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**CENTRE FOR RESEARCH ON INTRODUCED MARINE PESTS**

**TECHNICAL REPORT NUMBER 25**

**DISTRIBUTION AND BIOLOGY OF THE INTRODUCED GASTROPOD,  
*MAORICOLPUS ROSEUS* (QUOY AND GAMARD, 1834) (CAENOGASTROPODA:  
TURRITELLIDAE) IN AUSTRALIA**

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## SUMMARY

The turritellid gastropod, *Maoricolpus roseus* was first recorded in Australian waters by Greenhill in 1963. Anecdotal evidence suggests it may have been introduced from New Zealand to south-eastern Tasmanian waters in the 1920-30's. It has subsequently spread up the east coast of Tasmania, across Bass Strait and is currently recorded as far north as Botany Bay in New South Wales. Despite its presence throughout the south-eastern Australia out to the continental shelf depths to depths of at least 80 m, little is known about this species. This report compiles the currently available information on this species in the literature, information on museum collections around Australia, anecdotal evidence from commercial fishermen and amateur shell collectors and the results of several short-term field studies in an effort to increase our knowledge of the biology, ecology and distribution of *M. roseus*.

*M. roseus* is found burrowing in and on sediments and occurs on a range of substrata from silts and sands to crevices in rock walls and sheltered pockets on exposed reefs in the shallow subtidal zone out to the continental shelf. A suspension feeder, it can reach densities of up to several hundred per square metre, and grows to a length of 90 mm. However, so little is known about this species it is unclear what impacts the dense beds of *M. roseus* are having on our native fauna in south-eastern Australia. Similarly it is not clear whether its spread up Australia's east coast was a natural dispersal in prevailing currents, or whether its spread was facilitated by other vectors such as fishing vessels and dredges.

Given its wide temperature, depth and substrate tolerances, *M. roseus* has the potential to survive all around the southern Australian coastline out to a depth of at least 80m, and possible 200m. However, because prevailing currents run west to east, *M. roseus* is likely to remain restricted to east of Bass Strait unless carried to the west by other vectors. Management of those vectors will determine the risk that this species poses to the west coasts of Tasmania and Victoria and the Great Australian Bight. Appropriate management actions are needed before accidental translocation occurs.



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We are grateful to Margaret Richmond (amateur shell collector) for her enthusiasm in sharing her valuable 20 year database of beach-collected data with us, enabling us to include her results in this report.

We also thank the CSIRO Microalgae Research Centre for supplying phytoplankton cultures to enable us to maintain *M. roseus* in aquaria.



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## 1 INTRODUCTION

The extent of the introduced marine species problem in Australia became apparent with the outbreaks of highly visible introduced species (eg. *Asterias amurensis* in Hobart and Port Phillip Bay and *Mytilopsis* sp. in Darwin) capable of adversely affecting and impacting industry, aquaculture and biodiversity (Morrice 1995; Goggin, 1998; Ferguson, 2000). Baseline surveys in ports and adjacent environments by CSIRO's Centre for Research on Introduced Marine Pests (CRIMP) and State agencies, literature searches and museum collections have indicated that there are more than 200 introduced and cryptogenic species in Australia (C. Hewitt, CRIMP; pers. comm.). This number is an underestimate as only 21 of the 72 trading ports in Australia have been surveyed and 165 introduced and cryptogenic species were identified from Port Phillip Bay alone (Hewitt *et al.* 1999).

The majority of introduced marine pest species are restricted to shallow waters in areas subjected to a high volume of shipping activities such as port environments, although this is also where most biological surveys have been conducted. However, extensive benthic surveys in continental shelf waters off Southeast Australia have not reported large numbers of invasive species, with the exception of *Maoricolpus roseus* (Bax and Williams 2000). In its native region (New Zealand), *M. roseus* is found on all substrata from soft sediments to exposed rocky habitats, living in crevices on rock walls, and sheltered pockets on more exposed reefs from low-water to approximately 200 metres depth (reviewed by Scott 1997). In Australian waters, *M. roseus* has now spread out to the 80 metre depth contour off the eastern Victorian and New South Wales coasts (Bax and Williams 2000). Due to the wide range of habitats occupied, the potential exists for *M. roseus* to have greater ecological and environmental impacts over larger areas than many of the more high profile introduced pest species currently restricted to specific inshore environments. Given its wide temperature, depth and substrate tolerances, *Maoricolpus roseus* has the potential to expand its current distribution and successfully establishing itself further along the southern Australian coastline.

The economic cost of the impacts of aquatic exotic species is significant. Pimental *et al.* (2000) estimated conservative economic costs attributable to exotic fishes in the United States at US\$1 billion annually. Again in the United States, 1993 estimates put damage caused by and control efforts for the zebra mussel (*Dreissena polymorpha*), Asiatic clam (*Corbicula fluminea*) and the European green crab (*Carcinus maenas*) at US\$4.4 billion annually, while the aquatic weed, purple loosestrife cost US\$45 million annually and aquatic weed control cost US\$110 million annually (Hall and Mills 2000).

Large populations of introduced filter feeders (eg. *Mytilus edulis*, *Mercenaria mercenaria* and *Dreissena polymorpha*) have been known to reduce phytoplankton levels and can contribute to the decline of algal blooms as well as outcompeting native bivalve species for space and food (Takeda and Kurihar 1994; Welker and Walz 1998; Caron and Lonsdale 1999a, 1999b; Rensel and Martin 2000). The burrowing bivalve, *Mya arenaria* alters sulphur reduction rates in the sediments, most likely caused by substrate enrichment due to organic excretions (Hansen *et al.* 1996). It caused a transformation of the benthic communities of the Black Sea, through competitive exclusion of native bivalves (Leppakoski, 1994). *Ensis directus* another benthic bivalve is known to alter community structure due to its dense populations (Gollasch *et al.* 1999). These dense populations may also have an impact of the sediment structure by their burying activities and may decrease the stock of other filter feeders such as cockles and mussels (Armonies and Reise, 1999). While mats of the mussel, *Musculista senhousia* have a detrimental effect on existing sediment and infaunal assemblages in New Zealand (Crooks 1998), this effect is localised and only occurs where extensive beds are formed. Given the ephemeral nature of these beds, the environmental effects at a site are likely to be short-lived (Creese *et al.* 1997). It is unknown whether the dense beds of the burrowing and filter feeding

*M. roseus* around south-eastern Australia are having a similar negative impact on our native species. This is of particular importance as the Bass Strait scallop industry is virtually all that is left of the once highly profitable industry in southern Australia and stocks have been decreasing for some years.

*Maoricolpus roseus* was most likely introduced to Tasmania, either as semi-dry ballast in timber vessels from New Zealand, dumped over board on arrival in Tasmanian waters or it may have accidentally been transported from New Zealand with live oysters. *Tiostrea chilensis* and/or *Crassostrea glomerata* were sporadically imported to Tasmania from the late 1800's (1885, 1887, 1926) to bolster the failing local oyster industry, and particularly from Bluff, in about 1920. The New Zealand oysters were kept for sale at the Hobart Fish Market, where they were kept alive in crates in the water, during the 1920's to the late 1930's (Dartnall 1969).

Several other species of New Zealand origin are also introduced to Tasmania and initially were only found in the D'Entrecasteaux Channel region (Dartnall 1967). These species include the molluscs: *Venerupis largillierti*, *Neilo australis*, *Chiton glaucus*, the crustaceans: *Petrolisthes elongatus*, *Cancer novaezelandiae*, *Halicarcinus innominatus*, the branchiopod: *Terebratulula rubicunda* and the asteroids: *Patirella regularis* and *Astrostole scabra*. Details of the life history and distribution patterns of these species may help to shed some light of the life history of *M. roseus* and in the prediction of its future spread.

## 2 TAXONOMY

*Maoricolpus roseus* (Quoy and Gaimard, 1834) (Caenogastropoda: Turritellidae)

### 2.1 Synonyms

*Turritella rosea* Quoy and Gaimard, 1834

*Gazameda rosea* (Quoy and Gaimard, 1834)

*Turritella difficilis* Suter, 1908

*Maoricolpus roseus* (Quoy and Gaimard, 1834) Finlay 1927

*Maoricolpus roseus roseus* (Quoy and Gaimard, 1834) Powell 1931

### 2.2. Common names

Rosy screwshell

Rosy turritella

New Zealand screwshell

“Twirlies” (Tasmanian scallop fishermen)

### 2.3. Description

Shell large, solid with broadly conical spire; to 87 mm in length and 25 mm in width, with up to 18 whorls, slightly concave at the centres, with numerous threads and striae. Colour fawn to reddish or purplish brown, faintly marbled or streaked in darker brown; operculum thin, horny, circular and multispiral (Powell 1979).

The species is divided into two subspecies: *Maoricolpus roseus roseus* and *Maoricolpus roseus manukauensis* (Powell 1931). *Maoricolpus roseus manukauensis* is constantly narrower than the typical *M. roseus roseus* and has the whorls more tightly coiled and its distribution is restricted to the Manukau, Raglan and Kawhia Harbours in New Zealand, whereas *Maoricolpus roseus roseus* is found around most of New Zealand (Powell 1979). The Tasmanian subspecies was determined to be *Maoricolpus roseus roseus* by Greenhill (1965) who compared the dimensions of the Tasmanian specimens with those given in descriptions for the two subspecies in Powell (1931).



### 3 ECOLOGICAL ATTRIBUTES

#### 3.1 Geographic distribution in Australia

The first published record of *Maoricolpus roseus* in Australian waters was by Greenhill (1965), who stated that large quantities of live specimens were dredged in the D'Entrecasteaux Channel in 1964 by Mr. John Farnell while fishing for scallops, in depths from 2 to 10 fathoms. Greenhill (1965) reported that Mr. Farnell had specimens of *M. roseus* collected over 20 years previously (ie prior to 1945), and estimated that the species had become established in the D'Entrecasteaux Channel in the last 20-40 years. It was believed that *M. roseus* was rapidly increasing in numbers in the D'Entrecasteaux Channel. Hilary Reynard and Robin Seward, senior commercial scallop fishermen from the D'Entrecasteaux Channel area, report that *M. roseus* was commonly dredged there from at least 1938 when they started in the fishery as young boys, and was more common then in the southern end of the Channel than further north. The species was not recorded by May (1923), who had conducted an extensive amount of dredging for molluscs in the area prior to 1920, so it is most likely that the species arrived in Tasmanian waters post 1920 (Figure 1). If it was already common in the southern D'Entrecasteaux Channel by 1938, it most likely arrived during the 1920's, and most likely arrived in the southern D'Entrecasteaux Channel area or nearby, as that was where the first large numbers were collected.

Other Tasmanian records of *M. roseus* included by Greenhill (1965) were of worn specimens from the Huon Estuary (Brabazon [One Tree] Point & Randalls Bay) and two dead specimens from Macquarie Harbour on the west coast. The Huon Estuary records have been supported by later collections, including some live dredged material (see Appendix 1.). The record from Macquarie Harbour was the only one from the Tasmanian west coast until the year 2001 when a small 3mm individual was collected in northern Macquarie Harbour by an environmental consultant company (Adam Davey, Aquenal, pers. comm.). The 1960's specimens cannot be found in any museum collection. As they were noted to be dead collected, it is possible that they were dead shells transported to Macquarie Harbour, most likely either by a fishing vessel (transporting them from the D'Entrecasteaux Channel area) or by a timber vessel (transporting them either from New Zealand or the D'Entrecasteaux Channel). Dead collected specimens of *M. roseus*, particularly when they are the only records and only a few in number, should be accepted with great caution as a record of the species living in the area.

Greenhill (1965) also reported that *M. roseus* had not been collected in the littoral zone, and dead specimens were very rare on beaches. When Hope Macpherson revised May's (1923) Index for the 1958 reprint, based on published records and a survey of beach-collected material in the 1950's, *M. roseus* was not included amongst the new records for the State. However, apparently *M. roseus* was collected on the East coast by Macpherson (now Hope Black) at Stoop Rock in the Bay of Fires on the East coast but not included in the revision of May's work since it was not a native Tasmanian species (M. Richmond, pers. comm. following conversation with Hope Black, June 2001).

Beach-collected specimens of *M. roseus* are not necessarily common or even present in areas where the species is common sublittorally, particularly in areas where the species has recently established itself. Therefore, the absence of beach specimens of *M. roseus* is not conclusive to the absence of the species, and the first records of beach-collected specimens from an area usually postdate the arrival of *M. roseus* in that area by a number of years. A good example of this is that the first dredged material from Schouten Passage dates from 1977, but the first beach-collected material from Schouten Island is from 1987 (both TMAG collection). Many of the records of beach-collected material reflect collecting bias – samples were collected on an *ad hoc* basis, with no systematic surveys, and the species was in these areas long before any beach samples were collected.

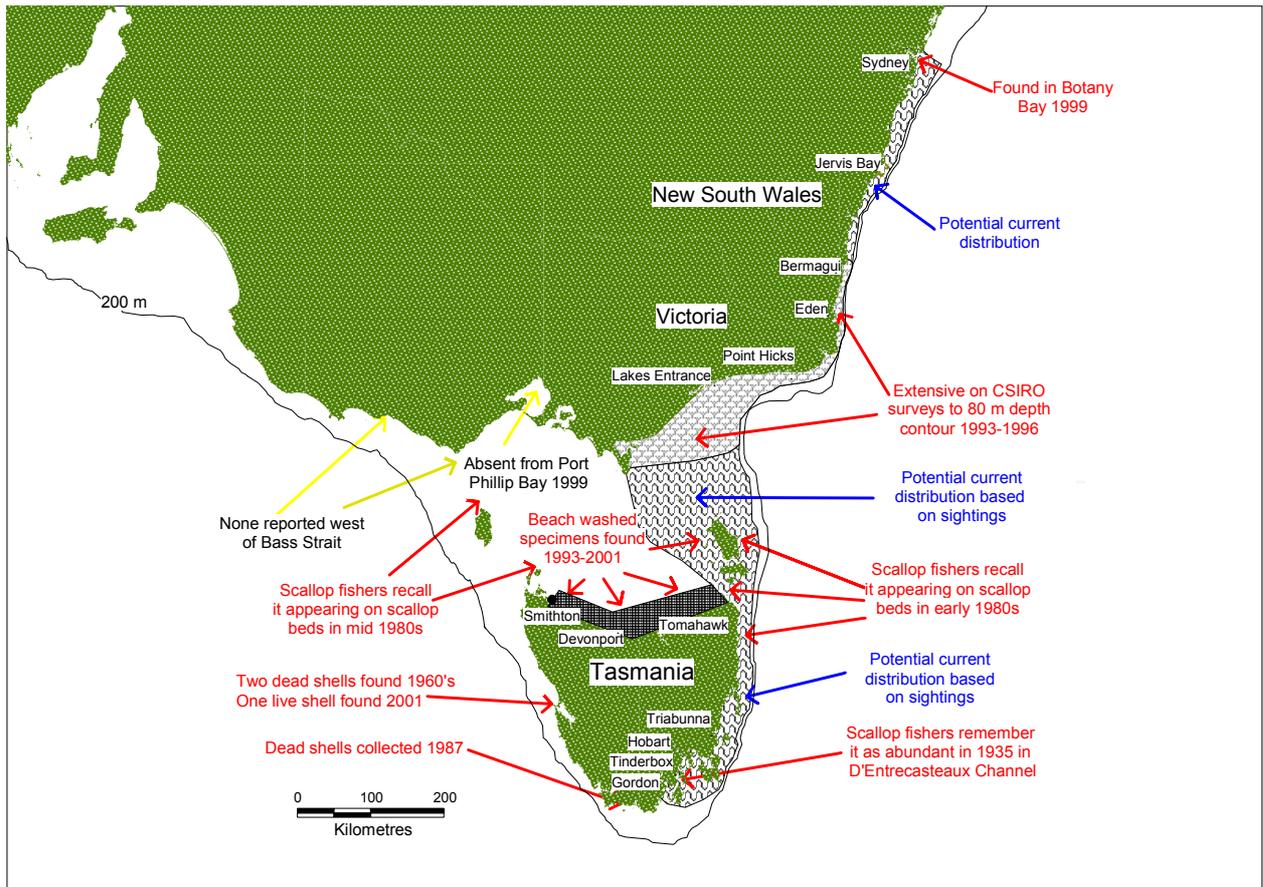
In 1981, Margaret Richmond, a Tasmania shell collector began regularly sampling beach-collected material (excluding the west coast) in order to produce a book on the 100 most commonly collected shells on Tasmanian beaches (Richmond 1990, 1992). She has an extensive database containing 20 years of records and ~600 mollusc species from numerous sites around Tasmania at various times through the years. From her records on beach-collected material there is a clear progression of *M. roseus* distribution around the State. In 1981, it was found in the south-east region at Tinderbox, South Arm, Lauderdale and Adventure Bay. In 1983, specimens were collected in many localities on the east coast from Orford to Scamander and then consistently afterward, expanding to include the Freycinet Peninsula and Stumpy Bay near Eddystone Point in 1985. The first beach-collected samples on the north coast were at Anthony Beach near Smithton in 1985 supporting anecdotal accounts from scallop fishermen who recall it appearing on scallop beds in the mid 1980's (G. Richie, pers. comm.). However, it was not collected again on the north coast until it was collected at the Bluff Beach at Devonport in 1993, Tomahawk in 1996, East Devonport in 1997, Anthony Beach in 1998 and Godfreys Beach, Stanley in 1999 (M. Richmond, unpublished data). Since the year 2000, *M. roseus* has repeatedly been collected as beach-collected specimens in the Devonport area. Several dead specimens have also been collected at the mouth of the Tamar River in 1995 (John Moverley, MOV, pers. comm.) and 2001 (Aquanel, pers. comm.).

The most southerly record of *M. roseus* in Tasmania from museum material is from Southport, beach-collected specimens in 1970 (TMAG collection). Margaret Richmond has single records from Cox Bight, in 1987 and Cockle Creek in 1988, given to her by two friends who had walked the south coast track from Melaleuca. It is perhaps surprising that there are no other records from Recherche Bay, given the large amount of timber trade that was going on there in the early part of this century. However, the lack of any other records from the southwest and west coast of Tasmania may be an artefact due to the inaccessibility of the regions and lack of sampling surveys in this region and therefore not indicative of the actual distribution of *M. roseus* in this area

The South Australian Museum holds the earliest authenticated record of this species from Bass Strait off Babel Island, east of Flinders Island (SAM D19059), dredged in 40 m by the FRV "Soela" on 11 October 1984. Beach-collected specimens were first collected on Flinders Island in 1995 at North East River and 1996 at The Patriachs and White Beach (M. Richmond, unpublished data). Bass Strait scallop surveys by CSIRO in 1986 and 1987 found "acres of twirlies" in Banks Strait (between Flinders Island and mainland Tasmania and also at several locations between Flinders Island and mainland Victoria (Figure 1) (R. Martin, CRIMP, unpublished data). The recent benthic survey for the Duke Energy gas pipeline along a transect line from Victoria to Tasmania found *M. roseus* present along the majority of the deeper water transects in central Bass Strait (Figure 1) (Butler *et al.* 2000). . No specimens of *M. roseus* have been collected by the three amateur shell collectors living on King Island (M. McGarvie, pers. comm.) or during the EIS for the new marine farm zone at Robbins Island (Ron Mawbey, Aquanel, pers. comm.). There are currently no confirmed records from western Bass Strait.

The range of *M. roseus* in Australian waters has been slowly extending northward, with specimens found out to the 80 m depth contour off the eastern Victorian and New South Wales coasts in a CSIRO survey in 1993-94 (Bax and Williams 2000), the Port of Eden in 1999 (C. Hewitt, CRIMP, pers. comm.) and Botany Bay in 1999 (Winston Ponder, AM, pers. comm) (Figure 1).

There is also a record of *M. roseus* from southern Queensland in Wilson (1993) based on a dead collected specimen with dubious locality and is regarded as a very doubtful record (see Appendix 1).



**Figure 1.** Historical observations of presence and absence of *Maoricolpus roseus* and inferred distribution based on dredged and beach-collected samples.

### 3.2 Habitat

*Maoricolpus roseus* is abundant around most of New Zealand, often occurring in vast beds of up to several hundred individuals per square metre on suitable soft bottom. They also occur in more rugged or exposed habitats, living in crevices on rock walls in areas like Fiordland, and in sheltered pockets on more exposed reefs. *M. roseus* is found from low-water to approximately 200 m depth on fine silt, mud, sand and gravel substrates in New Zealand (reviewed by Scott 1997). Greater densities were observed on shelly substrates than on sandy/silty beds (Allmon *et al.* 1994); other studies have found the greatest abundance on firm organically rich substrates (Rainer 1981, Probert and Wilson 1984). It prefers firm coarser substrates with moderate to strong currents (to supply adequate food for filtration). There is a positive correlation of abundance with availability of suspended food and a negative correlation with suspended terrigenous (land derived) sediment (Allmon *et al.* 1994).

It has a high spire, many whorls and a small aperture, characteristic features of turritellids and can move across sediments, or burrow into soft substrates (Kohn 1983). The striae (raised ridges in the direction of growth) found on the whorls of *M. roseus* and other gastropods are thought to be beneficial for holding the shell in substrate (Allmon 1988). *M. roseus* is much larger than any living native turritellid in southern Australian waters.

In New Zealand *M. roseus* can dominate the benthic community, in areas of muds and silty sands where few other infaunal species are present (McKnight 1969). In areas of shelly sand substrate it is found in association with many other species and is a subdominant member (Grange 1979). Seventeen

infaunal communities were described for the New Zealand continental shelf from 600 historic benthic samples (McKnight 1969). The “*Turritella*” community was dominated by *M. roseus* and the bivalve, *Nucula hartvigiana*. The community occurred on “shell” to “sand” substrates in depths from 5-20 m, but occurrence was restricted to the Manukau Harbour. The *Amphiura rosea* – *Dosinia lambata* community of sandy mud or mud substrates in depths of 1-50m from Tasman Bay north, also included *M. roseus* as a characteristic species. *M. roseus* occurred in 10 of the 19 samples and was numerically dominant in three sandy mud stations, although the remainder of the fauna was not noticeably reduced in species or numbers. The “*Maoricolpus* formation” and “*Maoricolpus* and *Dosinula* association” described by Powell (1936) are included in this community. They are typically associated with relatively coarse sediments, often associated with tidal scour channels. *M. roseus* was also present in the *Amphiura roseus* – *Dosinia greyi* community, comprising 13 stations on muddy sand to mud substrates in depths of 20-150 m and at 6 of the 10 stations of the *Nemocardium pulchellum* – *Dosinia lambata* community, found mainly in sheltered waters between 18-50 m on muddy sand to mud substrates, mainly mud.

## 4 BIOLOGICAL ATTRIBUTES

### 4.1 Feeding

*Maoricolpus roseus* has been described as a sedentary ciliary feeder (Morton and Miller 1968) relying on water currents carrying food. Ciliary suspension feeding is the most common feeding mode for the Turrnellidae (reviewed by Scott 1997), but some species eg. *Gazameda gunnii* can switch to deposit feeding when phytoplankton abundances are low (Allmon 1988). Whether or not *M. roseus* can switch modes is unknown, however the low stable isotope ratio for four specimens collected off southeast Australia ( $\delta^{15}\text{N} = 5.32$ ;  $N = 4$ , compared with particulate organic matter  $\delta^{15}\text{N} = 7.05$ ;  $N = 28$  and sediment  $\delta^{15}\text{N} = 6.97$ ;  $N = 42$ ) indicate that its food comes from low in the food chain – ie. a suspension or detritus feeder (Davenport and Bax 2002).

### 4.2 Growth

Shell lengths<sup>1</sup> of *Maoricolpus roseus* have been reported as 42.0-86.5 mm in New Zealand (Greenhill 1965; Powell 1979), 41.6-75.5 mm in the D'Entrecasteaux Channel, Tasmania (Greenhill 1965), 28-83 mm Tasman Peninsula, Tasmania (Scott 1997) and 16.9-72.9mm off Eastern Victoria and southern New South Wales at 25-80 m depth (N. Bax, unpublished data, Figure 2). Recent diver collections of *M. roseus* in southern and eastern Tasmania have found individuals between 29-90.8 mm at Tinderbox and 35-74 mm at Triabunna at ~5 m depth. The measurement of 90.8 mm is greater than any previous record in the literature. These data illustrate that length frequency (hence growth rates and/or age composition) varies between locations (Figures 2 and 3) and time (Figure 4). Growth rates and abundance of turrnellids have been shown to depend on environmental conditions such as degree of exposure, phytoplankton concentration, substrate, competition, density, predation and temperature (Allmon *et al.* 1994, Scott 1997).

There are several estimates of age and growth rates obtained from isotopic analysis ( $\delta^{18}\text{O}$ ) of shells. In one study, a 64 mm long, 14 whorl shell collected from Tinderbox, Tasmania, was estimated to be 3 years old and had 13 whorls by the second year (Allmon *et al.* 1994). The authors suggested that *M. roseus* has a maximum lifespan of 6-7 years, an average lifespan of 2-3 years and reproduces in its second or perhaps first year. In a second study, two shells (57 mm and 75 mm) from Pirates Bay were estimated to be 5 and 6 years old,

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<sup>1</sup> High spire gastropods such as turrnellids are difficult to measure accurately because they are prone to break at the tip and shell length and number of whorls measurements can be underestimated. By aligning homologous whorls with smaller specimens with entire apices, complete measurements of broken specimens can be estimated (Morris and Allmon 1994). Since the most rapid growth is when they are small, a missing tip of 2 mm length represents 5-6 whorls of growth, excluding the protoconch in *Maoricolpus roseus* (F. McEnnulty, unpublished data).

Qualitative diver collections of *Maoricolpus roseus* in southern and eastern Tasmania have failed to find any small specimens (<29 mm) amongst the larger shells. However quantitative grab samples around commercial aquaculture farms in the D'Entecasteaux Channel by the Tasmanian Fisheries and Aquaculture Institute have found juvenile specimens <20 mm as well as large specimens (C. Macleod, TAFI, pers. comm.). Given the burrowing nature of the species and its suspected nocturnal habits it likely they are hidden in the sediments during diver collections since collecting of shells by raking through sand by hand has been shown to undersample small individuals (Chilcott 1996).

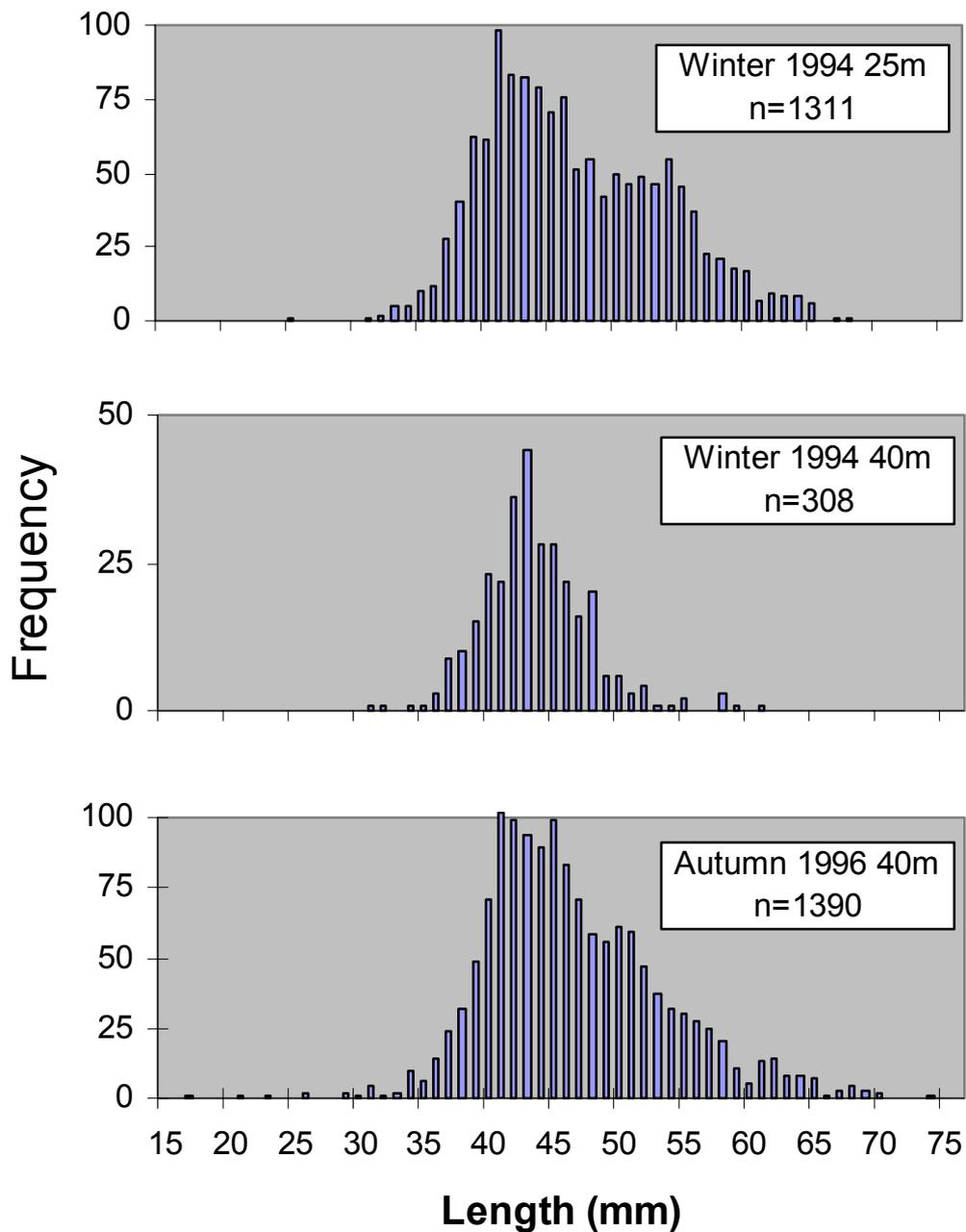
with a growth of only 8 whorls in the first two years (Scott 1997). These limited data further suggest that age and size of maturity may vary between locations.

By comparison, the average lifespan reported for the native turrnellid *Gazameda gunnii* from direct observation is 6-7 years and reproduction begins at 2.5-3 years (Carrick 1980 as cited in Allmon *et al.* 1992). Based on size and growth line counts, *Turritella communis* from the northern Atlantic may live 10-15 years, but most individuals probably live 2-3 years (Allmon 1988).

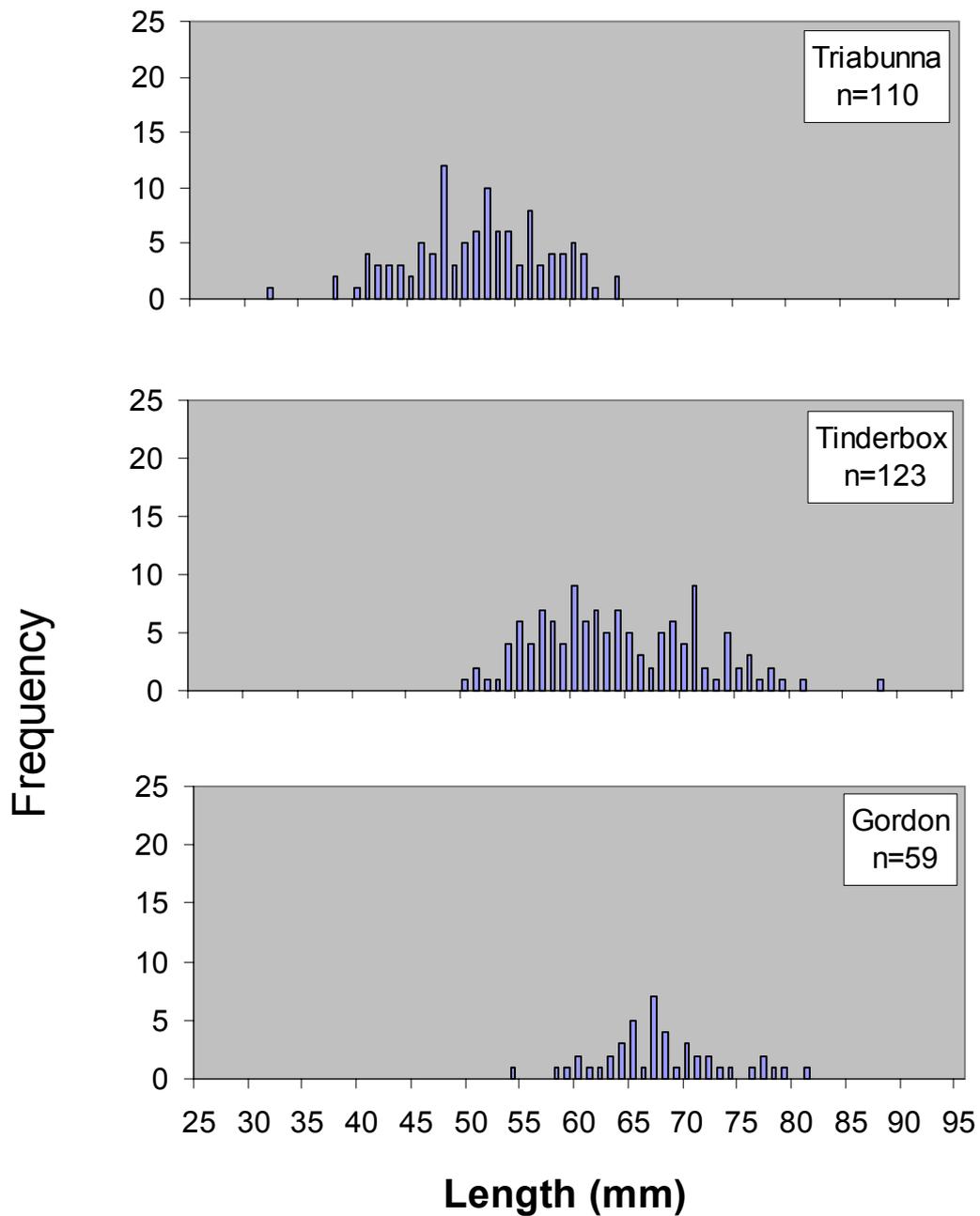
*Maoricolpus roseus* grows faster and lays down greater amounts of shell when younger and smaller. The reduction in shell growth with age almost certainly reflects an ontogenic decline as more investment is put into reproduction. Growth is seasonal, with the most rapid seasonal growth during the warmest months, particularly in the first year of life. Growth ceases at temperatures below 13°C and above 17°C but *M. roseus* is capable of very rapid growth to maturity under favourable conditions (Scott 1997).

Gonad development in relation to shell length was examined for 558 *M. roseus* collected at Tinderbox and Triabunna between December 2000 and March 2001 (Table 1). The smallest two females from Tinderbox (29.7 mm and 36.6 mm shell length) and one female from Triabunna (44.0 mm shell length) were immature (possessed no developed gonads), although specimens as small as 39.2 mm from Triabunna were mature. Egg capsules were found in specimens from 63.9-78.4 mm shell length (Tinderbox) and 41.9-71.8 mm shell length (Triabunna). Overall, egg capsules were found in 5% of the samples (10% of females). There was negligible difference between December (10% total, 25% females) and January (11% total, 17% females) samples from Triabunna. However, fewer individuals at Tinderbox in January had egg capsules (3% total 10% females). All male specimens, even those as small as 32.9 mm possessed actively swimming sperm.

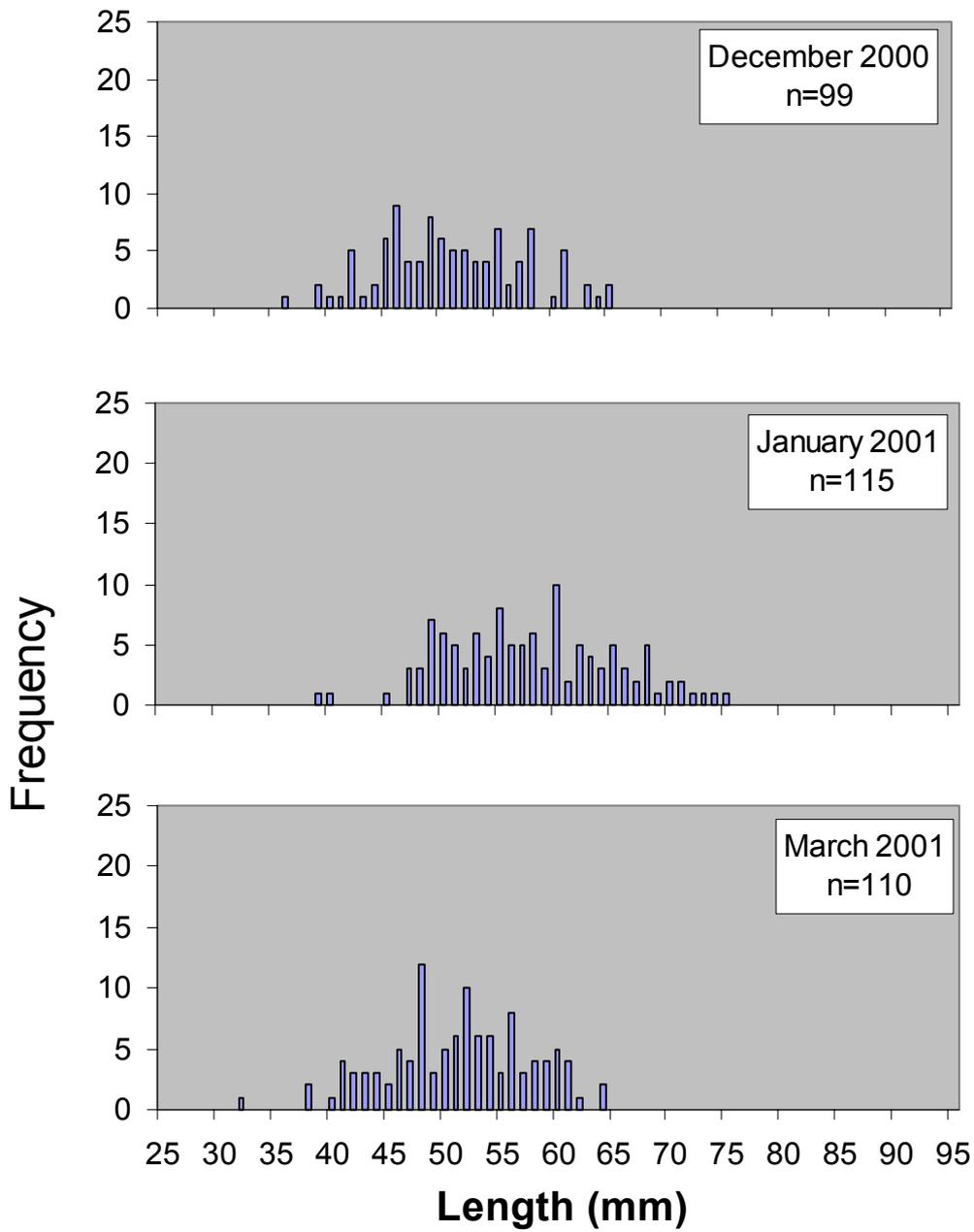
The smallest shell length at maturity for females was 38.9 mm (Triabunna) and 47.2 mm (Tinderbox); males possessed sperm at the smallest sizes examined 35.8 mm (Triabunna) and 39.6 mm (Tinderbox). The smaller size at maturity for the Triabunna population may be explained by the smaller maximum size (74.4 mm) compared to Tinderbox (90.8 mm). The shells of the Triabunna population were older in appearance and more stunted and heavily fouled than the specimens collected from Tinderbox, which had generally cleaner shell surfaces. This may be due to a higher shell density at Triabunna; the collection of specimens were from soft sediments between rocky reefs rather than open soft sediments as at Tinderbox; the greater exposure to wave action at Triabunna; or to a range of other environmental factors not considered here.



**Figure 2.** Length frequency compositions of *Maoricolpus roseus* sampled with a benthic sled on the continental shelf off Eastern Victoria and Southern New South Wales (Bax and Williams 2000 and unpublished data).



**Figure 3.** Length frequency compositions of *Maoricolpus roseus* sampled by diver collection at 5-10 metre depths in south-eastern Tasmania in March 2001 (CRIMP unpublished data).



**Figure 4.** Length frequency compositions of *Maoricolpus roseus* sampled by diver collection at 5-10 metre depths at Triabunna in south-eastern Tasmania (CRIMP unpublished data).

**Table 1.** Minimum and maximum shell lengths of immature and mature *Maoricolpus roseus*

Site Date	Triabunna 13-Dec-00	Triabunna 24-Jan-01	Triabunna 7-Mar-01	Tinderbox 17-Jan-01	Tinderbox 13-Mar-01	Gordon 10-Mar-01
Minimum size	35.8	38.3	32.9	29.7	50.9	45.1
Maximum size	65.0	74.4	64.3	90.8	88.3	81.2
Females						
Female minimum size	38.9	39.4	43.3	29.7	54.3	54.4
Female maximum size	65.0	74.4	64.3	90.8	88.2	81.2
Minimum size mature females without egg capsules	#	39.2	0	47.2	0	54.4
Maximum size mature females without egg capsules	#	74.4	0	90.8	0	81.2
Minimum size with embryos	41.9	54.1	0	63.9	0	0
Maximum size with embryos	65.0	71.8	0	78.4	0	0
Males						
Male minimum size*	35.8	38.3	32.9	39.6	50.9	45.1
Male maximum size*	64.3	61.6	62.1	87.5	74.6	73.4
n immature females	#	0	0	2	0	0
n mature females without egg capsules	#	60	57+	28	55	30
n with egg capsules	10	13	0	3	0	0
n male	60	42	53	76	68	28
n female	41	73	57	33	55	30
n Total	101	115	110	109	123	59

# not measured, \* all males possessed sperm, + female gonads regressed/shrunken.

Data not shown for n=6 Tinderbox samples collected 27/11/00, 3 male, 3 female, 2 with egg capsules.

### 4.3 Reproduction

Embryonic development in *Maoricolpus roseus* may be direct or indirect. If development is direct then the veliger stage occurs within the egg capsule, the egg capsules being retained by the adult, until either immediately before or immediately after the young hatch as crawling juveniles (Pilkington 1974; Lieberman *et al.* 1993). However, a review of the Turritellidae (Marwick 1956) suggested that the multispiral protoconch (3-4 whorls) indicates a long pelagic existence in the veliger stage (indirect development). A pelagic existence for the veliger stage would enable widespread current-enhanced dispersal of *M. roseus*; release of crawling juveniles would imply limited environmental dispersal.

Our laboratory observations indicate *M. roseus* has separate sexes with both males (red-brown gonads) and females (yellow-orange gonads) present across the size range sampled (Table 1). In contrast, the native *Gazameda gunnii* is a protandrous hermaphrodite so the larger size individuals are female.

*M. roseus* male gonads examined from Triabunna and Tinderbox had active sperm throughout December-March and November-March, respectively. The sperm are biflagellate with extremely long flagella (Figure 5) similar to other turritellid species. *M. roseus* female gonads were enlarged from November to January at both sites. However, females from Triabunna in March had regressed gonads while the Tinderbox females' gonads were still plump (Table 1).

Released sperm is taken up by the female on the inhalant current (Allmon 1988). Eggs are deposited within egg capsules (~1 mm diameter) (Pilkington 1974) and are retained as a conspicuous yellow mass within the female's mantle cavity (Figure 6). Egg capsules were present in females from at least November 2000, when sampling started in this study, until the following January (~1.3 mm diameter). February was not sampled and no egg capsules were

found in March (Table 1). Fertilised eggs (not observed) developed to an early stage embryo (~50 µm) (observed December-January) through to a trochophore stage (75-150 µm length) (Figure 7) (observed November to January) to a veliger (100-200µm in shell length, reaching 1.5 whorls) (observed November to January). Trochophores and veligers were mobile within the egg capsules. Up to 300+ very early stage embryos were observed within egg capsules in December, but only 50-100 veligers of 100-200 µm size (Figure 8) in January, indicating number of embryos per capsule decreases as embryo size increases.

Early stage embryos in New Zealand *M. roseus* were opaque and bright yellow in colour. Up to 100-150 spherical egg capsules (~1mm diameter) (Pilkington 1974) were found per female in September 1969; late stage veligers were found in March 1973 (Pilkington 1974). Late stage egg capsules were colourless and transparent (~1.40 mm diameter), had ~60 embryos per capsule but only 7-8 veligers. Pilkington (1974) concluded that while many eggs were laid per capsule, most embryos abort and serve as food for the remaining few embryos. Veligers were small, bilobed, with colourless vela and a shell of 1.25 whorls, 300 µm long, tinged pink with a short pointed beak and sculptured with faint spiral rows of ornate minute tubercles (Pilkington 1974). Egg capsules containing veligers were maintained in aquaria for 10 days at 12°C after which the shell was 400 µm long and the velum had a faint line of red pigment along the post-oral ciliary band. A small propodium was present and the tentacles enlarged (Pilkington 1974).

In this study, aquarium-held specimens released the occasional mass of egg capsules with the masses being larger and more diffuse in January than those observed in November-December. Attempts to rear the trochophores and veligers in these egg capsules in beakers of filtered seawater failed despite repeated attempts, due to contamination by ciliates and fungal infections despite daily washing and water changes.

Observations of shells of *M. roseus* have found the protoconch was conic, multispiral somewhat styloform in shape with 2.5 whorls and 400 µm in diameter (Marwick 1956; Lieberman *et al.* 1993). Veliger larvae of the Turritellidae are characterised by initiation of spiral ribs at the protoconch-teleconch boundary (as figured for *Turritella gonostoma* in Allmon (1988)). Examination of plankton samples taken in early March 2001 near Gordon in south-east Tasmania where *M. roseus* occurs in high densities, found larvae with a morphology similar to the above description, 400 µm in size with 3 whorls and the last whorl with 2-3 spiral ribs (F. McEnulty, pers. obs.). These larvae are suspected belong to the superfamily Cerithiacea of which the Turritellidae is a member, whether or not they are *M. roseus* is uncertain and more research is needed to determine this (e.g. genetic sequencing and rearing up of plankton samples).

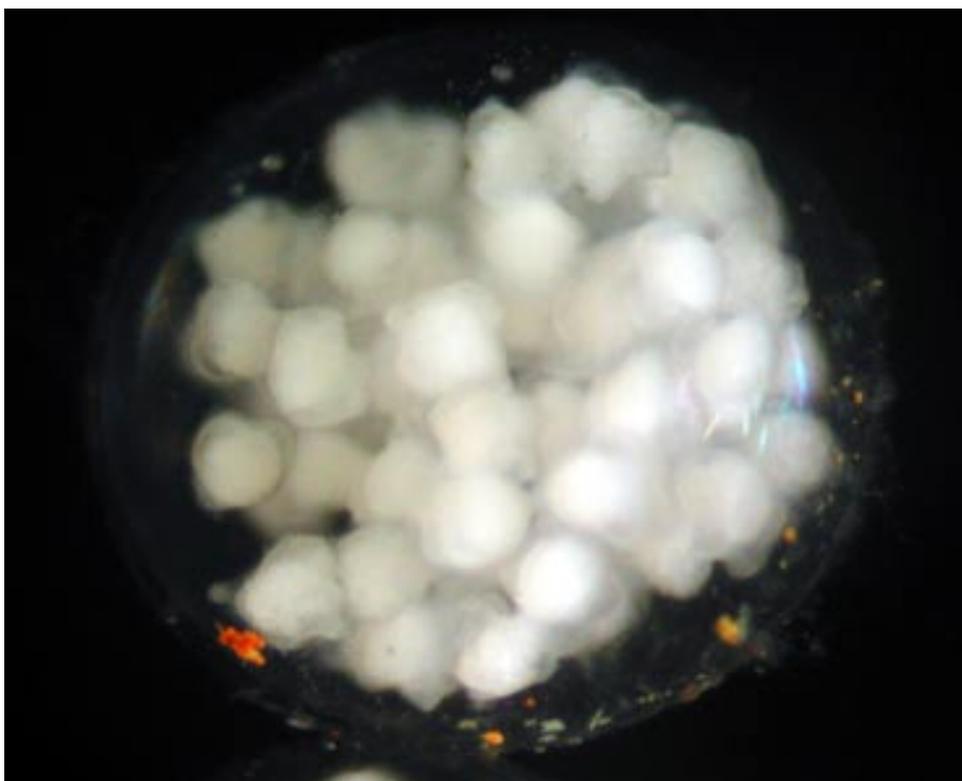
In this study, no egg capsules were found in March 2001, supporting the conclusion that larvae are likely hatched in late summer to autumn with declining temperatures (Scott 1997). This is further supported by the isotopic analysis by Allmon *et al.* (1994) that suggested that (post-larval) shell whorl formation began in the (austral) late winter-earliest spring (Allmon *et al.* 1994).



**Figure 5.** Biflagellate sperm of *Maoricolpus roseus* showing very long flagella



**Figure 6.** *Maoricolpus roseus* with mass of egg capsules protruding from within the mantle cavity (outermost whorl of shell broken away)



**Figure 7.** Trochophore larvae of *Maoricolpus roseus* inside egg capsule (egg capsule 1 mm diam.)



**Figure 8.** Veliger larva of *Maoricolpus roseus* removed from egg capsule (200  $\mu\text{m}$  length)

#### 4.4 Predators

Between 1993 and 1996, 5864 specimens of 100 fish species were sampled for gut analysis (excluding those with evacuated stomachs) on the southeast Australian continental shelf (Bulman *et al.* 2001). Seventeen species were recorded with *Maoricolpus roseus* or remains (Table 2). Frequencies of occurrence were generally low, although they were above 20% for six species, typically those species with strong mouthparts and/or fused mouthparts suited to crushing resistant prey (Bax *et al.* 1999). Occurrence of *M. roseus* parts in gut contents may overestimate actual predation, as in some cases, eg. *Diodon nichthermus*, no shell fragments were found, only opercula that may have been “hoovered” up off the bottom with other benthic matter.

**Table 2.** Presence of *Maoricolpus roseus* in stomachs of demersal fish species sampled on the southeast Australia continental shelf between 1993 and 1997 (Bax and Williams, unpublished data)

Species name	Common name	Stomachs sampled	Frequency of occurrence	Minimum count	Maximum count	Average wet weight (g)
<i>Heterodontus portusjacksoni</i>	Port Jackson Shark	11	1.00	2	20	2.19
<i>Parascyllium ferrugineum</i>	Rusty Catshark	92	0.02	1	2	0.14
<i>Asymbolus sp. D</i>	Orange-spotted Catshark	9	0.44	3	57	0.31
<i>Urolophus cruciatus</i>	Banded Stingaree	130	0.01	1	1	0.01
<i>Myliobatis australis</i>	Southern Eagle Ray	8	0.50	1	40	2.61
<i>Chelidonichthys kumu</i>	Red Gurnard	20	0.10	1	3	0.31
<i>Neoplatycephalus richardsoni</i>	Tiger Flathead	229	0.00	1	1	0.38
<i>Nemadactylus macropterus</i>	Jackass Morwong	328	0.00	1	1	0.00
<i>Notolabrus tetricus</i>	Blue-Throated Wrasse	9	0.33	2	4	1.05
<i>Pseudolabrus psittaculus</i>	Rosy Wrasse	12	0.17	1	4	0.22
<i>Ophthalmolepis lineolatus</i>	Maori Wrasse	11	0.09	2	2	0.12
<i>Kathetostoma laeve</i>	Common Stargazer	15	0.07	1	1	0.01
<i>Synchiropus calauropomus</i>	Common Stinkfish	121	0.06	1	19	0.10
<i>Parika scaber</i>	Velvet Leatherjacket	66	0.02	1	1	0.00
<i>Meuschenia freycineti</i>	Six-Spined Leatherjacket	71	0.28	0	94	0.75
<i>Diodon nichthermus</i>	Globefish	103	0.40	0	34	1.08
<i>Allomycterus pilatus</i>	Deepwater Burrfish	20	0.05	2	2	0.19
	TOTAL	1,255	0.08			

Countersunk boreholes indicative of predation by Nactidae gastropods have been observed in Tasmanian *M. roseus* shells of various lengths and on various whorls. Smooth straight-sided boreholes, often along suture lines of the shell indicative of Muricidae gastropods have been observed at a lower frequency (Scott 1997). Similar frequencies of predation by these two boring families were found for *Turritella leucostoma* and *T. gonostoma* in the Gulf of California (Tull and Bohning-Gaese 1993). The nactid species *Polinices didymus* and *P. conicus* and several muricid species have been collected in subtidal grab samples along with *M. roseus* in the D'Entrecasteaux Channel (C. Macleod, TAFI, pers. comm.). The muricid gastropod *Xymene ambiguus* eats *M. roseus* in New Zealand (Allmon *et al.* 1994) and the fasciolariid gastropod *Pleuroploca australasiae* has been observed feeding on *M. roseus* through the aperture (enveloping prey) in Tasmania (Edgar 2000 and K. Gowlett-Holmes, pers. obs.).

Peel and repair scars indicate predation by decapods, seastars, and octopus. The seastars, *Uniophora* spp. and *Patiriella regularis* and a number of unidentified stingrays eat *M. roseus* in Tasmania, while the seastars *Luidia* and *Astropecten* eat native turritellids in southern Australian waters (Allmon *et al.* 1994; F. McEnulty and K. Gowlett-Holmes, pers. obs.). In New Zealand, the red cod *Pseudophycis bachus*, the smoothhound *Mustelicus lenticulatus* and the eleven-armed seastar *Coscinasterias calamaria* eat *M. roseus* (Allmon *et al.* 1994).

## 5 IMPACTS

*Maoricolpus roseus* is so abundant in some areas that the benthic habitat has been altered from one of fine sand or mud to one with a dense cover of live and dead shells and faecal pellets (C. MacLeod, TAFI, pers. comm. in Scott 1997). It is also suggested that the mucus produced by turrnellids during faecal deposition and for sediment consolidation during burial, not only consolidates the sediments but also leads to an increase in the bacterial load. This may impact larval settlement and post settlement survival of a variety of benthic organisms.

The impacts of dense populations of filter feeding *M. roseus* on native species have yet to be substantiated. Native screwshells in Tasmania, primarily *Gazameda gunnii*, as well as commercial scallop species have declined in abundance since the appearance of *M. roseus* (unsubstantiated comment in Allmon *et al* 1994; Caton and McLoughlin 2000). The scallop fishery in Tasmania first became established in the D'Entrecasteaux Channel in the early 1900's. During the 1950's the fishery shifted to the east coast of Tasmania and not long afterwards the Channel fishery collapsed (after being on the verge of collapse for decades). It is unclear whether the expansion of *M. roseus* throughout the region contributed to the crash or whether it resulted from severe overfishing in the prior 50 years. When scallop catches in Port Phillip Bay declined due to overfishing in 1969, fishermen from Victoria and Tasmania moved to Bass Strait, off Lakes Entrance in 1970 and later, off Flinders and King Islands (Gwyther *et al.* 1991). The Furneaux region of Bass Strait became depleted of scallops in 1984 (coinciding with the first report of *M. roseus* in the area) due to a lack of control over fishing pressure (Gwyther *et al.* 1991) and beds have yet to recover despite more rigorous fishing legislation (Caton and McLoughlin 2000).

If *M. roseus* contributed to the decline of native screwshells and scallops it was probably not by predated the larvae (filtered from the water column during feeding). *G. gunnii* larvae hatch as crawling juveniles direct from the female mantle cavity (Scott 1997) and scallop larvae would probably be too large to be consumed directly by *M. roseus* which it thought to feed on microalgae and fine particulate matter.

*M. roseus* could possibly reduce numbers of native screwshells and scallops via direct competition for food and space as they are all filter feeding species with overlapping habitat requirements. The empty shells of *M. roseus* that are used as homes for hermit crabs in New Zealand (Paguridae: *Pagurus cooki* and *P. spinulimanus*) (Rainer 1981) and Australia (Paguridae: unidentified spp. and Diogenidae: *Dardanus* sp.) (CRIMP unpublished data) could also indirectly impact other benthic organisms. *M. roseus* shells are robust and together with their high abundance provide a novel habitat for hermit crabs in sandy sediments previously unavailable to them in areas occupied by scallops in eastern Tasmania. It has not been demonstrated that predation by hermit crabs impacts native screwshells and scallops. However, the abundance of *M. roseus* is so high and their shells so persistent, that even a low level of predation could be expected to have a large impact on the post-settlement survival of native screwshells and scallops.



## 6 TRANSLOCATION VECTORS

Planktonic larvae could explain the rapid spread of the screwshell from the D'Entrecasteaux Channel up the Australian east coast, but not the initial colonisation event from New Zealand as the trans-Tasman currents flow west to east (Garrard 1972). Planktonic larvae could also be transported in the bilge or ballast water of vessels from New Zealand (dependent on the duration of the larval stage). However, it is still unclear if *M. roseus* even has a planktonic larval stage. Adult shells could have been transported with mud and other debris collected during maritime operations such as dry ballasting, bottom trawling or dredging. It is unclear how big a role (if any) Tasmania's fishermen have played in expanding the distribution of *M. roseus* around the State. Potential methods include specimens caught up in dredges and relocated to the next fishing site or amongst oysters dredged in one location and then laid to the seabed in another location to depurate before human consumption).

Several other marine species of New Zealand origin are also introduced to Tasmania (as mentioned in introductory section) and initially were only found in the D'Entrecasteaux Channel region as was *M. roseus* (Dartnall 1967). Of these species, the ones with planktonic larvae have become well established and more widely distributed eg. *Petrolisthes elongatus* (Recherche Bay to Devonport, including the East coast and Flinders Island), *Cancer novaezelandiae* (D'Entrecasteaux Channel to Devonport including the East coast and Flinders Island, also mainland Australia: Gippsland Lakes, Victoria and Eden, New South Wales), and *Venerupis largellerti* (Southern and Eastern Tasmania, Derwent River to Pirates Bay, Coles Bay and Ansons Bay). *Maoricolpus roseus* has a similar distribution to these species with planktonic larvae supporting the theory of a planktonic phase in its lifecycle.

However, commercial scallop fishermen from the D'Entrecasteaux Channel area reported that *M. roseus* was commonly dredged there from at least 1938, and was more common then in the southern end of the Channel than further north. This may suggest that *M. roseus* was introduced further down the Channel region perhaps with semi-dry ballast dumped overboard by New Zealand timber boats or with imported oysters dumped overboard down the channel. The actual vector for introduction of *M. roseus* to Tasmania remains unknown.



## 7 CONCLUSIONS

Introduced marine pests have caused considerable environmental and economic damage in Australian nearshore waters. However, only one introduced marine pest, *Maoricolpus roseus*, has colonised the open continental shelf and the potential impacts of this species on native biodiversity and benthic habitat are only gradually becoming recognised. Despite its widespread distribution in New Zealand and south-eastern Australia, little is known on the biology, ecology and impacts of *Maoricolpus roseus*. How *M. roseus* was introduced to Australia remains unknown and the current known distribution is based on anecdotal evidence, beach-collected material and a few unrelated surveys, with absences in Figure 1 primarily due to a lack of survey data.

The limited distributional data that are available indicate that *M. roseus* is impacting a larger geographical area of the Australian coast than any other introduced marine species, and its abundance in those areas where it occurs suggests its impacts may be substantial. Impacts are not confined to the live animal, as its empty shell provides suitable habitat for native hermit crabs that may have a secondary impact on native fauna, especially newly settling larvae.

We need to understand the mechanisms that have led to the dispersal of *M. roseus* from southern Tasmania to Sydney in ~70 years. If this is natural dispersal in water currents then there is a possibility that *M. roseus* will not colonize the large continental shelf of the Great Australian Bight, because currents through the Bight run predominantly west to east. If however, dispersal has been assisted by other vectors (as was the first introduction to Australia), then there is an immediate risk that *M. roseus* can be spread to the Bight by those same vectors.

The Great Australian Bight, extending 2500 km from Western Australia through South Australia to Western Victoria sits off the world's longest east-west shoreline. The continental shelf of the Bight extends to 200km offshore and includes marine protected areas set aside for the conservation of benthic communities and whales. It is the site of active finfish and shellfish fisheries as well as some of Australia's most profitable aquaculture operations. While we have the means to reduce the risk of *M. roseus* colonizing these areas, it is incumbent on us to act and to act quickly. Understanding the mechanisms that led to the current distribution of *M. roseus* would be an important first step.



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## APPENDIX 1. MUSEUM COLLECTIONS AROUND AUSTRALIA

### South Australian Museum, Adelaide (SAM)

W.L. May Collection – William May was a very keen conchologist based in Hobart, who collected extensively, particularly in southeastern Tasmania, including a lot of dredging. His collection was the basis of his booklet “An Illustrated Index of Tasmanian Shells” published by the Government Printer, Tasmania in 1923, a comprehensive coverage of all molluscs known to occur in Tasmanian waters at that time. May’s primary types were mainly deposited in the Tasmanian Museum and Art Gallery collections, but his main collection was purchased by Sir Joseph Verco and donated to the South Australian Museum in Adelaide. There are no specimens of *Maoricolpus roseus* in the May Collection in SAM, and there is no listing of the species in his Index. May was a very thorough worker, and the absence of this species in the collection indicates that the species was not present when May was collecting, and supports the view that the species arrived in Tasmanian waters post 1920.

Other South Australian Museum material – of more than 40 lots of *M. roseus* in the SAM collections, only four are from Tasmania – an unlocalised lot of dry shells labelled “Tasmania” with no other data, and three live collected lots in spirit. One of the spirit lots (SAM D19059) is from off Babel Island, east of Flinders Island in Bass Strait, dredged in 40m by the FRV “Soela” on 11 October 1984 and contains 7 specimens. This is the earliest authenticated record of this species from Bass Strait. The other two lots were both collected on SCUBA in July 1991, one from Frying Pan Point, Port Arthur, and the other from Tinderbox. Both of the latter lots were photographed in situ, slides of which are in the SAM Photoindex.

### Tasmanian Museum and Art Gallery, Hobart

There are over 50 lots of *M. roseus* from Tasmanian waters in the TMAG collections, all dry. The earliest samples are those referred to by Greenhill (1965), from the southern D’Entrecasteaux Channel dredged live in 1963 (TMAG E3851 & 18328/E2804). There are several other lots of specimens dredged from the D’Entrecasteaux Channel during the 1960’s, and another dredged lot collected in 1977 from Schouten Passage on the east coast, but all the remaining specimens in the collections were beach-collected.

From the beach-collected records, the most southerly record of *M. roseus* is a lot from Southport (1970), and also from Cloudy Bay on Bruny Island (1979). The earliest records from the Derwent Estuary and Hobart are from Tinderbox (1981) and Roaring Beach, South Arm (1981), Blackmans Bay (1985), Battery Point (1986). The earliest record from the eastern side of Bruny Island is from Adventure Bay (1981). There are no records from the Port Arthur area until 1982. While dredged samples were recorded from Schouten Passage in 1977, the earliest beach-collected samples from the general area were from 1983 from Coles Bay and 1984 from Wineglass Bay. The earliest records of beach-collected material from the Furneaux Group in eastern Bass Strait is 1990.

### Australian Museum, Sydney

Only part of the collection was accessible, and as it was possible for computerised records to be purchased, the only lot of *M. roseus* checked in detail was the one from southern Queensland mentioned by Wilson (1993). This is a single specimen collected dead by Tom Darragh, and the locality is listed as dredged off Stradbroke Island. Some of the Darragh specimens in the AM have been shown to have erroneous data, probably having been mixed up at some time. As this is an isolated sample, dead collected, from an area where no other examples of this species have been found, at this stage, it should be regarded as a very doubtful record, probably with incorrect locality data.

There are no specimens of *M. roseus* in the AM from NSW or Victoria. All Australian specimens of this species in the AM were from Tasmania, mostly beach-collected and dating from post 1970. None of the dry collection material examined predates the TMAG samples. From discussions with the curatorial staff, there may also be some dredged specimens from Bass Strait from FRV “Soela” bycatch, dating from the mid-late 1980’s, but this could not be confirmed as that part of the collection was not accessible. The collection also contained many samples of this species from various parts of New Zealand.

#### **Museum of Victoria, Melbourne**

The collection was being moved and was not accessible. From catalogue records and discussions with the curatorial staff, there are no specimens of *M. roseus* from mainland Australia in the MoV. All Australian specimens in the collections were from Tasmania, and like the AM, mostly beach-collected and dating from post 1970, although some of the dredged D’Entrecasteaux Channel samples from the early 1960’s are also lodged in the MoV. None of the samples predate the TMAG samples. The collections also contained many samples of this species from various parts of New Zealand.

## APPENDIX 2: DATA ON REPRODUCTION FOR OTHER SPECIES IN THE FAMILY TURRITELLIDAE

Turritellid ecology is heterogeneous and different environmental variables may control distribution and abundance in different species and locations (Allmon *et al.* 1994). Turritellids do not exhibit determinate growth, but only large individuals are found associated with egg masses (Allmon 1988; Allmon *et al.* 1992). Most of the Turritellidae display seasonal reproduction (Pilkington 1974; Allmon 1988) and a variety of reproductive modes have been observed in the Turritellidae. Some species display ovoviviparity ie. retain eggs and juveniles within the shell of the mother for some time after their emergence from the egg (i.e. brood larvae). In females a portion of the mantle cavity may be modified into a brood pouch (Carrick 1980). This affords greater protection for the developing young. Other turritellid species display oviparity (lay egg capsules on the external substrate, outside the parent eg. in a mass of spawn). In both reproductive modes the young can be released from the egg in one of two forms of development. Either as planktonic veligers that settle after some time in the water column and metamorphose into the adult form (indirect development) or the veliger stage is passed through within the egg capsule to release crawling young onto the substrate (direct development).

In turritellids with a planktonic larval stage, it is generally only a short period since their size and organisation is the same or nearly the same, at the moment of hatching and at the moment of settling. The larvae may be able to feed in the plankton but it is likely in certain conditions they may settle without having taken in food during their short pelagic life. Feeding is of secondary importance to them, while the spreading of the larval stock and the chance of finding a suitable substratum seem to be the main requirements. The eggs are usually small or medium sized, but large eggs may also develop in this way (Thorson 1950).

### A2.1 Ovoviviparous turritellids

#### A2.1.1 Extant ovoviviparous turritellids

*Gazameda gunnii* Reeve, 1849 has direct development of the larvae, juveniles are released from within a specialised brood pouch in the adult shell as crawling juveniles (2.6-3.0mm size). Eggs are large (960-1000µm) and brooding time is 200 days in New South Wales, Australia (the longest known for prosobranch gastropods) (Peile 1922; Iredale 1924; Carrick 1980). Oviposition occurs during January and release of metamorphosed juveniles occurs during the maximum availability of phytoplankton in August –January (Carrick 1980). *G. gunnii* is a protandrous hermaphrodite, the eggs produce only male individuals. The males undergo a metamorphosis at a later stage to an individuals displaying both male and female characteristics, finally developing into (and remaining) a mature female (Allmon 1988). Hence males are substantially smaller than females (always in protandric hermaphrodites). Reproduction begins when the females are 2.5-3 years of age and is repeated through a lifespan of 6-7 years (Allmon *et al.* 1992). Larger individuals have more eggs. Isotopic analysis found the estimated lifespan of *G. gunnii* is 6-7 years (Allmon *et al.* 1994).

*Vermicularia spirata* R.A. Philippi, 1836 has indirect development as brooded embryos develop into veligers that are released from the adult shell to a brief planktonic larval phase. Juveniles then settle into a free-living stage and then cement themselves to various hard substrata to become uncoiled adults (Bieler and Hadfield 1990).

#### A2.1.2. Fossil records of ovoviviparous turritellids (taken from Marwick (1971))

Records of ovoviviparity are more common in the fossil species than in living species and palaeontologists have found preserved specimens with numerous immature shells within the adult shell

*Turritella cumberlandica* Conrad, Miocene, Maryland, USA (Burns 1899)

*T. indentata* Conrad, Miocene, Maryland, USA (Burns 1899)

*T. alumensis* Mansfield, Miocene, Florida, USA (Sutton 1935)

*T. pilsbryi* Gardner, Miocene, Virginia, USA (Gardner 1948; Palmer 1958)

*T. alticostata* Conrad, Miocene, Florida, USA (Antill 1976)

*Zeacolpus taranakiensis* Marwick, Miocene, New Zealand (Marwick 1969)

## **A2.2. Oviviparous turritellids**

### **A2.2.1. Examples of oviviparous turritellids**

*Turritella gonostoma* Valenciennes, 1832 lays eggs in masses of 200-300 egg capsules (2-3mm diameter) in shallow water in February- April (late winter-early spring), which hatch as veligers that undergo a 2-3 week planktonic larval stage (indirect development). Just prior to hatching egg capsules contain 1-12 veligers (the average is 3); Figures 6-7 in Allmon *et al.* (1992). Veligers added at least one full whorl to the shell during their planktonic period and newly settled juveniles has 2.5 whorls. Large, apparently adult individuals are often found associated with egg masses, either individually or in large aggregations or 100-1000's (Allmon 1988). It lives in shallow water <5m where average monthly temperatures range from 13.8°C (Jan) -29.4°C (August). Higher densities being observed between December – May. The most rapid seasonal growth occurs during the warmest months, particularly in the first year of life, but estimated lifespan is only 2-3 years in the Gulf of California (Allmon *et al.* 1992).

*Turritella variegata* (Linnaeus, 1758) was thought to undergo indirect development of the larvae that develop from spawn on substrates such as pebbles and resemble a bunch of grapes in the Caribbean coast of Columbia. The spawn mass has 200-300 egg capsules each containing 16-18 yellowish eggs. After 5 days actively swimming veligers are seen within the capsule. After 16-18 days the veli-concha will hatch that can swim as well as crawl. After another 2-3 days the veli-concha have completed their metamorphosis and are able to crawl only (Bandel 1976). However, recent work by Lieberman *et al.* (1993) suggests that *T. variegata* has non-planktonic larval stages (Scott 1997).

*Turritella communis* Risso 1826 was thought to undergo indirect development where encapsulated eggs attached to the substrate develop into veligers from which they escape to a brief planktonic larval phase (<1 week; Kennedy and Keegan 1992, 2-3 weeks Allmon 1988), in British Isles (Ireland, Scotland). Eggs are 139µm diameter and are found in egg capsules with ~28 eggs (Lebour 1933; Yonge 1946; Kennedy and Keegan 1992; Kennedy 1995). However, recent work by Lieberman *et al.* (1993) suggests that *T. communis* has non-planktonic larval stages ie. direct development (Scott 1997). Sexes are separate, with (aphallic) males releasing sperm into the water for transferral to the female's mantle cavity via the inhalant current (Allmon 1988). Wright (1956) in Allmon *et al.* (1992) observed well developed gonads in individuals as small as 23mm in length (maximum size is 45mm), which according to growth curves by Cadee (1968) in Allmon *et al.* (1992) corresponds to an age of less than one year.