

Pelagic Squid Associations with a Warm-core Eddy of the East Australian Current

Stephen B. Brandt

Division of Fisheries Research, CSIRO Marine Laboratories, P.O. Box 21, Cronulla, N.S.W. 2230;
Present address: State University Research Center at Oswego;
King Hall, Oswego, New York, U.S.A. 13126.

Abstract

Cephalopods were sampled at night by midwater trawling in the upper 500 m in and near warm-core eddy F during summer. In all, 29 species (1019 specimens) were caught. Of the five dominant species, the squid *Pterygioteuthis giardi* and *Brachioteuthis riisei* were most numerous inside the eddy and *Abraliopsis gilchristi* and *Pterygioteuthis gemmata* had length-frequency distributions that were significantly larger outside than inside the eddy. *A. gilchristi* was also concentrated in warmer water and *Pyroteuthis margaritifera* was more common at 250 m than at shallower depths. Cluster analysis established a clear association of overall composition and relative abundances of cephalopod species with water temperature and location with respect to the eddy.

Extra keywords: Tasman Sea; rings; mesopelagic.

Introduction

Squid represent the highest level of development among the invertebrates and form an important link in oceanic food webs (Clarke 1966; Zuev and Nesis 1971; Packard 1972). Yet little is known about the distribution and ecology of oceanic squid because many of the fast swimming species can avoid standard oceanographic sampling nets (Clarke 1977; Roper 1977). Data on oceanic squid in the Tasman Sea are notably scant (Nesis 1979).

Warm-core eddies generated by the East Australian Current cause much of the mesoscale hydrographic variability in the western Tasman Sea (Nilsson and Cresswell 1981). These eddies differ in nutrient cycling, phytoplankton productivity and fish species composition from surrounding waters (Tranter *et al.* 1980; Brandt 1981). In this preliminary study, the effects of a warm-core eddy on squid have been examined by comparing abundance, species composition and size distribution and sex ratio of common species among samples collected inside, outside and at the edge of a warm-core eddy in summer. Samples were taken with a commercial midwater trawl and the number of specimens examined here represents the largest collection reported for the Tasman Sea.

Materials and Methods

Study Area

Warm-core eddies of the East Australian Current (EAC) are described by Andrews and Scully-Power (1976) and Nilsson and Cresswell (1981). Briefly, eddies form off south-eastern Australia when a meander of the East Australian Current breaks off into a closed ring structure. Warm-core eddies can exist as relatively isolated bodies for up to 18 months, mix with or be completely reabsorbed by the EAC, divide into two eddies or coalesce (Cresswell 1982). The counterclockwise (anticyclonic) flow has surface currents up to 2 m s⁻¹ and entire eddies can move at an average of 0.15 m s⁻¹ or about 13 km day⁻¹ (Nilsson and Cresswell 1981). Eddies are identified by an isothermal-isohaline thermostad that is formed during winter cooling.

Eddy F was studied from 28 November to 13 December 1978, and was 7–10 months old by this time (Tranter *et al.* 1980). A physical description of eddy F is given by Brandt (1981). During the study, eddy F was centred at 36°30'S, 151°42'E. and had a diameter of about 120 km at a depth of 250 m as defined by the 15°C isotherm. The eddy thermostad was 17.4–17.7°C with a salinity of 35.59×10^{-3} and extended to depths of at least 290 m. The thermostad was overlaid by a 50–100-m layer of 18–19°C water, which was probably formed by surface heating rather than an overflow of the East Australian Current (Tranter *et al.* 1980). In the surrounding Tasman Sea, temperatures in the upper 250 m ranged from 12 to 22°C and salinities from 35.00×10^{-3} to 35.70×10^{-3} .

Hydrography

Temperature to 450 m was measured using expendable bathythermographs (see fig. 1 in Brandt 1981). Temperature and salinity were measured from water samples collected with reversing Nansen bottles at 25-m intervals to 300 m.

Squid Collections

Brandt (1981) details sampling methodology and discusses some of the limitations of the sampling strategy. Only night samples are considered fully here because cephalopods were rare or absent (<3% of total numbers) during day collections. At night, squid were sampled in the upper 500 m of the water column using a 308 meshes \times 800 mm Engel midwater trawl ($n = 17$) with a 10-mm stretch mesh liner in the cod end. This net opens vertically about 12 m and samples an estimated area of 450–600 m². The trawl was towed horizontally at depth for 30 min at a speed of about 1.5 m s⁻¹. A Simrad FB Trawl Eye monitored trawl depth, temperature and vertical opening.

Trawl samples were classified on the basis of water temperature at a depth of 250 m (T_{250}) since the position of the 15°C isotherm at 250 m most closely approximates the eddy boundary (Boland 1973). Samples collected at a T_{250} between 14 and 16°C were defined as being from the eddy edge; a T_{250} warmer or cooler than this was considered inside or outside the eddy, respectively. At least two trawl samples were taken near 50, 150 and 250 m depth inside and outside the eddy and near 250 m at the eddy edge. Additionally, one deep tow (475 m) was taken near the eddy centre and one tow at 150 m at the eddy edge. Time of sampling within a night was random. Mean temperatures during the trawl ranged from 10.5 to 18.3°C (see table 1 in Brandt 1981).

Cephalopods were weighed *en masse* to the nearest 5 g and then either preserved in 10% buffered seawater-formalin or frozen. Subsequently, specimens were identified and, for the more common species, sexed and dorsal mantle length (M.L.) measured to the nearest 0.1 mm. Assignment of individuals to the species *Abraliopsis gilchristi* is tentative and is open to a later revision of this genus. *A. gilchristi* may, in fact, include more than one species (C. C. Lu, personal communication).

Statistics

Samples were grouped by temperature (>17°C, $n = 10$; <16°C, $n = 7$), depth (c. 50 m, $n = 5$; c. 150 m, $n = 5$; c. 250 m, $n = 6$; c. 475 m, $n = 1$), and location with respect to the eddy (inside, $n = 8$; edge, $n = 3$; outside, $n = 6$). Catch rates (number of individuals per trawl sample) of common species were compared within each of these groups using the non-parametric Kruskal–Wallis (KW) test (Conover 1971). Sizes within a species were compared using the Kolmogorov–Smirnov (KS) test on cumulative percentage frequency distributions (Conover 1971).

A percentage similarity index and cluster analysis were used to examine which factors (location with respect to the eddy, temperature or depth) more closely corresponded with trawl species composition. The percentage similarity index emphasizes the relative proportion of species within a sample whereas the cluster analysis calculates a similarity measure based on the actual numbers of individuals caught in each sample. The percentage similarity index (S) was calculated as

$$S = 100 - 0.5 \sum_i |P_{ij} - P_{ik}|,$$

where P_{ij} and P_{ik} represent the percentage of the i th species in samples j and k , respectively (Whittaker 1975). Cluster analysis for abundance ('root–root' transformation of number of individuals per trawl sample) of the 29 species for the 17 night samples was based on the Bray–Curtis similarity index (see Field *et al.* 1982).

Results

Species Composition

In all, cephalopods were represented by 1019 specimens, 14 families and at least 29 species (Table 1). Only 28 specimens were caught during the 14 samplings with the Engel trawl during day and only six specimens were caught in eight samplings with a Frank and Bryce trawl (see Brandt 1981 for information on day samples). The remaining 96.7% of the total catch was taken by the Engel trawl at night and these data form the basis of the results. Trawl samples are related to temperature and salinity in Fig. 1.

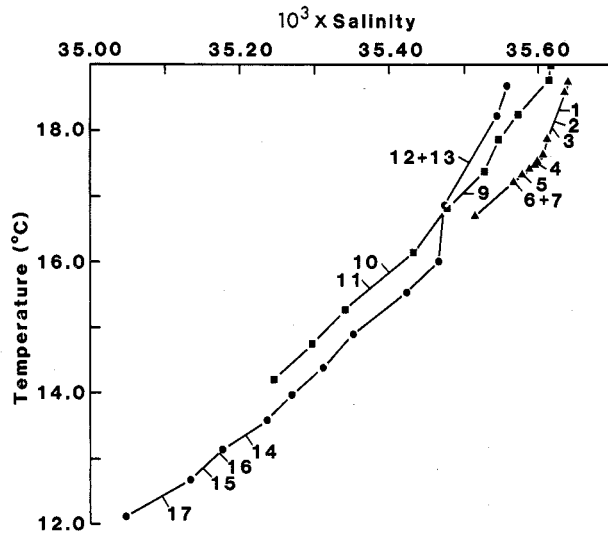


Fig. 1. Temperature and salinity of the upper 300 m inside (▲), outside (●) and at the edge (■) of eddy F in summer. Numbers represent the Engel trawl samples at night, numbered sequentially from table 1 in Brandt (1981).

Cephalopod biomass per sample ranged from 50 to 1010 g at night and did not differ among depths, temperatures or locations. Day catches were always less than 100 g.

Squid of the family Enoploteuthidae dominated (86.4% of total) the catches. The five most abundant species caught were *Abraliopsis gilchristi* (49.9% of total catch by number), *Pterygioteuthis gemmata* (21.8%), *Pterygioteuthis giardi* (6.1%) and *Pyroteuthis margaritifera* (5.9%) of the family Enoploteuthidae, and *Brachioteuthis riisei* (2.4%) of the family Brachioteuthidae. Each species is discussed separately below.

Distribution of Individual Species

Abraliopsis gilchristi was the most abundant species inside (42%), outside (56%) and at the eddy edge (66%), and was caught in all but one of the night trawl samples (Table 1). Catches were higher ($P < 0.05$, KW test) in the warmer water ($\bar{x} = 42.7$ specimens per trawl sample) than in cooler water ($\bar{x} = 10.3$) and in each location the largest catch occurred in the shallowest, warmest sample (Table 1, Fig. 1). Catches did not differ significantly with depth or location with respect to the eddy.

Sizes of *A. gilchristi* ranged from 10.7 to 66.8 mm (M.L.). The size-frequency distributions of males and females did not differ significantly, although females had a mode of abundance slightly larger than males (Fig. 2). Within each sex, the size-frequency distribution of individuals caught inside the eddy was significantly smaller ($P < 0.05$, KS

Table 1. Species list and catch of cephalopods by location
 Percentage occurrence for night samples and total day catch are given. *n*, number of trawl samples

Taxa	Day Total (<i>n</i> = 14)			Inside eddy (<i>n</i> = 8)			Night Eddy edge (<i>n</i> = 3)			Outside eddy (<i>n</i> = 6)			Total catch
	Mean	Range	Occurrence (%)	Mean	Range	Occurrence (%)	Mean	Range	Occurrence (%)	Mean	Range	Occurrence (%)	
Order: Sepioidea													
Family: Sepiolidae													
<i>Heteroteuthis serventi</i>	5	1.5	0-8	25	2.0	0-4	67	0	0	0	0	23	
<i>Heteroteuthis</i> sp.	0	0	0	0	0-3	0-1	33	0	0	0	0	1	
Order: Teuthoidea													
Family: Eupoloteuthidae													
<i>Eupoloteuthis</i> sp.	0	0	0	0	0-3	0-1	33	0	0	0	0	1	
<i>Abralia</i> sp.	0	0-1	0-1	13	0-3	0-1	33	0	0	0	0	2	
<i>Abraliopsis gilchristi</i>	9	27.6	3-64	100	43.7	5-120	100	24.5	0-86	83	508		
<i>Abraliopsis</i> sp.	0	0	0	0	0-3	0-1	33	0-2	0-1	17	2		
<i>Ancistrocheirus</i> sp.	0	0	0	0	0-3	0-1	33	0	0	0	1		
<i>Pyroteuthis margaritifera</i>	0	4.0	0-11	88	2.3	0-5	67	3.5	0-9	83	60		
<i>Pyroteuthis gemmata</i>	0	16.4	5-36	100	9.0	5-17	100	10.0	2-21	100	222 ^A		
<i>Pyroteuthis giardi</i>	5	6.0	2-9	100	2.3	1-4	100	0.2	0-1	17	62 ^A		
Enoplateuthidae unidentified	0	2.5	0-19	25	0	0	0	0.3	0-2	17	22		
Family: Octopoteuthidae													
<i>Octopoteuthis</i> sp.	0	0.1	0-1	13	1.0	0-3	33	0.2	0-1	17	5		
Family: Onychoteuthidae													
<i>Onychoteuthis</i> sp.	0	0.8	0-2	38	0	0	0	0	0	0	6		
<i>Moroteuthis</i> sp.	0	0	0	0	0-3	0-1	33	0	0	0	1		
Family: Lepidoteuthidae													
<i>Tetronychoteuthis</i> sp.	0	0.1	0-1	13	0	0	0	0	0	0	1		
Family: Histiototeuthidae													
<i>Histiototeuthis bonnelli</i>	0	0.1	0-1	13	0	0	0	0	0	0	1		

<i>Histioteuthis meleagrateuthis</i>	3	0.2	0-2	13	0	0	0	0	0	0	0	0	5
<i>Histioteuthis</i> sp.	0	1.6	0-6	50	0.3	0-1	33	1.2	0.4	50	21		
Family: Ctenopterygidae													
<i>Ctenopteryx</i> sp.	0	0.6	0-2	38	0	0	0	0.5	0.2	33	8		
Family: Brachioteuthidae													
<i>Brachioteuthis risei</i>	1	2.1	0-8	63	1.7	0-3	67	0.2	0-1	17	24		
Family: Ommastrephidae													
<i>Ornithoteuthis volatilis</i>	1	0.5	0-2	38	0.3	0-1	33	0.3	0.2	17	9 ^A		
Ommastrephidae unidentified	0	0.1	0-1	13	0	0	0	0	0	0	1		
Family: Chiroteuthidae													
<i>Chiroteuthis</i> sp.	0	0.1	0-1	13	0	0	0	0	0	0	1		
Family: Cranchiidae													
<i>Cranchia scabra</i>	2	0.2	0-2	13	0	0	0	0	0	0	4		
<i>Leachia</i> sp.	0	0	0	0	0	0	0	0.7	0.4	17	4		
<i>Megalocranchia megalops</i>	0	0.2	0-1	25	0.7	0-1	67	1.2	0.4	50	11		
<i>Megalocranchia abyssicola</i>	0	0.1	0-1	13	0	0	0	0	0	0	1		
<i>Megalocranchia</i> sp.	0	0.2	0-2	13	0	0	0	0	0	0	2		
Cranchiidae unidentified	0	0.1	0-1	13	0	0	0	0.2	0-1	17	2		
Order: Octopoda													
Family: Bolitaenidae													
<i>Japetalia</i> sp.	0	0.1	0-1	13	0	0	0	0	0	0	1		
Family: Ocythidae													
<i>Ocythoe tuberculata</i>	0	0.1	0-1	13	0	0	0	0.2	0-1	17	2		
Family: Argonautidae													
<i>Argonauta</i> sp.	2	0	0	0	0	0	0	0.2	0-1	17	3		
Octopoda unidentified	0	0	0	0	0	0	0	0.2	0-1	17	1		
Cephalopoda unidentified	0	0	0	0	0.3	0-1	33	0	0	0	1		
Biomass (g), mean (range)	280	473	(154-1010)	216	(92-430) ^B	386	(50-940)						
Total No. of specimens	28	527	197			261						1019 ^A	

^A Includes six specimens caught in eight tows of a Frank and Bryce trawl. ^B Excludes one specimen weighing approx. 2 kg.

test) than of those caught outside the eddy or at the eddy edge (Fig. 3). Length-frequency distributions were bimodal outside the eddy, particularly for males; the larger size mode was nearly absent inside the eddy.

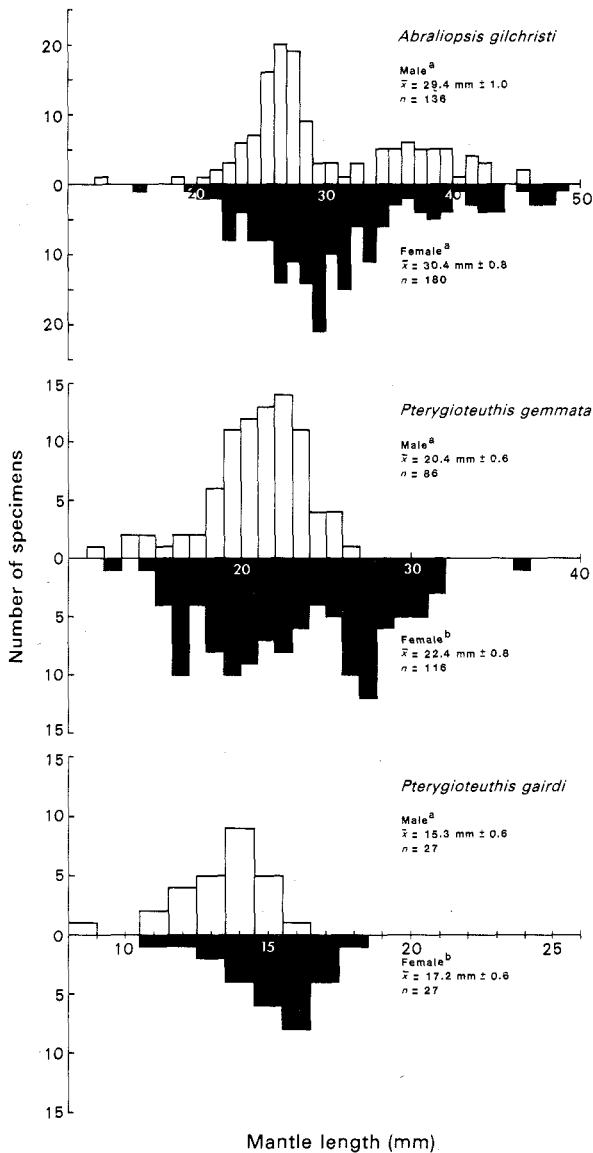


Fig. 2. Frequency distribution of mantle lengths of male and female *Abraliopsis gilchristi*, *Pterygioteuthis gemmata* and *P. gairdi*. Superscripts a and b denote significant differences in length-frequency distributions within species (Kolmogorov-Smirnov test).

Large *A. gilchristi* were confined to shallower depths ($P < 0.05$, KS test). Only one specimen (out of 106) larger than 33 mm was in the samples taken at 250 or 475 m depth. Mean mantle lengths of males were 25.9 mm ($n = 32$), 29.6 mm ($n = 41$) and 31.2 mm ($n = 63$) at depths of 250, 150 and 50 m, respectively. Mean lengths of females for the same depths were 27.3 mm ($n = 31$), 32.1 mm ($n = 77$) and 30.1 mm ($n = 72$), respectively.

The female to male sex ratio was 0.90 ($n = 95$) outside the eddy, 2.06 ($n = 55$) at the eddy edge and 1.44 ($n = 166$) inside the eddy. Length of immature specimens (too young to sex) ranged from 11 to 23 mm ($n = 46$). Most (65.2%) were caught in the shallowest trawl sample (32 m) taken inside the eddy. Many (82%) of the frozen specimens caught at 150 m at the eddy edge were damaged and could not be sexed.

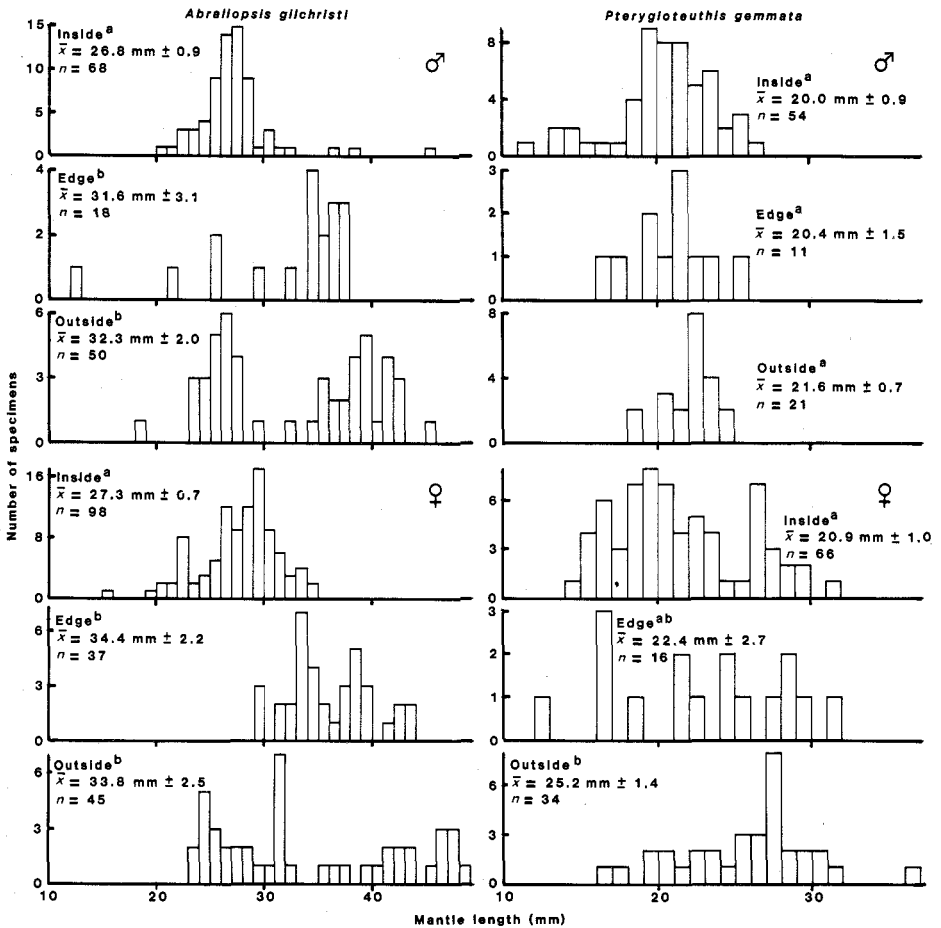


Fig. 3. Frequency distribution of mantle lengths of male and female *Abraliopsis gilchristi* and *Pterygioteuthis gemmata* caught inside, outside and at the edge of eddy F. Superscripts a and b denote significant differences in length-frequency distributions (Kolmogorov-Smirnov test).

Pterygioteuthis gemmata was caught in all trawl samples and was the second most abundant species at all locations (Table 1). Catch rates did not differ among depths, temperatures, or locations. Mantle lengths ranged from 11.2 to 36.4 mm. Females were generally larger than males (Fig. 2) and the size-frequency distributions of females ($P < 0.05$, KS test) and males ($P < 0.1$, KS test) caught inside the eddy were significantly smaller than of those caught outside (Fig. 3). Females were generally larger at 50 m ($\bar{x} = 25.1$ mm, $n = 20$) than at 150 m (23.3 mm, $n = 42$, $P < 0.1$, KS test) and 250 m (20.6 mm, $n = 49$, $P < 0.05$, KS test). Sex ratio (female:male) was 1.62 ($n = 55$) outside the eddy, 1.22 ($n = 120$) inside the eddy, and 1.45 ($n = 27$) at the eddy edge.

Pterygioteuthis giardi was caught almost exclusively inside the eddy (85.7% of total catch) or at the eddy edge (12.5%) (Table 1). Catch rates were significantly ($P < 0.01$, KW

test) higher inside the eddy ($\bar{x} = 6.0$ individuals per trawl sample) than at the eddy edge ($\bar{x} = 2.3$) or outside the eddy ($\bar{x} = 0.2$). Mantle lengths ranged from 10.4 to 24.7 mm and did not differ among depths or temperatures. Females were significantly ($P < 0.1$, KS test) larger than males (Fig. 2). The sex ratio was 1.00 ($n = 54$).

Pyroteuthis margaritifera was the fourth most abundant squid and catch rates did not differ among temperatures or locations. Catch rates were significantly higher ($P < 0.05$, KW test) at 250 m ($\bar{x} = 5.8$ individuals per trawl sample) than at shallower depths ($\bar{x} = 1.8$). Mantle lengths ranged from 16.9 to 39.2 mm and did not differ among depths, temperatures, or locations. Specimens were not sexed.

A total of 24 individuals of *Brachioteuthis riisei* was caught. Most ($P < 0.1$, KW test) of the specimens were caught inside the eddy (75.0% of total catch) or at the eddy edge (20.8%) (Table 1). Mantle lengths ranged from 24.9 to 57.3 mm. One specimen was caught outside the eddy at 150 m and had a mantle length of 25.0 mm. Specimens were not sexed.

Table 2. Percentage similarity indices among sample groups
Depths and temperatures are means (one to three samples)

	Outside eddy			Edge of eddy		Inside eddy			
	54 m, 17.5°C	151 m, 13.1°C	255 m, 12.8°C	165 m, 17.0°C	252 m, 15.7°C	42 m, 18.1°C	156 m, 17.4°C	255 m, 17.3°C	475 m, 10.5°C
Outside eddy									
54 m, 17.5°C									
151 m, 13.1°C		50							
255 m, 12.8°C		46	67						
Edge of eddy									
165 m, 17.0°C				91	43	40			
252 m, 15.7°C				28	61	54	22		
Inside eddy									
42 m, 18.1°C						66	66	63	60
156 m, 17.4°C						52	77	71	45
255 m, 17.3°C						49	68	77	43
475 m, 10.5°C						22	40	42	16
									53
									46
									43
									40

Community Analyses

In all, 19 species were caught inside the eddy ($n = 7$ samples) in the upper 250 m, 16 species were caught at the eddy edge ($n = 3$) and 14 species were caught outside the eddy ($n = 6$). Shannon's diversity index was significantly different ($P < 0.05$, Zar 1974) in the three locations (although see Hulbert 1971). The eddy was most diverse ($H = 0.70$); the outside ($H = 0.57$) and edge ($H = 0.53$) did not differ in diversity. Numbers of species per sample were higher in deeper water and at colder temperatures ($P < 0.1$, KW test). For only the samples taken at 250 m, 13 species were caught at the eddy edge, compared to 9 and 10 for outside and inside the eddy, respectively.

To compare composition and relative abundance of species among samples, a percentage similarity index was calculated for samples grouped by depth, temperature and location with respect to the eddy (Table 2). Within locations, the percentage similarity index ranged from 67 to 85% ($n = 4$) for samples taken at similar temperatures and from 22 to 50% ($n = 6$) for samples taken at different temperatures. Comparisons between sample locations (inside and outside the eddy) within the upper 250 m ranged from 49 to 77% ($n = 9$) and species compositions were most similar at corresponding depths. The sample taken in warm water at 150 m at the eddy edge was most similar to the samples taken in warm water at 50 m depth outside the eddy (91%) and most different from the samples taken in cold water at 250 m depth at the edge (22%) and at 475 m (16%) inside the eddy. The species composition of the samples taken at 250 m in cold water at the eddy edge was

intermediate in nature to that of samples taken inside (53–71%) and outside (54–61%) the eddy except for the samples taken at 50 m outside the eddy (28%).

Trawl samples were also clustered on the basis of the Bray–Curtis measure of similarity in species composition (see Field *et al.* 1982). The 'root-root' transformed abundances of all 29 species in the 17 night samples were used for these analyses. Results are represented on a dendrogram (Fig. 4) with successive clusters representing decreasing similarity (i.e.

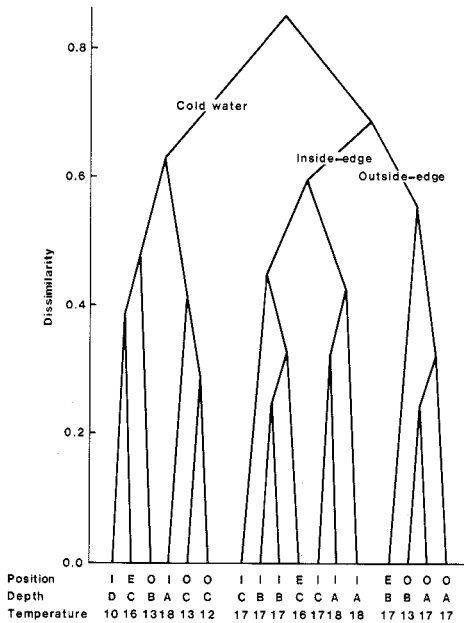


Fig. 4. Dendrogram showing clusters of 17 trawl samples based on 29 cephalopod species. Successive clusters represent increasing dissimilarity. Trawl samples have been categorized as inside (I), outside (O) or on the edge (E) and approximate depths are given by the letters A (50 m), B (150 m), C (250 m) and D (475 m). Sample temperatures have been rounded off to the nearest 1°C.

dissimilarity). Groups were defined at the 0.65 level of dissimilarity and tested for independence of temperature, depth and location with respect to the eddy (χ^2 contingency tables). For this purpose, temperatures were lumped into warm ($>17.0^\circ\text{C}$) and cold ($<16.0^\circ\text{C}$) samples. Basically, three main groups were recognized (Fig. 4). Sample groups were significantly correlated with temperature and location inside or outside the eddy ($P < 0.05$, χ^2 contingency tables). Each group contained one edge sample. Group I consisted of six trawl samples taken mainly at colder temperatures ($<16^\circ\text{C}$) except one sample, which was the shallowest (32 m) taken inside the eddy. All depths sampled were represented in this group. Group II consisted of seven samples all taken inside the eddy or at the eddy edge. It included all samples taken inside the eddy at 150 and 250 m and two of the three samples at 50 m. Total temperature range of these samples was $15.8\text{--}18.1^\circ\text{C}$. Group III consisted of four samples taken outside the eddy or at the eddy edge. These samples were taken at depths less than or equal to 150 m and had a temperature range of $12.8\text{--}17.5^\circ\text{C}$.

Discussion

These samples, although limited in time, space and number, provide evidence that (1) warm-core eddies do affect the distributions of oceanic squid in the Tasman Sea and that (2) water temperature may be an important factor defining the boundaries of oceanic squid communities. Four of the five most common species either had nocturnal distributions restricted to the eddy (*Pterygioteuthis giardi* and *Brachioteuthis riisei*) or to warm water (*Abrialiopsis gilchristi*) or had length-frequency distributions that differed inside and outside the eddy (*A. gilchristi* and *Pterygioteuthis gemmata*). Cluster analysis of relative

abundances and composition of species also grouped samples on the basis of either water temperature or location with respect to the eddy.

Lu and Roper (1979) also found that the passage of warm-core eddies across dumpsite 106 in the western North Atlantic altered the cephalopod community in the region. Some species (e.g. *Abraliopsis pfefferi*) were concentrated in warm-core eddies whereas others were caught primarily in slope water outside the eddy although patterns were not always consistent across seasons. *P. gemmata* had widespread distributions in both the Tasman Sea and the western North Atlantic.

The works of Pickford (1946), Clarke (1966), Roper (1969), Nesis (1977) and McSweeney (1978) suggest that general distribution patterns of some cephalopods are limited to particular ocean basins or water masses. In fact, the large-scale zoogeography of many oceanic taxa has often been linked with the physical structure of the ocean, and, in particular, to water-mass boundaries (see reviews by Ekman 1953; Ebeling 1962; McGowan 1971; Briggs 1975; van der Spoel and Pierrot-Bults 1979). Often major geographic patterns coincide from taxon to taxon, most notably for the holoplankton. The mechanisms for these associations are unclear. Water temperature most closely corresponds with faunal boundaries, although other factors seem important for particular groups of animals (see discussions in Hutchins 1947; McGowan 1971; Briggs 1975).

So little is known about the ecology of oceanic squid that it is only possible to speculate on the mechanisms through which eddies might affect squid. In particular, data on the zoogeography and life history of cephalopods off Australia and New Zealand are notably scant (Nesis 1979) and, for example, it is not yet known if the two eddy species *B. riisei* and *P. giardi* occur commonly in eddy source water of the Coral Sea. On a worldwide basis, the five major species in this study have widespread zoogeographic distributions (Clarke 1966; Nesis 1979).

Clearly one of the more immediate physical effects of eddies is to change the vertical thermal structure. Depths of particular isotherms are closely linked to the location and dynamics of an eddy and eddy location itself is defined by temperature. Temperature was an important correlate of both squid and fish (Brandt 1981) distributions in eddy F. Fishes are known to have very precise thermal requirements and often behaviourally regulate their environmental temperature very precisely (Magnuson and Beiting 1978). However, squid are physiologically quite different from fishes but with similar motility and behavioural capabilities (Packard 1972; O'Dor 1982). Unfortunately, few studies have been done on the thermal requirements or thermoregulatory ability of oceanic squid.

Squid distributions were probably more precise than this study shows because of the variability inherent in the sampling technique. At least two major sources of variability were probable (see Brandt 1981): contamination from shallower depths in open tows and variations in flow rates through the net (and thus volume sampled) due to subsurface currents. In this study, trawl depth and temperature may really only represent the maximum depth and minimum temperature of a water-column sample. An opening and closing net with accurate measures of sampling volume would be required to discriminate fine-scale habitat selection.

Most non-larval squid of the families Enoploteuthidae and Brachioteuthidae make diel vertical migrations, occupying depths of 200–800 m during day and migrating to the upper 200–300 m at night (Clarke 1966; Lu and Clarke 1975; Roper and Young 1975). Thus, if migrations are similar in the Tasman Sea, the temperatures at both day and night depths would differ inside and outside the eddy because eddy structure extends to at least 1500 m (Hamon 1965). One of the immediate effects of eddies may be to alter the extent of the vertical migration by changes in the thermal structure.

Lu and Clarke (1975) document changes in species number and composition of cephalopods with latitude in the North Atlantic, which corresponded with changes in thermocline depth. Similar trends have been observed for mesopelagic decapods (Foxton 1972) and planktonic ostracods (Fasham and Angel 1975). Boyd *et al.* (1978) found that

cold-core rings of the Gulf Stream affected the vertical distribution of the euphausiid *Nematoscelis megalops*, causing a reduction in food availability and ultimate decline in populations. Perhaps the differences in size distribution of *A. gilchristi* and *P. gemmata* across the boundary of eddy F may reflect more subtle effects of eddies on growth, spawning times, reproduction or survival. Without basic data on the life history and ecology of these oceanic squid in the Tasman and Coral Seas, the importance of these factors cannot be assessed adequately.

Light, prey availability and predation pressure may also affect squid distributions and are known to vary across the physical boundary of a warm-core eddy (e.g. Tranter *et al.* 1980; Brandt 1981; Brandt *et al.* 1981). Light seems to be important in the responses of some species of euphausiid to cold-core rings of the Gulf Stream (Wiebe and Flierl 1983).

In summary, this study on oceanic squid adds to the growing body of data on the biological contrasts across boundaries of warm-core eddies in the Tasman Sea and suggests that eddies can be considered at least partially closed biological systems. Isolated eddies are known to differ from the surrounding Tasman Sea in seasonal nutrient cycling and phytoplankton production, species composition of copepods, decapods, and fishes and abundance of tunicates (Tranter *et al.* 1980, 1983; Brandt 1981; Brandt *et al.* 1981; Griffiths and Brandt 1983). These eddies may thus be responsible for much of the large-scale patchiness in pelagic distributions in the western Tasman Sea and may be functionally analogous to Gulf Stream cold-core rings in the western North Atlantic (Wiebe *et al.* 1976).

How faunal associations are originally established and how (or if) they persist through time is largely speculation. The eddy 'community' was likely established during eddy formation when a group of organisms was trapped within the eddy and transported with it. The subsequent biological future of eddies appears to be species specific and perhaps dependent on motility (Brandt and Wadley 1981). Questions concerning the rate of species or population mixing across the warm-core eddy boundary, the mechanisms involved, and the evolution of populations within an eddy have yet to be adequately addressed.

Acknowledgments

I thank Dr C. C. Lu and V. A. Wadley for identifying the cephalopods, the crew and scientific staff of the F.R.V. *Courageous* for help at sea, and M. Dunning, V. A. Wadley and an anonymous reviewer for useful suggestions on the manuscript.

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Manuscript received 27 November 1981, accepted 10 December 1982