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FAUNAL RELATIONSHIPS BETWEEN THE NEW ZEALAND PLATEAU AND THE NEW ZEALAND SECTOR OF ANTARCTICA BASED ON ECHINODERM DISTRIBUTION

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SUMMARY

The problem of New Zealand–Antarctic faunal relationships is discussed on the basis of echinoderm distribution. The limitations of the data upon which past zoogeographical speculations have been based are pointed out.

Macquarie Island (occupying an intermediate geographical position between the New Zealand Plateau and the Antarctic) shows definite relationships with New Zealand, and the submarine Macquarie Ridge may have provided a connecting migration route. However, only four species of echinoderms are shared between the Ross Sea–Balleny Islands area (the New Zealand sector of the Antarctic Region) and the New Zealand Plateau–Macquarie Island area (the New Zealand Region). Although the as yet unsampled part of the Macquarie–Balleny Ridge may reveal other faunal similarities, the present systematic sampling has made possible a sounder understanding of the zoogeographical affinities of the two regions.

INTRODUCTION

Recent literature contains many attempts to review the knowledge of the Antarctic fauna (*e.g.*, Pantin *et al.* 1960; Carrick, Holdgate and Prévost 1964; Priestley, Adie and Robin 1964; Van Mieghem and Van Oye 1965; Hatherton 1965; Llano 1965; Llano and Schmitt 1967; Arnaud *et al.* 1967; Petrovskaya 1968; Bushnell and Hedgpeth 1969). For some groups, such as birds or mammals, a fairly clear picture can be seen of zoogeographical relationships both within and beyond the Antarctic (Bonner and Laws 1964; Falla 1964; Fraser 1964; Laws 1964; Murphy 1964; Stonehouse 1964, 1965; Voous 1965; Austin 1968). For marine invertebrates, however, the overall picture is not so clear (Broch 1961; Holme 1964; Dell 1965) because many collections of important groups still await examination (Dell 1968, p. 115) and some geographical areas have not yet been sampled (*cf.* Mortensen 1936, p. 203). Hedgpeth's recent summary of Antarctic biogeography also reveals these points; his outline of the usage of the terms "Region", "Subregion" and "Province" is also particularly helpful (Hedgpeth 1969, p. 4, Fig. 10).

Although little is known of the biology of many of these animals—often no information is available about breeding habits, nature of larvae, length of larval life, or depths and temperature ranges—weakly based generalisations and speculations continue to be made. Workers

in other groups may therefore gain mistaken impressions of established zoogeographical relationships, impressions which override the limitations both of the material reviewed and of the extent of sampling of the Southern Ocean. Inadequate sampling, in particular, has sometimes led to erroneous conclusions. For example, speculations on the relationships of the molluscan fauna of Macquarie Island (Powell 1957) have been based on only a few shore collections in the intertidal zone and one shallow water dredging (BANZAR Expedition, Sta. 83) off the south-east coast.

Although extensive cruises across the Southern Ocean are now being made, the problems which have beset zoogeographers still exist. Analysis of the distribution of a single group of abundantly represented benthic animals—the Echinodermata—is offered here and the choice of this group perhaps ensures that the conclusions reached are sounder than those derived from less ubiquitous material (*cf.* Broch 1961).

COLLECTION OF INFORMATION

Until recently, zoogeographical data for the New Zealand Region (the geographic area depicted by Lawrence's (1967) chart) has come mainly from isolated random collections.

Several expeditions, notably those of the Philosophical Institute of Canterbury in 1907, Mortensen's "Pacific Expedition, 1914–16", and the wartime Cape Expedition of coast-watchers, added to the knowledge of the intertidal and shallow water fauna of the Subantarctic Islands of New Zealand (Auckland, Campbell, Bounty, Antipodes and Snares Islands) but the benthic fauna existing between these islands was unknown and there was little information about bathymetry and submarine geology.

The Chatham Islands 1954 Expedition associated physical information with specimens collected for the first time and gave a glimpse of the nature of the deep-water fauna on the Chatham Rise east of New Zealand (Knox 1957). Elsewhere in the New Zealand Region, the nature of the archibenthal fauna remained largely unknown and the shelf fauna was inadequately sampled.

In 1960, the New Zealand Oceanographic Institute* began a systematic survey of the New Zealand shelf to depths of 200 m. About 400 benthic stations were sampled along lines spaced latitudinally at 40-mile intervals around the New Zealand coast (McKnight 1969, Fig. 2). The distribution, ecology, sediment preferences, and zoogeographical relationships of the echinoderms from this survey are being analysed, and have now been published for echinoids (McKnight 1969).

A similar survey of the archibenthal areas of the New Zealand Plateau—defined as "the area of sea floor immediately surrounding New Zealand extending to the mid-depths of the marginal continental slopes" by Brodie (1964, pp. 24, 35–6, Fig. 19), and including the

*Subsequently referred to as NZOI.

Challenger Plateau and Lord Howe Rise to the north-west of Cook Strait, the Chatham Rise to the east of the South Island, and parts of the Campbell Plateau to the south, as well as the steep slopes linking these wide flat areas (*see, e.g.*, Pawson 1968a)—is now almost completed. Particular attention has been given to the benthos of the Chatham Rise because of its critical position in relation to the Subtropical Convergence; here 40 species of echinoderms, some of them new records for the New Zealand Region, have been added (McKnight 1967) to the 54 species reported from the Chatham Islands 1954 Expedition by Fell (1960).

Systematic sampling of some 300 benthic stations south of New Zealand, carried out as part of the New Zealand Antarctic Research Programme (Dawson 1963, 1964), with associated studies on hydrology (Burling 1961; Houtman 1967) and geology (Summerhayes 1969) now permits a more soundly based assessment of the relationships of the New Zealand–Subantarctic marine fauna.

A joint New Zealand and United States Expedition in 1965 in USS *Glacier* surveyed the bathymetry, sediments and bottom-living animals of the western margin of the Ross Sea and the Balleny Islands (*see* Forbes *et al.* 1968; Brodie 1970). This expedition traced the Balleny-Macquarie Ridge northwards to Macquarie Island to link up with the previously investigated New Zealand region. Attempts to collect benthic samples from the ridge between 57°S and the Balleny Islands at latitude 66°S were, however, thwarted by topography and weather, and samples from this region have yet to be obtained.

ECHINODERM FAUNA OF THE NEW ZEALAND REGION*

ASTEROIDEA

The known New Zealand fauna of asteroids is 65 species, 34 of which occur on the shelf (McKnight, in prep. a). This fauna is of Indo-Pacific derivation; 79% of the species are endemic, 16% occur in Australia, and 5% range widely in the Indo-Pacific. Some of the Indo-Pacific species, such as *Zoroaster spinulosus* Fisher and *Crossaster japonicus* (Fisher), have been collected in abundance south to latitude 50°S on the Campbell Plateau. None of the species is found in the Antarctic, although some occur at Macquarie Island. Four elements are distinguishable in the New Zealand shelf fauna (omitting five species of infrequent occurrence)—Northern 21%; Central (occupying the Cook Strait–Chatham Rise area) 21%; Southern 26%; and Widespread 17%.

At Macquarie Island, of three species of *Henricia* identified from NZOI collections, two occur in New Zealand in both shallow and archibenthal depths (Dawson 1965, Fig. 5). Those representatives of this notoriously difficult genus which extend to other Subantarctic and Antarctic areas have recently been reviewed by A. McG. Clark (1962). A *Pteraster* species and a *Smilaster* of circumpolar affinity occur at

*Includes New Zealand Plateau and Macquarie Island (*see* Lawrence 1967).

Macquarie Island and also one or more species of *Odontaster* and of *Ceramaster*, allied to or possibly identical with New Zealand Plateau species, as well as a species of *Hymenaster* which has also been taken in depths of over 1,000 m further north on the New Zealand Plateau. Of special interest is the first recorded occurrence (McKnight, in prep. c) off Macquarie Island of *Porania antarctica* Smith, a starfish of very wide distribution (Kerguelen, Marion, Bouvet, and Falkland Islands, the Magellanic Region (off Chile northwards to 30°S and off Argentina to 35°S), South Georgia and Shag Rocks, South Shetlands and Clarence Islands, Bellingshausen Sea, Enderby Land and east to the Ross Sea). Without knowledge of the biology of this starfish we can only speculate on how it got to Macquarie Island but not to New Zealand. Four other species of starfish occur at Macquarie Island (*see* Table 1) in shallow water, three being known so far only from Macquarie Island.

OPHIUROIDEA

The ophiuroid fauna of New Zealand now comprises at least 87 species of which 45 are found in shallow water, and about 80 occur in deeper water (McKnight, in prep. b). Omitting about six unusual species, a division yields three elements within the New Zealand shelf fauna—Northern 48%; Central 12%; Southern 22%. Although 60% of the shelf species are endemic, Indo-Pacific elements are apparent in the total fauna. Comparison with the Macquarie Island fauna is difficult because some material from earlier expeditions at Macquarie Island has not been reported on. Madsen (1967) lists only three Macquarie ophiuroids. The NZOI material from Macquarie Island is not yet completely identified but at least four genera and 13 species have been found (McKnight, in prep. c) of which 4 species certainly occur on the New Zealand Plateau as well (*see* Table 1). *Ophiopyren regularis* Koehler and *Toporkovia antarctica* (Lyman), recorded by Fell (1961) from the Ross Sea, have now been found off Macquarie Island. The Campbell Plateau has 17 recorded species of ophiuroids (McKnight, in prep. b) 3 of which have been found at Macquarie.

One species, *Amphiodia* (*Hemilepis*) *joubini* (Koehler)*, is known from two occurrences in the archibenthal zone of the New Zealand Region (Cook Strait and Bay of Plenty, 360 m and 750 m) and is also circumpolar in the Antarctic and Subantarctic at 80–1,000 m. According to Fell (1961, p. 42) it is ". . . notable as being the only ophiuroid known to be shared by the faunas of New Zealand and Antarctica". It was collected at 12 NZOI stations in the Ross Sea.

ECHINOIDEA

The echinoids are represented by 49 species in the New Zealand fauna, 28 of which occur on the shelf shallower than 200 m (Baker 1968; McKnight 1969). Analysis of these species shows that New Zealand may be considered as part of the Indo-Pacific region, the southern

*The names of amphiurid ophiuroids used here were valid before their revision by A. McG. Clark (1970).

limit of the New Zealand Plateau at 50°S latitude forming the southern boundary to a number of widely ranging, deep-water Indo-Pacific species such as the very toxic, collapsible urchins *Phormosoma bursarium* A. Agassiz and *Areosoma thetidis* (H. L. Clark); 58% of the species are endemic, 24% occur in Australia, and 18% range widely in the Indo-Pacific. Within the New Zealand shelf area, three main faunal elements can be distinguished—a Northern element, comprising 55% of the total fauna, extending south more or less to the Subtropical Convergence zone, a Southern element, 28% of the total, extending south of this zone, and a widespread element (17%) throughout the whole shelf area (McKnight 1969). Distinct faunal provinces corresponding with those proposed for New Zealand molluscs by Finlay (1925) and perpetuated by Powell (1961) are not recognisable (*cf.* also Pawson 1961; Dell 1962).

No species within the New Zealand Region are found in the Antarctic, but one, *Pseudechinus novaezealandiae* (Mortensen), extends south along the Macquarie Ridge as far as Macquarie Island and this species, at least, may have reached Macquarie Island along the ridge rather than from the west by epiplanktonic drift as suggested by Fell (1962a) who said of *Pseudechinus*—"One suspects that the genus set out from New Zealand long ago, circumnavigated the globe, and like Magellan's sailors, arrived back where it started, but from the other direction".

HOLOTHUROIDEA

The holothurian fauna of New Zealand totals 36 species (Pawson, in press). Of six species found at Macquarie Island, two occur in New Zealand (Pawson 1968a; Pawson 1968c) and two are circumpolar in the Subantarctic. Again the Macquarie Ridge may possibly have linked or be linking these two areas. No New Zealand species have been found in the Antarctic, but there are no reports available yet on the Ross Sea fauna.

ECHINODERM FAUNA OF THE N.Z. SECTOR OF ANTARCTICA

Monographs on two groups of echinoderms of the Ross Sea have been published so far: Ophiuroidea (Fell 1961) and Asteroidea (H. E. S. Clark 1963). These collections, and the material from the Balleny Islands Expeditions of 1964 and 1965, allow possible faunal links between New Zealand and the Antarctic to be examined.

Compiliations of the available data on the distribution of Antarctic echinoderms have been published recently by Dearborn and Rommel (1969) (Crinoidea); Pawson (1969a) (Holothuroidea); Pawson (1969b) (Echinoidea); Fell and Dawsey (1969) (Asteroidea); Fell, Holzinger and Sherraden (1969) (Ophiuroidea). Their distribution maps do not include the new records of the Balleny Islands Reconnaissance Expedition 1964 (Dawson, *in* Hatherton, Dawson, and Kinsky 1965) nor subsequent NZOI records from the Balleny Islands (Dawson, in prep.) and from Macquarie Island (McKnight, in prep. c).

ASTEROIDEA

Before the NZOI surveys were carried out, 21 species of starfish were known from the Ross Sea. H. E. S. Clark's report (1963) on the NZOI collections bought this up to 37 species. During a preliminary 2-day reconnaissance expedition to the Balleny Islands in 1964 (Hatherton, Dawson, and Kinsky 1965) 12 species of starfish were collected, all but 2 of which were already known from the Ross Sea. One of these two, a spectacular multi-rayed species *Labidiaster annulatus* Sladen, was previously known only from Kerguelen, Heard Island, the South Orkneys and off South Georgia. The 1965 Ross Sea and Balleny Islands Expedition collected starfish in abundance; 28 species from the western side of the Ross Sea, and 21 from around the Balleny Islands. Of the 37 species known from the Ross Sea 17 have not been found at the Balleny Islands but of the 21 Balleny Islands species only 1 has not also been found in the Ross Sea.

The starfish *Porania antarctica* Smith, now known from Macquarie Island, was abundant at the Balleny Islands; this is the only asteroid species so far known to be common to both ends of the Balleny–Macquarie Ridge.

OPHIUROIDEA

The previously known Ross Sea fauna of 17 species was brought to 34 species by the NZOI material (Fell 1961). One of the species, *Ophiopyren regularis* Koehler, is now known from off Macquarie Island. The 1964 Balleny reconnaissance expedition collected 16 species (Hatherton, Dawson and Kinsky 1965), 3 of which were new records for this sector of the Antarctic: *Ophiogona doederleini* (Koehler), previously known from Kerguelen and the South Shetlands; *Ophiura meridionalis* (Lyman) from South Georgia and the Falkland Islands; and *Ophioperla koehleri* (Bell) which has a circumpolar Antarctic and Magellanic range north to 54°S at South Georgia. Ophiuroid material collected by the 1965 Balleny Islands Expedition is only about two-thirds identified and analysed, and this work may therefore amend the conclusions presented here, but the 14 species so far identified are also known from the Ross Sea.

The Third Antarctic Expedition, 1964–65, of t.s. *Umitaka-Maru* from the Tokyo University of Fisheries collected ophiuroids at 3 stations in the Ross Sea area; 11 species were found, including 1 new species, *Ophiura umitakamaruae*, and 2 new records were made (Senô and Irimura 1968). The new records were *Gorgonocephalus chilensis* (Philippi), previously known from Patagonia, South Georgia, Magellan Straits, and Kerguelen Archipelago, and *Ophiosteira senouqui* Koehler, known from the western Antarctic. The occurrence of *Gorgonocephalus chilensis* provides a close link with the New Zealand fauna in which a very similar, perhaps identical, species, *Gorgoncephalus novaezelandiae* Mortensen, occurs. Fell (1962b, p. 55), and later Fell, Holzinger and Sherraden (1969), regarded the New Zealand form as distinct but Bernasconi (1965, p. 144) included it within *G. chilensis* (*see also* Alarcón 1968, p. 16). *Amphiodia joubini* (Koehler) and *Toporkovia*

antarctica (Lyman) have already been mentioned as occurring in both the Ross Sea and in the New Zealand Region. The record of *Ophiacantha imago* Lyman from the Ross Sea (figured by Fell, Holzinger and Sherraden 1969), reputed to be another link with the New Zealand Region, is probably based on an early misidentification of *Ophiacantha antarctica* Koehler (*cf.* Fell 1961, p. 34).

ECHINOIDEA

Preliminary identifications of NZOI echinoid material from the Ross Sea have yielded 18 species (Dr A. Chesser, pers. comm.). Fell's (1961) photographs of the Ross Sea bottom fauna show two of these, *Ctenocidaris perrieri* Koehler and *Sterechinus neumayeri* (Meissner). The 1964 Balleny Islands Reconnaissance Expedition took about 200 specimens of *Sterechinus antarcticus* Koehler, a circumpolar Antarctic species occurring north to South Georgia. The 1965 Balleny Islands Expedition took specimens of all three species.

HOLOTHUROIDEA

No reports are available yet on the holothurians from the Balleny Islands and from the Ross Sea although Pawson's (1969a, pl. 22) recent charts show what is at present known of Antarctic distributions.

DISCUSSION

Table 1 is a summary of present knowledge of echinoderm distribution (excluding the Crinoidea) in the New Zealand, Macquarie, Balleny Islands and Ross Sea areas. The New Zealand crinoid fauna is not yet sufficiently well known but contains at least 26 species (McKnight, in prep. d). According to Dearborn and Rommel (1969, p. 35) ". . . there have been no major taxonomic reports on southern crinoids since . . . 1937, 1938, 1939". They also remark: "There exist at present large collections of Antarctic and Subantarctic crinoids yet to be reported on". The NZOI collections from the Macquarie Island area (McKnight, in prep. c) reveal five species of crinoids, two of which are endemic species belonging to Indo-Pacific genera, another two are widespread Indo-Pacific species, and the last is an indeterminate specimen of the Antarctic genus *Ptilocrinus* possibly close to *P. antarcticus* Bather.

Only those species of echinoderms occurring in more than one of these areas are of significance in the present discussion. Twelve or possibly 13 species of echinoderms are common to the New Zealand Plateau and Macquarie Island; *Amphiodia joubini* (Koehler) occurs in the Ross Sea and on the slope of the New Zealand Plateau; 3 species, *Ophiopyren regularis* Koehler, *Porania antarctica* Smith and *Toporkovia antarctica* (Lyman) occur at Macquarie Island and in the Ross Sea; 37 species at the Balleny Islands and in the Ross Sea; and 4 or perhaps 5 species are common to the Ross Sea and the New Zealand Region.

ZOOGEOGRAPHY OF MACQUARIE ISLAND

Because Macquarie Island was for a long time thought to be separated from the New Zealand Plateau by water of 4,000 m or deeper (*cf.* Adie 1963, p. 460, Fig. 2), which led zoogeographers to look away from New Zealand for faunal affinities, its marine fauna was thought to be distinct and related either to the Subantarctic (*e.g.*, the Kerguelen Archipelago) or more directly to the Antarctic.

Following a detailed bathymetric and geological survey of Macquarie Island and the associated sea floor, Brodie and Dawson (1965) have shown that—

(1) a submarine ridge extends north of Macquarie Island to the south-west corner of the New Zealand shelf;

(2) much of this ridge is shallower than 2,000 m and has individual high areas which form shallow banks at 100 m or less;

(3) the maximum distance between the shallower parts of the ridge is 35 miles. Hence, benthic animals with restricted larval life and specific depth tolerances could have spread between New Zealand and Macquarie Island.

The Macquarie Ridge also extends south towards the Balleny Islands on the fringe of the Antarctic continent and might further serve as a faunal exchange route. The New Zealand–Antarctic link which Fell (1961) and Clark (1963) regarded as non-existent on topographic and faunal information then available now needs to be re-examined (*cf. also* Pawson 1968b).

In my review of work on the New Zealand Subantarctic fauna (Dawson 1965), my analysis supported Dell's (1964) conclusion that the marine fauna of Macquarie Island has a distinctive mixed character related to the Kerguelen, New Zealand, Heard Island and circum-Subantarctic biotas as a result of its geographical and hydrological position. However, Kusakin (1967, transl. 1968, pp. 354–5), from an examination of the isopods and tanaidaceans of Macquarie Island, concluded that the faunas are similar "not so much to the New Zealand or Antarctic as to the Kerguelen and Subantarctic American fauna".

The morphology of the Macquarie Ridge south of Macquarie Island and its associated features have been broadly determined, but no benthic samples have been collected along a 500-mile section of it between 57°S (about 200 miles south of Macquarie Island) and the Balleny Islands at about latitude 66°S. Possible faunal routes along the ridge (*e.g.*, high banks comparable with those on the ridge to the north between Macquarie Island and New Zealand) are not evident so far.

NORTH–SOUTH FAUNAL RELATIONSHIPS

Excluding wide-ranging latitudinal (*i.e.*, circum-Antarctic) relationships (as discussed by Fell and Dawsey 1969, for example), we can now examine more closely the north–south (or meridional) relationships. The Macquarie Island fauna (a total of 33 species known) has 12 species in common with the New Zealand Plateau. Most of the Balleny Islands

TABLE 1—Echinoderm species (excluding Crinoidea) common to the New

ASTEROIDEA

NEW ZEALAND REGION	NEW ZEALAND PLATEAU	Total fauna 65 species	
	MACQUARIE ISLAND	*Henricia aucklandiae* *H. lukinsii* *Hymenaster* sp. *Ceramaster* sp. ? *Odontaster* sp.	*Porania antarctica*
		Total fauna 13 species	
ANTARCTIC REGION	BALLENY ISLANDS	Total fauna 21 species	
	ROSS SEA	*Macroptychaster accrescens* *Leptychaster flexuosus* *Bathybiaster loripes obesus* *Psilaster charcoti* *Luidiaster gerlachei* *Odontaster meridionalis* *O. validus* *Acodontaster capitatus* *A. hodgsoni* *Perknaster densus* *P. fuscus antarcticus* *P. sladeni* *Cuenotaster involatus* *Lophaster gaini* *Peribolaster powelli* *Pteraster stellifer stellifer* *Notasterias armata* *Lyasterias joffrei* *Diplasterias brucei*	
		Total fauna 37 species	

Zealand Plateau, Macquarie Island, the Balleny Islands and the Ross Sea

OPHIUROIDEA	ECHINOIDEA	HOLOTHUROIDEA
Total fauna 87 species *Ophiuroglypha irrorata* *Monamphiura magellanica* *Axiognathus squamata* *Pandelia angularis* *Amphiodia joubini*	Total fauna 49 species *Pseudechinus novaezealandiae*	Total fauna 36 species *Ocnus brevidentis* *Trochodota dunedinensis*
Total fauna at least 13 species *Toporkovia antarctica* *Ophiopyren regularis* →	Total fauna 1 species	Total fauna 6 species
Total fauna 16 species ← *Ophiopyren regularis* *Astrotoma agassizi* *Astrochlamys bruneus* *Astrohamma tuberculatum* *Ophiacantha antarctica* *O. pentactis* *O. vivipara* *Amphiura belgicae* *Ophionotus victoriae* *Ophioperla koehleri* *Ophiomastus bispinosus* *Ophiurolepis gelida* *Ophioceres incipiens* *Amphiodia joubini*	Total fauna 3 species *Ctenocidaris perrieri* *Sterechinus antarcticus* *S. neumayeri*	Total fauna not yet determined
Total fauna 36 species *Toporkovia antarctica*	Total fauna 18 species	Total fauna not yet determined

echinoderms are shared with the Ross Sea and only four species, *Porania antarctica, Ophiopyren regularis, Amphiodia joubini* and *Toporkovia antarctica* link the Macquarie–New Zealand and Macquarie–Balleny–Ross Sea areas.

Amphiodia joubini regarded by Fell as "a cold-water eurybathic form", is a deep-water link between the Antarctic and the New Zealand region: ". . . where all water zones are cold, it has colonised the shelf. In the south temperate region, where the surface waters are at a higher temperature, it is presumably unable to occupy the shelf" (Fell 1961, pp. 42–3). *Gorgonocephalus chilensis* may be another species common to the Antarctic and the New Zealand regions, depending on its taxonomic status.

There are, therefore, close links between the Balleny Islands and Ross Sea areas and somewhat looser links between the New Zealand Plateau and Macquarie Island areas, but only rather tenuous links between the northern and southern ends of this potential migration route for benthic organisms. The present analysis provides a documented basis for earlier assumptions that these two regions, New Zealand and the Antarctic, must be regarded as distinct faunal entities. Hence, the demonstrated submarine connections (*see* Lawrence 1967) between Macquarie Island and New Zealand and the probable similar connections between the Balleny Islands and Macquarie Island have probably not functioned as particularly effective migration routes for echinoderms. Despite the substantial deep-water gap between the Balleny Islands and the continental shelf edge of the Ross Sea (Dawson 1970) the close relationship between the Balleny and Ross Sea faunas suggests that circum-Antarctic epiplanktonic drift may be more significant in their dispersal.

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