter and summer), and in each case was completed within a 2–3-day period, depending on the weather. Three or four boats were used during each sampling period, i.e. one or two in each sampling region, so that the three regions could be sampled at the same time. Between 12 and 14 samples were taken in each season at the two western regions, and 15–18 samples were taken in the Esperance region. Due to poor weather conditions, fewer samples were taken offshore, i.e. the continental shelf edge, during winter.

Vertical tows were taken during the day from a depth of 70 m, or from the bottom in shallower water. The tows were made using two conical nets in a bongo arrangement, with a centrally located bridle so that no towing apparatus lay in front of the mouths of the nets. Each net had a mouth diameter of 0·6 m and was constructed of 500-µm mesh. The nets were winched to the surface at a speed of 1 m s^{-1}. The volume of water sampled was measured with a flowmeter and averaged 50 m^3. The samples were fixed in buffered 5% formalin and seawater.

Sea-surface temperature was measured at each sampling location with a mercury thermometer. Large-scale oceanographic variations in sea-surface temperature during each sampling period were assessed using NOAA AVHRR (advanced very high resolution radiometer) satellite images.

Laboratory procedures

Hydromedusae, siphonophores, chaetognaths and raptorial copepods were counted under a dissecting microscope, and their abundances were expressed as concentrations, i.e. number of individuals 100 m^{-3}. Siphonophores typically break apart when collected in plankton nets. Physonects were thus counted only when the pneumatophore and colony stem could be found, rather than relying on dislodged nectophores. Likewise with the calycophorans, counts refer to anterior nectophores only, since the posterior nectophores were often dislodged. The unidentified gonophores of diphyids could usually be recognized as belonging to a certain type (although unidentified) of eudoxid, i.e. from which they had broken away. Thus, the category ‘gonophores’ consisted only of those which could not be ascribed to a particular type of eudoxid. The hydromedusae were generally in poor condition and difficult to identify. Although 15 different species of hydromedusae could be recognized, only the Trachymedusae *Auglaura hemistoma* could be identified to species level (Table 1). The remainder were identified to family using Kramp (1968). Siphonophores were identified using Totton (1965), Rengarajan (1973) and Pagès and Gili (1992).

TABLE 1. Mean (+SD) concentrations (no. 100 m^{-3}) of carnivorous zooplankton recorded in continental shelf waters off southern Western Australia in July 1992 (winter) and January 1993 (summer)

Taxa	Winter	Summer
Cnidaria		
Hydromedusae		
Anthomedusae	22·5 (30·0)	32·2 (52·3)
Leptomedusae	43·5 (65·1)	4·6 (11·7)
Limnomedusae	2·0 (5·8)	5·0 (16·7)
Trachymedusae		
Auglaura hemistoma	59·6 (155·1)	17·8 (5·88)
All hydromedusae	127·6	59·6
Siphonophora		
Physonectae (two species)	5·4 (13·6)	0
(*Agalma elegans*)		
(*Rhizophysa* sp.)		
Calycophorae		
Sulculeolaria sp.	0·3 (1·7)	0
Diphyidae		
Unidentified larvae	9·0 (22·1)	253·9 (422·0)
Unidentified gonophores	2·0 (4·3)	13·0 (64·7)
Lensia subtilis	1·7 (6·8)	0
Lensia subtiloides	2·0 (8·3)	0
Chelophyes appendiculata	4·2 (13·3)	281·7 (518·1)
C. appendiculata eudoxids	19·0 (56·5)	565·4 (938·5)
Eudoxoides spiralis	11·7 (47·8)	0
E. spiralis eudoxids	34·6 (112·4)	5·3 (23·0)
Abyliidae		
Abylopsis eschscholtzi	13·3 (55·0)	0
Abylopsis tetragona	1·6 (8·0)	0
Bassia bassensis	8·6 (26·2)	0
All siphonophores	102·1	852·4
No. of species	10	3
Chaetognatha		
Pterosagitta draco	114·6 (380·5)	8·5 (21·0)
Sagitta bipunctata	11·5 (42·0)	0
Sagitta enflata	105·3 (122·6)	0
Sagitta hexaptera	6·4 (19·6)	1·1 (4·8)
Sagitta lyra	1·9 (8·8)	0
Sagitta minima	44·8 (66·4)	259·7 (590·9)
Sagitta regularis	7·8 (35·3)	0
Sagitta robusta	16·9 (36·2)	1·2 (4·9)
Sagitta serratodentata atlantica	14·9 (35·3)	2·6 (7·2)
All chaetognaths	324·1	273·1
No. species	9	5
Copepoda		
Candacia bipinnata	31·0 (55·8)	7·1 (16·6)
Euchaeta marina	42·1 (103·5)	5·4 (23·8)
All copepoda	73·1	13·5
Total number species identified	23	10

The means are based on data pooled across regions in each season.

Chaetognaths were identified using the keys in Thomson (1947) and O'Sullivan (1983), along with the figures in several works including those of Burfield and Harvey (1926), Tokioka (1940) and Furnestin (1957, 1958). The copepods were identified using the monograph by Dakin and Colefax (1940). Given their greater concentrations, this paper focuses on the siphonophores and chaetognaths.

Data analyses

Prior to analyses, all abundance data were $\log_{10}(n+1)$ transformed to homogenize variances. The variability in the concentrations of the 12 more abundant taxa (those for which the mean concentration in either winter or summer exceeded 25 ind. 100 m^{-3}) were analysed between seasons, coastal regions and distance from shore (i.e. cross-shelf positions) using three-factor ANOVAs. However, Bartlett's test (Zar, 1984) indicated that for 10 of the 12 taxa, variance remained heterogeneous following transformation. To decrease the chances of making a Type I error in these cases, a significance level of $P<0{\cdot}01$ was chosen. Only six of 84 F values resulting from the ANOVAs had probabilities between 0·05 and 0·01.

Preliminary examination of the data revealed differences in the number of species between seasons, regions and the inshore and offshore sampling stations. Stepwise regression indicated that there were both longshore and offshore trends in the numbers of species. To help elucidate spatial patterns in the distribution of species, contour plots were made of the total numbers of species and the numbers of siphonophore and chaetognath species found at each station. Contour intervals were assigned by a software package which interpolated node values from the given data. The results of eight different methods of interpolation were examined with the view of choosing that which best represented the structure of the data identified by stepwise regression, i.e. the longshore and offshore trends in numbers of species. Kriging with linear drift (e.g. see Legendre & Fortin, 1989) was the method of producing contours which most closely reflected the actual values of the original data.

Results

Sea-surface temperature

In July 1992, the sea-surface temperature data obtained during the survey and from the NOAA satellite thermal images indicated that the Leeuwin Current was flowing strongly close to the coast in the region west of Albany (Figure 2). In the Albany region, the landward edge of this band of relatively warm water was located about 10 km offshore. The current was further offshore in the Bremer Bay ($\sim$16 km) and Esperance ($\sim$26 km) regions, and was also considerably weaker than at Albany, due in part to a major southerly offshoot at 119°E. Surface waters within the current ranged from 18·5 to 19·0 °C, whereas outside of its influence, they were only 16·5–17·9 °C.

The water temperatures and satellite image for January 1993 indicated that the Leeuwin Current was either not present off southern WA at this time or had temperatures similar to those already present along the southern coast, resulting in the detection of little or no thermal contrast (Figure 2). The sea-surface temperatures in the study area during January varied between 19·0 and 21·5 °C.

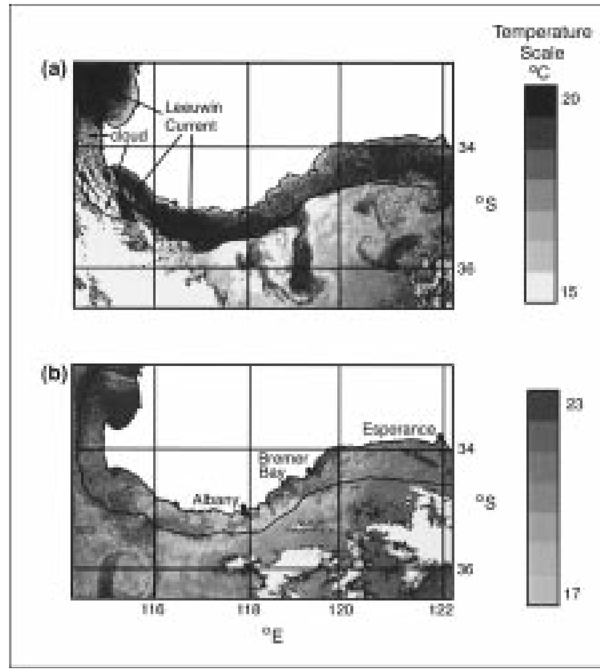

FIGURE 2. NOAA-AVHRR (advanced very high resolution radiometer) thermal images of the ocean off southern Western Australia during (a) winter (July 1992) and (b) summer (January 1993). Separate temperature scales are provided for each image since the variations in the range of sea-surface temperatures between summer and winter necessitated compiling the images at different levels of contrast. Note that some areas have cloud cover. The Leeuwin Current can be seen in (a) as a dark band, with a southerly offshoot at 119°E, covering much of the continental shelf along the southern coastline.

Taxa composition

The carnivorous zooplankton caught in this study consisted of 10 species of siphonophores, nine chaetognaths, two copepods and one species of Hydromedusae (Table 1). Representatives of three other families of Hydromedusae were also found. The number of species differed significantly ($P<0{\cdot}001$, t-test) between seasons, with 23 identified species recorded during winter and only 10 during summer.

During winter, the total number of species of carnivorous macrozooplankton decreased in an eastward direction ($P<0{\cdot}001$, ANOVA), with up to 18 species per sample being recorded in the Albany to Bremer Bay region, but a maximum of only 11 species per

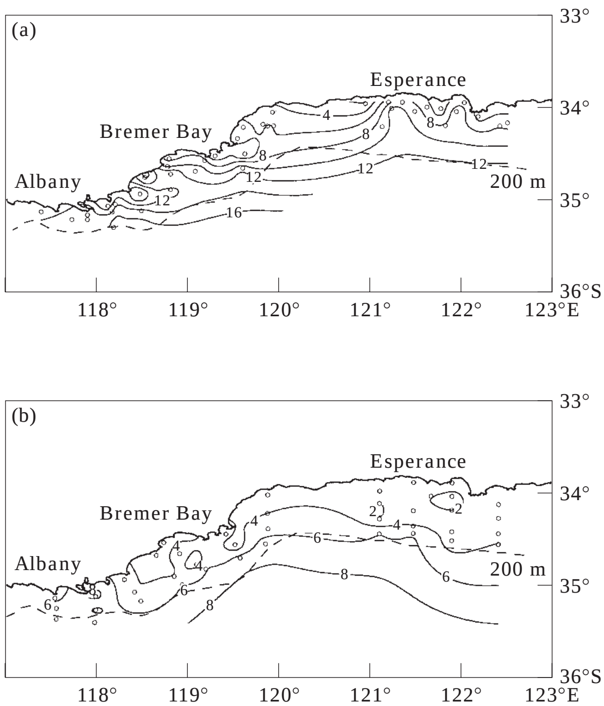

FIGURE 3. The number of species of carnivorous zooplankton per sampling station on the continental shelf off southern Western Australia in (a) winter (b) summer. ○, sampling stations. The contour intervals were produced by a software package using the kriging method, which incorporated linear drift while interpolating node values. Note that the contours have been allowed to extend beyond the sampling regions in order to clarify the large-scale spatial trends indicated by the data. The same contouring method was also used in Figures 4 and 5.

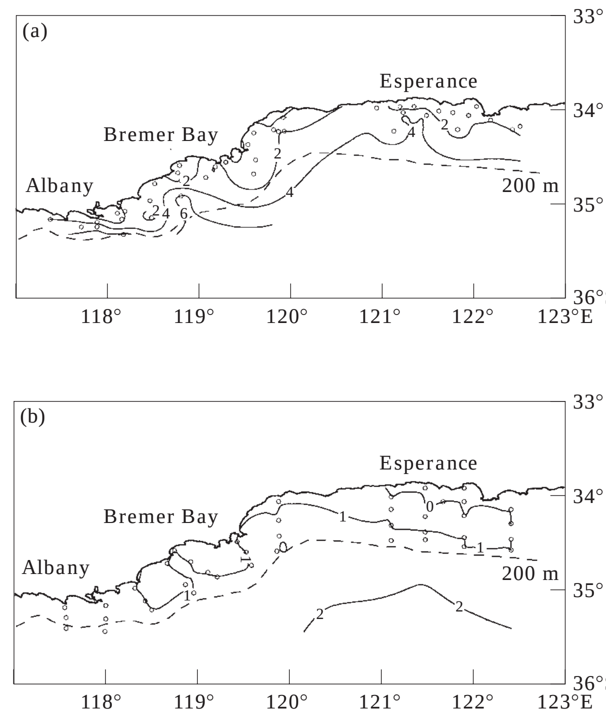

FIGURE 4. The number of species of siphonophores at each sampling station on the continental shelf off southern Western Australia in (a) winter and (b) summer.

sample in the Esperance region [Figure 3(a)]. By contrast, such longshore differences, although still significant ($P<0{\cdot}01$), were less well defined during summer, when the overall number of species was much lower [Figure 3(b)]. These patterns are reflected by the species richness of chaetognaths and siphonophores (Figures 4 and 5).

The number of macrozooplankton species increased in an offshore direction ($P<0{\cdot}01$) in both summer and winter (Figures 3–5). However, stepwise regression of the total number of species against distance offshore and distance east (from the most westward station) indicated that the longshore differences accounted for 70% of the variation in species richness in both summer and winter.

Overall, siphonophores were about eight times more abundant in summer (mean = 852·4 ind. 100 m^{-3}) than in winter (mean = 102·1 ind. 100 m^{-3}), whereas the mean concentrations of the copepods and the hydromedusae were higher in winter (Table 1). In summer, the mean concentrations of the polygastric and eudoxid stages of *Chelophyes appendiculata* were 281·7 and 565·4 ind. 100 m^{-3}, respectively, whereas the highest mean concentrations for any one species of siphonophore in winter were only 11·7 and 34·6 ind. 100 m^{-3} for the polygastric and eudoxid stages of *Eudoxoides spiralis*, respectively.

The abundance of the chaetognaths as a group varied little between seasons (winter = 324·1 ind. 100 m^{-3}, summer = 273·1 ind. 100 m^{-3}). However, *Pterosagitta draco* (mean = 114·6 ind. 100 m^{-3}) and *Sagitta enflata* (105·3 ind. 100 m^{-3}) dominated the chaetognaths in winter, while *Sagitta minima* (259·7 ind. 100 m^{-3}) dominated in summer.

Seasonal and spatial variability of the more abundant taxa

Three-factor ANOVAs were performed for those 12 taxa or developmental stages for which the mean concentration exceeded 25 ind. 100 m^{-3} in either season (Table 2). In most cases, there were significant differences ($P<0{\cdot}01$–$P<0{\cdot}001$) in abundance between seasons, regions or both. The Anthomedusae were the main exception to this, and with no differences in abundance between either seasons or regions, while *S. enflata* showed a significant difference for season

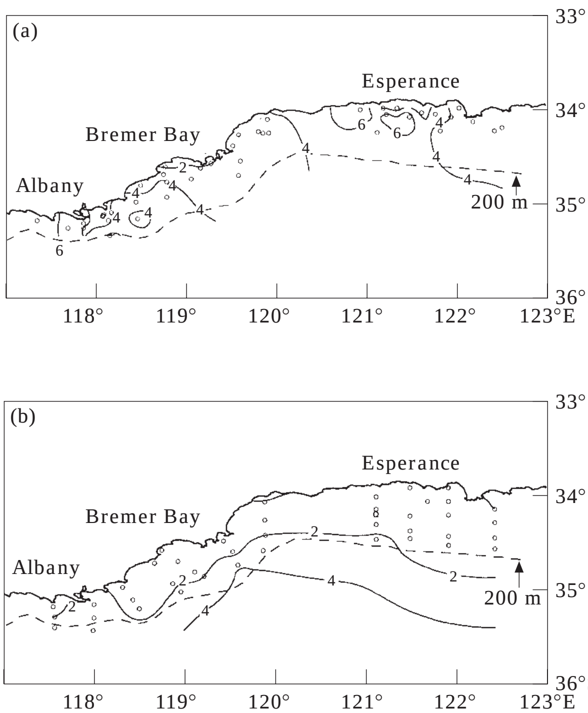

FIGURE 5. The number of species of chaetognaths at each sampling station on the continental shelf off southern Western Australia in (a) winter (b) summer.

only. The following descriptions of the variability in abundance of the various taxa are based on the significant differences for the main effects and the interaction terms, either singly or, where appropriate, in combination (Table 2).

Seasonal variations. Calycophoran larvae, *C. appendiculata*, the eudoxids of *C. appendiculata* and *E. spiralis*, and *S. minima* were significantly more abundant in summer (Tables 1 and 2). In contrast, *Candacia bipinnata*, *Euchaeta marina*, Leptomedusae, *A. hemistoma*, *P. draco* and *S. enflata* were significantly more abundant in winter. Also, several of the less abundant taxa were present only during winter (Table 2).

Regional variations. Most of the species that were only found in winter were present in the Albany region alone. *Auglaura hemistoma*, *E. spiralis* eudoxids and *E. marina* were significantly ($P<0{\cdot}01$) more abundant at Albany than at the other two regions, whereas *C. bipinnata* was more abundant at Albany and Esperance than at Bremer Bay. Both stages of *C. appendiculata* were present during winter in the Albany region alone, but were abundant through to Esperance during summer, resulting in significant ($P<0{\cdot}01$) season × region interaction terms. *Sagitta minima* and *P. draco* also had significant ($P<0{\cdot}01$) season × region interactions. *Sagitta minima* was more abundant at the Albany and Esperance regions in winter, but had similar concentrations at each region in summer. The abundance of *P. draco* was much higher in Albany than at either Bremer Bay or Esperance during summer, but was higher at both Albany and Bremer Bay than at Esperance during winter.

Cross-shelf variations. The abundance of eight of the 12 taxa differed significantly with distance from shore

TABLE 2. Significance results of three-way ANOVAs comparing concentrations of the more abundant carnivorous zooplankton in continental shelf waters of southern Western Australia between seasons (summer and winter), regions (Albany, Bremer Bay and Esperance) and distances offshore

Taxa	Season (S)	Region (R)	Distance from shore (D)	S × R	S × D	R × D	S × R × D
Leptomedusae	*						
Anthomedusae			*				
Auglaura hemistoma	*	*	*				
Larval calycophorans	*					†	
Chelophyes appendiculata	*	†	*	*		†	
C. appendiculata eudoxids	*	†	*	*	†	†	
Eudoxoides spiralis eudoxids	*	†			†		
Pterosagitta draco	*	*	*	†		†	
Sagitta minima	†	†	*	†			
Sagitta enflata	*						
Candacia bipinnata	*	†					
Euchaeta marina	*	*	†				

*$P<0{\cdot}001$, †$P<0{\cdot}01$. Blank spaces represent non-significant results.

(i.e. cross-shelf position), the exceptions being Leptomedusae, larval calycophorans, *E. spiralis* eudoxids and *S. enflata* (Table 2). Anthomedusae was the only taxa which tended to be more abundant inshore, while both stages of *C. appendiculata*, *A. hemistoma*, *P. draco*, *S. minima* and *E. marina* were typically more abundant offshore. Eudoxids of *C. appendiculata* and *E. spiralis* were the only taxa for which there was a significant ($P<0{\cdot}01$) seasonal change in cross-shelf distribution (Table 2), with greater abundances offshore in summer and inshore during winter. There were also differences in cross-shelf abundance between regions for larval calycophorans, both stages of *C. appendiculata* and *P. draco*. The first three of these groups were more abundant inshore at Albany and Bremer Bay than at Esperance, whereas *P. draco* was more abundant offshore at Bremer Bay than at Albany.

Discussion

Species richness in relation to the Leeuwin Current

The composition and distribution of carnivorous macrozooplankton off southern WA appear to be affected by the presence and absence of the Leeuwin Current, and were characterized by low species richness and high variability in abundance between seasons and regions. Each species of siphonophore and chaetognath recorded in this study has a wide geographic distribution, and in most cases occurs in each of the Indian, Pacific and Atlantic oceans, with most characteristic of warm to temperate waters (Alvariño, 1965, 1971; Mackie *et al.*, 1987; Pagès & Gili, 1992). Whilst several are known to be tropical to sub-tropical species (e.g. *A. elegans*, *S. enflata*, *S. regularis*), no cold-water forms were found.

Since the main factors that influence the geographical distribution of chaetognaths and siphonophores are large-scale hydrographic features, such as the presence and location of different water masses (Alvariño, 1965; Mackie *et al.*, 1987), the higher species richness of these groups off southern WA in winter than in summer was probably due to the intrusion of the Leeuwin Current along the continental shelf in this region during winter. Thus, although water temperature was generally about 2 °C higher in summer, during winter there appeared to be more tropical and subtropical species being advected into the southern shelf waters by the current which originates in tropical waters off northern WA and includes subtropical water entrained from off the west coast of WA (Cresswell & Peterson, 1993). The lack of cold-water species off southern WA was, therefore, a consequence of the presence of relatively warm water throughout the year and the limit of sampling to warmer surface (<70 m) waters. Furthermore, there are no known areas of persistently strong upwelling or intrusion of cold subantarctic waters onto the continental shelf in the study region. Short periods of upwelling near the coast may sometimes occur, while intrusions of subantarctic water either mix with, or are over-run by, the Leeuwin Current (Cresswell & Peterson, 1993).

Further evidence of the influence of the Leeuwin Current during winter was the distinct decrease in the number of species of both chaetognaths and siphonophores in the direction that the current was flowing, i.e. west to east, in conjunction with the weakening and increasing distance offshore of the current in that direction. Indeed, the winter pattern in the shelf waters between Albany and Esperance resembled the north-south gradient in the number of siphonophore species in shelf waters of south-west Africa which resulted from the southward intrusion of a warmer water mass into the Benguela system (Pagès & Gili, 1991). Likewise, gradients in the distribution of gelatinous zooplankton off the west coast of North America have been attributed to the California Current (Colebrook, 1977) which flows from north to south in that region.

The west to east decrease in the number of species off southern WA during summer, when there were fewer species, implies that the Leeuwin Current was still flowing, albeit weakly, along the coast at this time, despite the fact that there was apparently insufficient thermal contrast for it to show up on the AVHRR images. Besides the effect of a weaker Leeuwin Current, the fewer species in summer could also be attributed to the larger contribution by subtropical water, rather than tropical water, to the current during summer (Cresswell & Peterson, 1993).

Distributions of the dominant taxa

Chelophyes appendiculata, the dominant siphonophore in summer, is one of the most common and abundant siphonophores, being widely distributed in warm and temperate waters throughout the world (Pagès & Gili, 1992). The increase in abundance offshore for *C. appendiculata* in coastal waters off southern WA has also been found in both India and south-west Africa (Rengarajan, 1975; Pagès & Gili, 1991). Despite the fact that this species is generally considered to be oceanic, it is not clear whether the differences in cross-shelf abundance of *C. appendiculata* between seasons and regions resulted from its own population dynamics or hydrographic events. For example, at a region of the northern Mediterranean, *C. appendiculata* is apparently brought inshore during summer by the advection of superficial oceanic waters (Patriti, 1964; in Mackie *et al*., 1987). If onshore advection occurred during the present study, it would have also been limited to summer since during winter, the stronger Leeuwin Current, which flows more or less parallel to the coast and pervades the entire water column on the shelf, would block cross-shelf transport. However, while found inshore at Albany during winter, *C. appendiculata* was not present during this period at the Esperance region where the Leeuwin Current was weaker. This therefore suggests that some factor(s) other than the blocking of cross-shelf advection may have been influencing this species' distribution in this season. A change in bathymetric distribution (Gili *et al*., 1987) during winter, whereby *C. appendiculata* were located deeper than the maximum sampling depth of 70 m, may have negated the capture of this species at even the more offshore stations at Esperance. The small, inshore populations at the Albany region during winter may have persisted due to higher productivity associated with river discharge (e.g. Gili *et al*., 1987), which is greater at this region than at Bremer Bay and Esperance. Alternatively, the inshore waters may have contained the remnants of populations that were present before the seasonal intrusion of the Leeuwin Current effectively isolated them near the coast. Thus, larger summer populations may be displaced by the Leeuwin Current during winter, resulting in both seasonal changes in abundance on the continental shelf and, depending on the position of the current on the shelf, variations in abundance with distance from shore. When the Leeuwin Current weakens, the distribution of oceanic species may then spread across the shelf, whether this be due to population growth or mixing of oceanic and shelf waters.

Eudoxoides spiralis, the most abundant siphonophore during winter, is widely distributed throughout temperate waters of the three great oceans (Pagès & Gili, 1992). Overall concentrations of *E. spiralis* off southern WA did not differ with distance from shore. Likewise, off south-western Africa this species is widely distributed on the shelf and in the oceanic zone (Pagès & Gili, 1992), but, unlike *C. appendiculata*, was not noted as an oceanic species. However, in southern WA, *E. spiralis* was more abundant offshore during summer and inshore during winter. As with *C. appendiculata*, it could not be determined whether the variations in the concentrations of *E. spiralis* found in this study were due to its own population dynamics or hydrographic events.

Sagitta minima, the only abundant chaetognath during summer, is a cosmopolitan, epiplanktonic species, and is apparently characteristic of regions where there is a mixing of neritic and oceanic waters or of different water masses (Alvariño, 1965). Considering the regular intrusion of warm water along the southern WA coast, the interannual variability in the strength of this current, and the marked weakening of the current between Albany and Esperance, the shelf waters of this region may be considered a mixing zone. Thus, the abundance of *S. minima* in summer may represent particularly successful population growth in waters which had presumably been mixed by the Leeuwin Current in previous months. The lower abundances of *S. minima* in winter may have resulted from displacement of shelf waters by the Leeuwin Current, as suggested above for *C. appendiculata*. Since the main core of the current is typically 100–150 m deep and its influences can extend to 300 m depth (Cresswell & Peterson, 1993), such displacement could affect the entire water column on the continental shelf.

Both *S. enflata* and *P. draco*, the dominant chaetognaths in winter, are also cosmopolitan, epiplanktonic species of warm to temperate regions (Alvariño, 1965). As found off southern WA, *S. enflata* was more abundant in coastal than oceanic waters off western India (Srinivasan, 1974). Both the presence and high concentrations of *S. enflata* in winter may have resulted directly from entrainment within the Leeuwin Current. In south-west Africa, the presence of *S. enflata* (and *S. regularis*, which also found only in winter off southern WA) is indicative of penetration by warm Agulhas Current water into the cooler Benguela system (Heydorn, 1959). Likewise, the higher concentrations of *P. draco* in winter and the decreased concentrations towards the coast also suggest that this species was entrained in the current.

Conclusions

Direct effects of major coastal currents on the distribution of macrozooplankton have not been described previously for the eastern Indian Ocean. This study has demonstrated that the Leeuwin Current influences the composition and distribution of carnivorous macrozooplankton on the continental shelf off southern WA, transporting some species into the region during winter, but apparently displacing others at the same time. There was also evidence that seasonal and regional differences in the abundance of some taxa may be related to the location of the current on the shelf. Any further studies on pelagic ecosystems in this region must, therefore, consider the potential effects of the current, and the possible implications of its interannual variability in strength and position on the continental shelf.

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