Biogeography of *Octopus* species (Cephalopoda: Octopodidae) from southeastern Australia

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Abstract: Seven species of inshore, benthic octopuses have been recorded from temperate waters off southeastern Australia. Studies on aspects of reproductive biology show that five species (*Octopus berrima* Stranks and Norman, 1993; *O. bunurong* Stranks, 1990; *O. kaurna* Stranks, 1990; *O. pallidus* Hoyle, 1885; and *O. superciliosus* Quoy and Gaimard, 1832) produce large eggs (8-14 mm long) in low numbers (10s or 100s), and have hatchlings that immediately adopt a benthic existence. Another two species (*O. maorum* Hutton, 1880, and *O. warringa* Stranks, 1990) produce small to medium eggs (2-7 mm long) in high numbers (1000s), with juveniles that are temporarily planktonic before settling out to the benthos. The distribution of these species is influenced by regional oceanographic factors such as the Leeuwin Current, West Wind Drift, and East Australian Current. The five species with direct development have limited means for dispersal, and are restricted in distribution to waters off southeastern Australia; the other two species with indirect development have the potential for long-range dispersal through the waters off southeastern Australia, the Tasman Sea, and New Zealand.

The family Octopodidae is typically characterized by the inshore, benthic octopus that possesses a saccular mantle and eight arms. The best-documented genus in the family is *Octopus*, which has a distribution in all coastal regions except for Arctic and Antarctic areas (Nesis, 1987).

There is a rich and diverse octopodid fauna in tropical to cold-temperate waters of the Australasian continental shelf region (Lu and Dunning, in press; Stranks, in press). During the past decade, the systematics of the regional fauna have been reviewed and revised by several workers, for example, the tropical fauna of Australia by Norman (1992a, b; 1993a, b, c), the cold temperate fauna of Australia by Stranks (1988a, b; 1990) and Stranks and Norman (1993), and the fauna of New Zealand by O'Shea (1990). These studies recognized 19 valid species of *Octopus* from Australia, and eight species from New Zealand. In addition, these works established distributional ranges for most of the valid species, and reported data on general biology where available.

Wilson and Allen (1987) included a general summary of molluscan biogeography from Australia. Lu and Phillips (1985) and Lu and Dunning (in press) have summarized available information on the distribution and biogeography of Australian cephalopods, but there has been little information published on the biogeography of octopodids from the region. Recent taxonomic work on the southeastern Australian fauna has facilitated a biogeographic study (see Stranks, 1988a). The present paper reports on the distribution of *Octopus* in this region related to biological and oceanographic factors.

METHODOLOGY

This study was based on a review of octopus specimens from southern Australian and New Zealand localities, held in collections in Australian museums: The Australian Museum (Sydney) (AM); Museum of Victoria (Melbourne) (NMV); Queen Victoria Museum and Art Gallery (Launceston) (QVM); South Australian Museum (Adelaide) (SAM); and Tasmanian Museum and Art Gallery (Hobart) (TMH). Additional material was examined from collections in New Zealand institutions: Canterbury Museum (Christchurch) (CMNZ); Museum of New Zealand (Wellington) (MONZ); and the Otago Museum (Dunedin) (OMNZ). Other abbreviations used are: CL, capsule length of mature ovarian or spawned egg; ML, mantle length; and TL, total length.

RESULTS

Seven valid species of octopuses have been recorded from southeastern Australian waters (Table 1).

Octopus berrima Stranks and Norman, 1993, is one of the most common *Octopus* species in southeastern Australia, occurring from the central Great Australian Bight (about 132°E) to Twofold Bay, New South Wales (about 37°S), including Bass Strait and Tasmania (Stranks and Norman, 1993). This species produces large eggs (10-14 mm CL) that are attached singly to the substratum (see vouchers NMV F52511 and F77664), and large hatchlings (4-5 mm ML) (see voucher NMV F77665). Mature females of *O. berrima* were recorded by Tait (1980) [as *O. australis* Hoyle, 1885] brooding clutches of 52-129 eggs.

Octopus bunurong Stranks, 1990, is distributed in southeastern Australia from the central Great Australian Bight (about 132°E) to southern New South Wales (about 37°S), including Bass Strait and northern Tasmania (Stranks, 1988a; 1990). Females have medium-sized mature ovarian eggs of 8-10 mm CL (see voucher NMV F53221). Method of egg attachment, clutch size, and hatchling size are unknown.

Octopus kaurna Stranks, 1990, is recorded in southeastern Australia from the central Great Australian Bight (about 132°E) to southern New South Wales (about 37°S), including Bass Strait and northern Tasmania (Stranks, 1988a; 1990). Females have mature ovarian eggs of 9-11 mm CL (see voucher NMV F1628). Method of egg attachment, clutch size, and hatchling size are unknown.

Octopus maorum Hutton, 1880, is a common species widely distributed in southeastern Australia and New Zealand (Fig. 1). The species is recorded on continental-shelf and upper-slope regions in southeastern Australia, from the central Great Australian Bight (about 132°E) to central New South Wales (about 33°S), and also in New Zealand from the North and South islands, and Chatham, Stewart, Auckland, and Campbell islands (Dell, 1952; Stranks, 1988a). The species produces medium-sized eggs (6-7 mm CL) that are attached singly to the substratum (see vouchers SAM D17981 and OMNZ A.'44.22). Batham (1957) reported a female *O. maorum* from New Zealand with a clutch of approximately 7000 eggs, and described morphology of the paralarvae (6.7-7.6 mm TL). Additional details of planktonic hatchling morphology and size (4.3-4.5 mm ML) were given by Hochberg *et al.* (1992). Larger planktonic hatchlings of 13-17 mm ML are also recorded from off eastern Tasmania (see vouchers NMV F77607-F77610).

Octopus pallidus Hoyle, 1885, is another common species in southeastern Australia (Fig. 2), recorded from continental-shelf and upper-slope regions, ranging from the central Great Australian Bight (about 132°E) to central New South Wales (about 33°S) including Bass Strait and Tasmania (Stranks, 1988a, b). One female was observed with a spawned clutch of 270 large eggs (11-13 mm CL) that were attached singly to the substratum (see voucher NMV F52502). The species produces large hatchlings (5-6 mm ML) (see voucher NMV F31563).

Octopus superciliosus Quoy and Gaimard, 1832, is recorded in southeastern Australia from the central Great Australian Bight (about 133°E) to Twofold Bay, New South Wales (about 37°S), including Bass Strait (Stranks, 1988a). The species produces large eggs (8-11 mm CL) that are attached singly to the substratum, and large hatchlings (4-5 mm ML) (see voucher NMV F59403). Clutch size is unknown.

Octopus warringa Stranks, 1990, has a wide distribution in southeastern Australia and New Zealand; it is recorded from the central Great Australian Bight (about 125°E) to eastern Victoria (about 38°S), and also in New Zealand from the North and South islands, and Stewart Island (Dell, 1952; Stranks, 1988a; 1990). The species produces small eggs (2-3 mm CL) that are attached in festoons to the substratum (see vouchers NMV F53216 and AM C92051). Brough (1965) reported on a female *O. warringa*

Table 1. Mature female size, egg size and number, hatchling type, and general distribution of *Octopus* species in southeastern Australian waters (*, measured from mature ovarian eggs; **, estimated from number of ovarian eggs).

Species	Female size at maturity (mm ML)	Egg size (mm CL)	Egg number	Hatchling size (mm ML)	Geographical distribution
		Small to Intermediate Egg Species with Planktonic Hatchlings			
Octopus maorum	90-255	6-7	7000	4-5	SE Australia-New Zealand
O. warringa	15-30	2-3	1000	2-3	SE Australia-New Zealand
		Large Egg Species with Benthic Hatchlings			
O. berrima	30-90	10-14	50-130	4-5	SE Australia
O. bunurong	45-50	8-10*	50-100*	?	SE Australia
O. kaurna	40-85	9-11*	50-100**	?	SE Australia
O. pallidus	50-130	11-13	270	5-6	SE Australia
O. superciliosus	10-30	8-11	50-100**	4-5	SE Australia

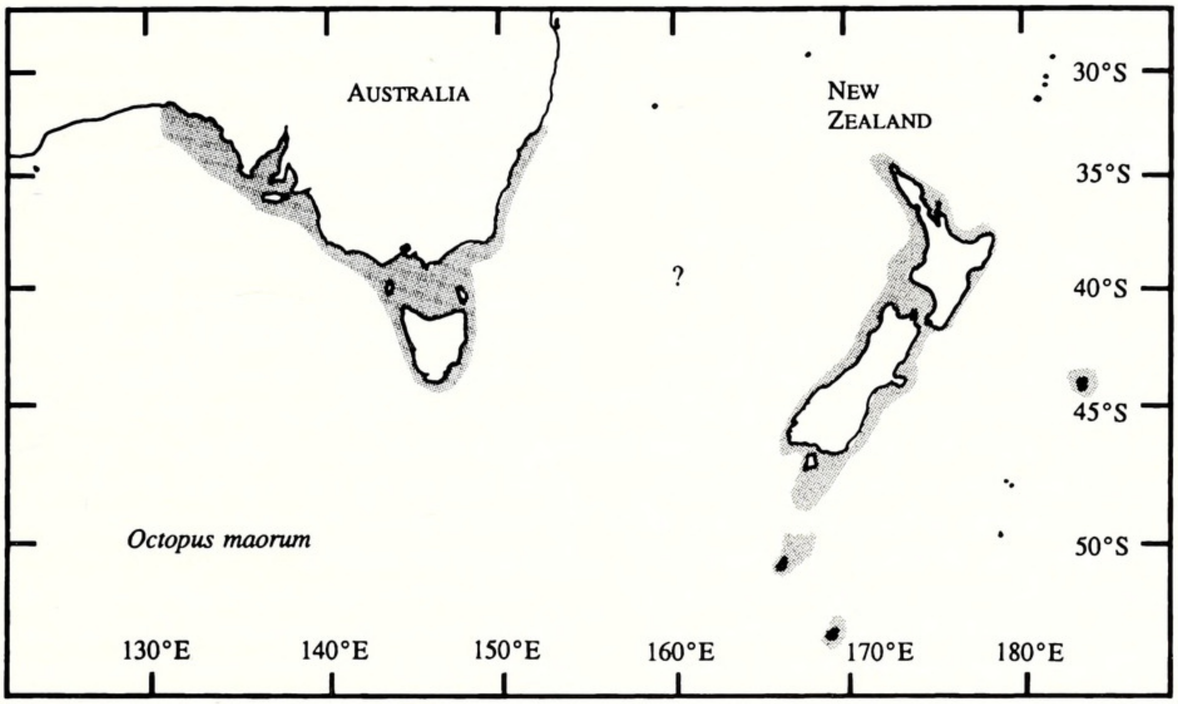

Fig. 1. Generalized geographical distribution of small- to medium-egg sized species around the southeastern coast of Australia, and around New Zealand and adjacent islands (based on the distribution of *Octopus maorum*).

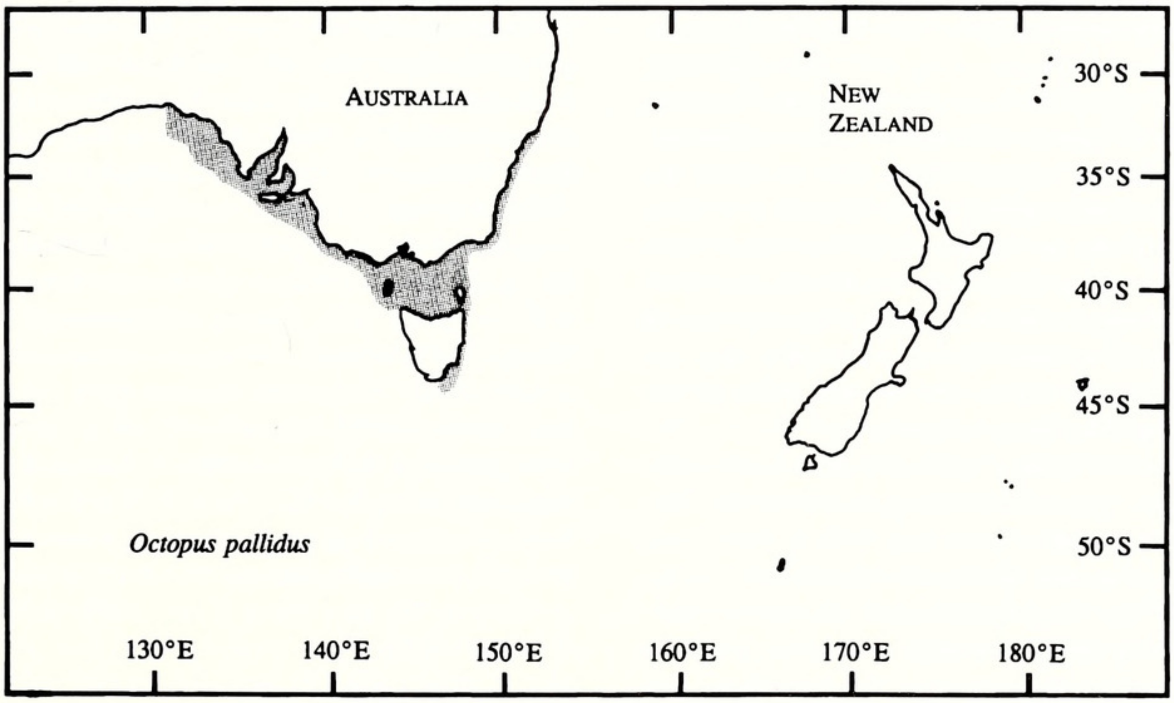

Fig. 2. Generalized geographical distribution of large egg sized species around the southeastern coast of Australia (based on the distribution of *Octopus pallidus*).

[as *Robsonella australis* (Hoyle, 1885)] brooding a clutch of about 1000 eggs, and on the morphology of the resulting hatchlings (3.6-4.0 mm TL). Further details of planktonic hatchling morphology and size (2.2-2.3 mm ML) were given by Hochberg *et al.* (1992).

DISCUSSION

The seven species of *Octopus* recorded in the present study have a localized distribution in the inshore temperate waters of southeastern Australia, and additionally with two cases, in New Zealand. The generalized distributional pattern of this species group on the Australian continent is from the Great Australian Bight to the southern or central New South Wales coast, including Bass Strait and the Tasmanian coastline. Those species also occurring in New Zealand are generally distributed around the North and South islands, and several of the smaller offshore islands. The author has not identified any of the seven *Octopus* species in areas outside these geographic limits, and on the basis of studies to date, all the species are considered endemic to the southeastern Australian and New Zealand region. This endemism at the species level corresponds well with the very high level of endemism (probably over 95%) of the southern Australian Mollusca in general (Wilson and Allen, 1987).

Adult inshore octopuses of southeastern Australia and New Zealand have a rather restricted distribution over the continental shelf and upper continental slope, from the intertidal zone to water depths of about 500 m. Adult animals can actively swim for short periods, but do not appear to migrate over extended ranges along the continental shelf, nor venture deep down the continental slope. Deep-sea trawling of mid- to lower continental slope benthos has failed to capture any of the mentioned species. Deep-sea regions could act as physical barriers to migration of these species. In this region, the Indian, Southern, and Pacific Oceans, as well as the Tasman Sea, can be considered as such oceanic barriers. Conversely, shallower stretches of water such as Bass Strait (between the Australian mainland and Tasmania) with water depths of less than 200 m do not appear to present any barrier to migration.

Apart from bathymetric isolation, other factors can influence the distribution of *Octopus* species along the continental shelf at the peripheries of their ranges. Several of the southeastern Australian species are restricted to waters east of the head of the Great Australian Bight (approximately 132°E). A local geographic feature that might present a barrier to migration of some species further west of this longitude is the cliffed Nullarbor coastline. From Eucla, Western Australia (129°E), to the head of the Great Australian Bight (132°E) is a long stretch of coast with very steep cliff frontage, extensive wave-cut platforms, and strong to extreme wave actions (Womersley and Edmonds, 1958). Whether *Octopus* species can survive in such a harsh environment is uncertain at present. Locality records for this area of the range are unfortunately sparse, so this distributional limit could to some extent be an artifact due to lack of sampling. Geographical features that might limit migration at the periphery of species' distributional ranges in eastern Australia are not obvious. Many of the *Octopus* species of southeastern Australia have ranges of distribution that extend along the eastern Australian coast as far northwards as southern or central New South Wales (32-37°S), but such distributions could be the result of hydrological rather than coastal topographical factors. This could also be reflected in the distributions of *Octopus* species around the coasts of New Zealand.

An important factor affecting the distribution of *Octopus* species in southeastern Australia and New Zealand appears to be water temperature. This temperate region has characteristic temperature profiles, described by Womersley and Edmonds (1958) and Knox (1975), that are distinct from those of neighboring areas. Distributional patterns of *Octopus* of southeastern Australia and New Zealand could be correlated with temperature regimes over these regions. Species in these temperate waters appear to tolerate temperature ranges from 10-17°C during the winter period, and 13-23°C through the summer season.

Hydrology of the temperate waters of southeastern Australia affects the distribution of inshore *Octopus* species, particularly where there is a meeting of cold and warm currents, marked by a sharp change in water temperature over a relatively short distance. The generalized temperate distribution of inshore *Octopus* species is confined in southeastern Australia, from about the center of the Great Australian Bight (130-134°E) to central or southern New South Wales (32-37°S), including Bass Strait and Tasmania. These distributional boundaries along the continental shelf in southeastern Australia could be correlated with effects of the Leeuwin Current in the west, and the East Australian Current to the east (Fig. 3). In summary, the Leeuwin Current carries warmer subtropical water around the southwestern coast of Western Australia to at least as far as the head of the Great Australian Bight (130°E) (Rochford, 1986), and can transport warm-water tropical fauna into the Bight (Maxwell and Cresswell, 1981). The East Australian Current carries warmer subtropical waters along the coast of eastern Australia, and can transport warm tropical fauna at least as far as central New South Wales (32-34°S) (Ekman, 1953).

Seawater salinity can be eliminated as a factor affecting distribution of *Octopus* species in southeastern Australia and New Zealand, as the surface salinity profiles are relatively uniform throughout this temperate region

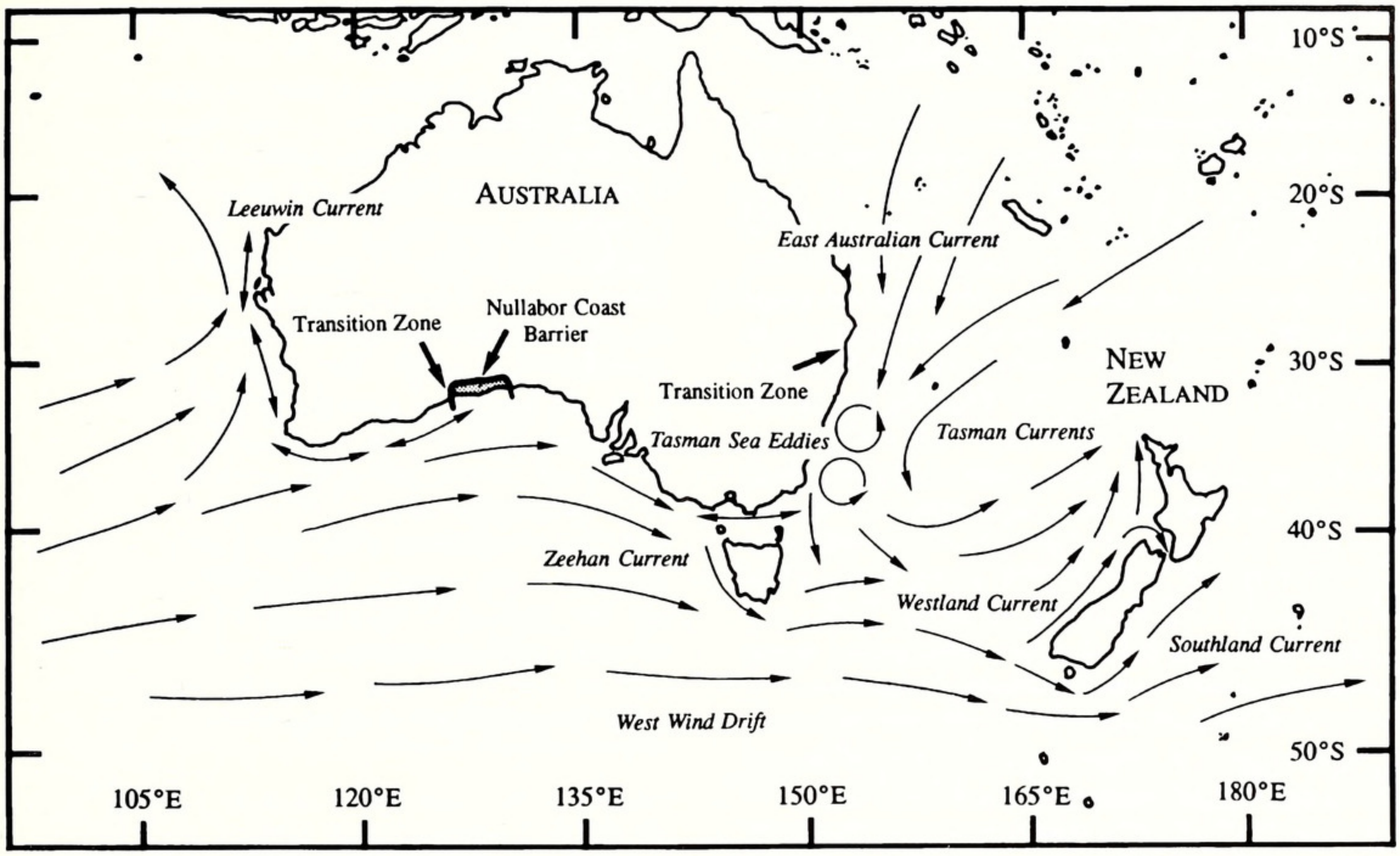

Fig. 3. Schematic chart of principal sea-surface currents influencing distribution of inshore benthic octopuses in the southeastern Australian and New Zealand region.

(Knox, 1975; Bunt, 1987).

Two alternate patterns of geographical distribution and reproductive behavior were noted. Two of the seven *Octopus* species have an extended distribution in southeastern Australian and New Zealand waters. The two taxa involved, *O. maorum* and *O. warringa*, are coincidentally the only species that produce small to intermediate sized eggs (2-7 mm CL) in very high numbers (*e. g.* 1000-7000), and whose hatchlings are relatively small and undergo a planktonic phase as paralarvae before settling out to the benthos (*i. e.* indirect development). The remaining five *Octopus* species are limited in their distribution to southeastern Australia. They produce large eggs (> 8 mm CL) in fewer numbers (*e. g.* 50-300), and the resulting hatchlings are relatively large and immediately adopt a benthic existence (*i. e.* direct development). Other mollusks that have shared distributions in Australia and New Zealand, and possess planktonic juvenile stages, have been reported by Wilson and Allen (1987).

Only the two *Octopus* species with planktonic juvenile stages occur in both Australia and New Zealand, suggesting that the distributional pattern in the region is the result of recent or on-going migration across the Tasman Sea, and not the result of previous land-mass connections between Australia and New Zealand. If the latter was the case, some of the species with non-planktonic stages might have been expected to occur in New Zealand as well as Australia.

Octopus species with benthic young do not have an alternate means for dispersal of individuals, and must rely on the relatively limited migration of adults. In other species with planktonic young, there is the potential for long-distance dispersal of juveniles across oceanic barriers. The Tasman Sea, with its submarine Tasman Trough at least 4000 m deep (Keast, 1959), appears to present a barrier to migration from southeastern Australia of *Octopus* species that have benthic juveniles and adults. However, species with benthic adults but planktonic paralarvae might have the potential for trans-Tasman migration. The distributional patterns of some *Octopus* species in southeastern Australia and New Zealand can thus be explained.

Pielou (1979) summarized requirements for successful transoceanic dispersal, noting the dependence on abundant offspring produced by the shore-dwelling adult, the probability of the juvenile being carried from coastal waters into open ocean circulation, the chances of the juvenile surviving the duration of the journey, and on chances of shifting back from oceanic to coastal waters after reaching the other shore. These factors will be examined with respect to predictions for trans-Tasman dispersal of planktonic juvenile *Octopus*.

Octopus maorum and *O. warringa* are species whose benthic adults live in inshore waters, and whose mature females are highly fecund, producing very large numbers of small or medium sized eggs, presumably to maximize chances of at least some planktonic juveniles surviving to adulthood. A mechanism for dispersal could involve hatched planktonic young being transported via the inshore coastal currents of southeastern Australia, into larger scale offshore movements of the Southern Ocean and Tasman Sea. The Tasman Currents, derived in part from the East Australian Current and also indirectly from West Wind Drift currents, appear to be the major agents for Tasman transportation. Movement of planktonic individuals in the Tasman Sea could be facilitated by strong currents and eddies. Prevailing easterly currents across the Tasman suggest that the movement and dispersal of individuals is unidirectional from Australia to New Zealand; there is no evidence for marked movement in the opposite direction. Individuals trapped in offshore Tasman Sea eddies can experience east to west transport over reduced distances for short periods, but there is no evidence that this movement would be significant enough to transport paralarvae back to shore.

At present, the duration that juveniles of *Octopus maorum* and *O. warringa* remain in the plankton before settling out to benthic existence is unknown. An indication of planktonic life is given by studies on other representatives of the genus: Yamashita (1974) calculated that juveniles of *O. dofleini* (Wülker, 1910) remain in the plankton for 2-3 months; Villanueva (1995) and Rees and Lumby (1954) estimated that juveniles of *O. vulgaris* Cuvier, 1797, remain planktonic for around two or three months respectively. Based on these figures, juveniles of *O. maorum* and *O. warringa* could have the potential to survive as plankton in oceanic currents for three months.

If juveniles of *Octopus maorum* and *O. warringa* are to reach New Zealand from Australia, the period that the juveniles remain planktonic must be correlated with the velocity of currents flowing from Australia to New Zealand. This could determine whether the young are able to be transported across the Tasman to the New Zealand coast in sufficient time, before their transition from plankton to benthos, or whether they perish before ever reaching the coast. Rates of current flow for the East Australian Current are estimated at 2 m/sec by Hamon *et al.* (1975), and for some Tasman Sea eddies at 1.3 m/sec by Cresswell (1983). Such movements for passively drifting planktonic material are deemed maximal, and will be reduced when animals are caught in slower flowing currents or entrapped in eddies. Distances from the coast of Australia to New Zealand range from approximately 1500 to 2200 km. By calculation, the fastest period in which an organism could be transported in plankton from Australia to New Zealand, under optimal conditions, would be about nine days. Because of variable current patterns and rates of flow, it is highly improbable that transportation occurs so rapidly. Nevertheless, given that *O. maorum* and *O. warringa* individuals might survive in the plankton for three months, it seems possible that juveniles could survive suspended in the plankton long enough to reach New Zealand from Australia. Hence, despite the isolation of adult populations of the two species in Australia and New Zealand, genetic exchange could be possible by continuous or sporadic transport of juvenile individuals across the Tasman Sea.

Elucidation of the distribution of *Octopus maorum* and *O. warringa* must await detailed studies of plankton systematics and ecology from off southeastern Australia and New Zealand. Collections are at hand to study the distribution of octopus paralarvae across the Tasman Sea, but until the author has completed further studies, some of the above comments must remain speculative.

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