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Demography of *Pristipomoides multidens* in northern Australia and a comparison within the Family Lutjanidae with respect to depth

Thesis submitted by

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For the degree of Doctor of Philosophy

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within the

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Statement on the Contribution of Others

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Abstract

Lutjanids are an important group of perciform reef fish distributed over a wide depth range throughout the world's tropical and sub tropical oceans. It has been noted by Newman and Williams (1996) that within this complex there is a separation of genera with respect to depth. Shallower waters <100 m are dominated by the genera *Lutjanus, Aprion, Macolor, Symphorichthys,* and *Symphorus*, while in the intermediate depths (100-200 m) *Pristipomoides,* and *Paracaesio* dominate, and in the deeper waters >200 m *Etelis* are more prevalent. Therefore the lutjanid complex offers a unique opportunity to observe whether there is a distinction in life history characteristics of genera within the same family with respect to different depth zones and consequently different environmental influences.

While many shallow water species have been well studied, there is a paucity of information on species in the intermediate and deeper waters where research is expensive and logistically difficult. The lack of information is a significant problem for many developing countries for which lutjanids are an important source of export revenue as well as food. In developed countries, attracting funding for small-scale "boutique" fisheries is very difficult, despite the recognised need to manage all fisheries in a sustainable manner. Therefore, in the absence of research data, managers and scientists are forced to use proxy values, but how valid is this approach?

To examine this question, I undertook a comparison of the demography of genera within the Family Lutjanidae within different depth ranges; shallow (<100 m), intermediate (100-200 m) and deep (>200 m). I conducted a detailed study of *Pristipomoides multidens* (intermediate depth range) and compared findings from this

study with information published for lutjanids from other depth ranges. This provided a framework within which to assess whether it is acceptable to use proxy values, and whether proxy values should preferentially be from lutjanids inhabiting the same locality possibly from different depth ranges, or the same depth range even if the information is from a different region.

The key findings were:

Significant differences are evident in age, growth and reproductive parameters for genera from the different depth ranges. Small shallow water lutjanids appear to show greater variability in growth across smaller scales compared species in intermediate and with deeper waters. A possible explanation for this observation may relate to the tendency for small lutjanids to be more reef-associated and hence their growth more strongly influenced by localised conditions compared with lutjanids in intermediate and deep waters.

The lutajnids (*Pristipomoides multidens*, *Lutjanus malabaricus* and *L. erythropterus*) in my study showed a general trend for a greater mean length at age for the Timor Sea when compared with the Arafura Sea. Likewise, my results showed, longevity (defined by the upper 20% of ages for a species) was also greater for fish from the Timor Sea when compared with those from the Arafura Sea. This is possibly due to the differences in depth as the Arafura Sea is considerably shallower than the Timor Sea. Samples taken from the Arafura Sea were caught at the 50-60 m depth range, while samples from the Timor Sea were taken in the 100-150 m depth range. However, fishing gear selectivity may confound these observed differences. Samples from the Arafura Sea were taken by trawling, and it is possible that larger, stronger fish may be able to swim faster than the trawled nets and therefore avoid capture. Timor Sea samples were taken by trap and dropline methods.

Lutjanids appear to exhibit different spawning patterns with respect to depth zonation. Shallow water lutjanids favour a restricted summer peak in spawning activity, compared with lutjanids inhabiting intermediate and deeper waters, which appear to show a more protracted spawning season with a peak in activity during summer months and in some regions two spawning peaks are observed. In my study, I observed a protracted summer spawning period for *P. mutidens*, which was consistent with findings for this species by Brouard and Grandperrin (1985), and *P. filamentosus* (Kikkawa 1984).

By comparing the results from my detailed study of *P. multidens* with lutjanids from other depth ranges I explored the validity of using proxy values for fisheries management for data-poor situations, and concluded that caution is needed in using proxy values from other lutjanids in stock assessment modelling. Similar species within the same genera or the same location should not automatically be chosen as a proxy. However, underlying patterns exist within populations and by exploring these relationships, information can be utilised from data-rich fisheries to assist in developing appropriate management strategies for data-poor fisheries.

In conclusion, my study has shown that within the lutjanid complex there are different life-history strategies for lutjanids inhabiting different depth ranges, which are influenced by the environmental conditions within these depth ranges. However there are also confounding effects such as fishing and genetics which may also contribute to observed demographic patterns.

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Chapter 1. General Introduction

Lutjanids are an important group of perciform reef fish distributed over a wide depth range throughout the world's tropical and subtropical oceans. Many species are fished commercially, but it has been the shallow water members of this group, which have been more heavily targeted. However, over-exploitation of inshore resources combined with advances in technology (in both efficiency and affordability), have resulted in a greater interest in developing the deeper water fisheries (Pauly et al. 2003).

While many of the shallow water species have been well studied, there is a paucity of information on species in the intermediate and deeper waters where research is expensive and logistically difficult. This is a problem for many developing countries for which lutjanids are an important source of export revenue as well as food for the local population. Similarly in many developed countries, attracting funding for developing fisheries, small–scale fisheries, non-target species and low values fisheries is very difficult, despite the recognised need to manage all fisheries in a sustainable manner.

To overcome the limitations that these data-poor fisheries present, there has been a trend towards using information from data-rich fisheries to provide additional information for assessment (Punt et al. 2005). The use of proxy values for stock assessment can be found during the early development of Australia's northern fish resources. In the absence of specific life history information for the key snapper species (including *Pristipomoides multidens*), biological values were used for *Lutjanus malabaricus* from the North West shelf (Ramm1994).

Although it may seem appropriate to use the biological values of a species within the same family as a proxy, how valid is this approach? Do species throughout the different depth ranges have similar life history characteristics? Have lutjanids developed specialised life history characteristics which are specific to the environment in which they live?

To examine these questions further, I have undertaken a comparison of the demography of genera within the Family Lutjanidae with respect to depth distribution, as different genera dominate different depth regimes. This provided an opportunity to look at different life history strategies within the different depth ranges. I did this by conducting a detailed study across spatial and temporal scales of *Pristipomoides mutidens*, which is found in greatest abundance in the intermediate depth range (100-200 m), and compared findings from this study with the demography of lutjanids in other depth ranges from the literature and a study of lutanids (*Lutjanus malabaricus*, *L. erythropterus*, *L. sebae*) which I collected in the same study area, but within a different depth range.

1.1. The lutjanid complex

The family Lutjanidae represents a diverse group of fish consisting of 17 genera and 103 species (Allen 1985). This family is found in a wide range of depth and habitat distributions, and consequently is exposed to a range of environmental conditions.

The four sub-families are Etelinae, Apsilinae, Paradichthyinae and Lutjaninae, which consist of the following genera:

Etelinae - *Aphareus*, *Aprion*, *Etelis*, *Pristipomoides*, *Randallichthys*

Apsilinae - *Apsilus*, *Lipocheilus*, *Paracaesio*, *Parapristipomoides*

Paradichthyinae - *Symphorichthys*, *Symphorus*

Lutjaninae - *Hoplopagrus*, *Lutjanus*, *Macolor*, *Ocyurus*, *Pinjalo*, *Rhomboplites*

Primarily inhabiting marine waters, some species have adapted to live in freshwater, and a number of juvenile species inhabit brackish estuaries (Allen 1985).

Within the lutjanid complex there is a separation of genera with respect to depth. Shallower waters (<100 m) are dominated by the genera *Lutjanus*, *Aprion*, *Macolor*, *Symphorichthys* and *Symphorus*, while in the intermediate depths (100-200 m) *Pristipomoides* and *Paracaesio*, dominate, and in the deeper waters (> 200 m) *Etelis* is more prevalent (Newman and Williams 1996a). Ralston and Polovina (1982) found similar genera segregated by depth in the Hawaiian fisheries.

Therefore the lutjanid complex offers a unique opportunity to observe the effects of depth partitioning, on the life history and biology of genera found within different environmental conditions.

1.2 Changes in environmental conditions with depth

With increasing depth there is a decrease in temperature, light and an associated decrease in food availability (Cailliet et al. 2001). These differences in environmental conditions with depth, result in fish evolving characteristics best suited to the environment they inhabit (Lowe-McConnell 1977). This is reflected in its shape, body structure and physiology. For example, body shape reflects a way of life, with the open water species having a more fusiform shape suited to chasing prey, than the deeper bodied reef-associated species, whose body shape enables it to maintain its position in turbulent conditions (Lowe-McConnell 1977). Behavioural differences also reflect different habitat associations. The open water species have highly developed schooling tendencies, whereas those associated with reefs tend to be more solitary, schooling only when travelling, or in the case of nocturnal species, during periods of inactivity during the day (Lowe-McConnell 1977).

Therefore, one would expect genera within the lutjanid complex to reflect physical characteristics best suited to the different environmental conditions they inhabit within the different depth partitions.

1.3. *Pristipomoides multidens study*

In this study I will investigate whether the more stable environment inhabited by *Pristipomoides multidens* leads to a greater stability in demographic patterns compared with shallow water lutjanids. I will examine the pattern and magnitude of demographic variation in age, growth, and reproduction of this species.

This study was conducted across northern Australia in the Northern Territory sectors of the Timor and Arafura Seas (Figure 1.3.2) with additional samples obtained from 6 sites in eastern Indonesia (Figure 1.3.1).

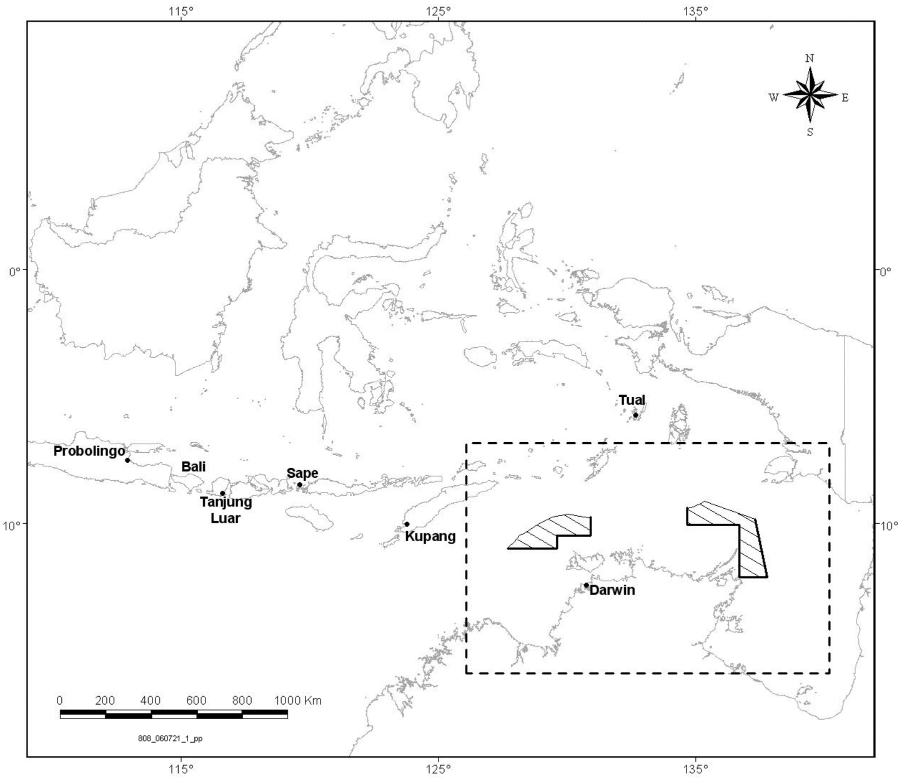


Figure 1.3.1. Sampling sites for joint Australian-Indonesian project. Australian sites (boxed area) are shown in more detail in Figure 1.3.2.

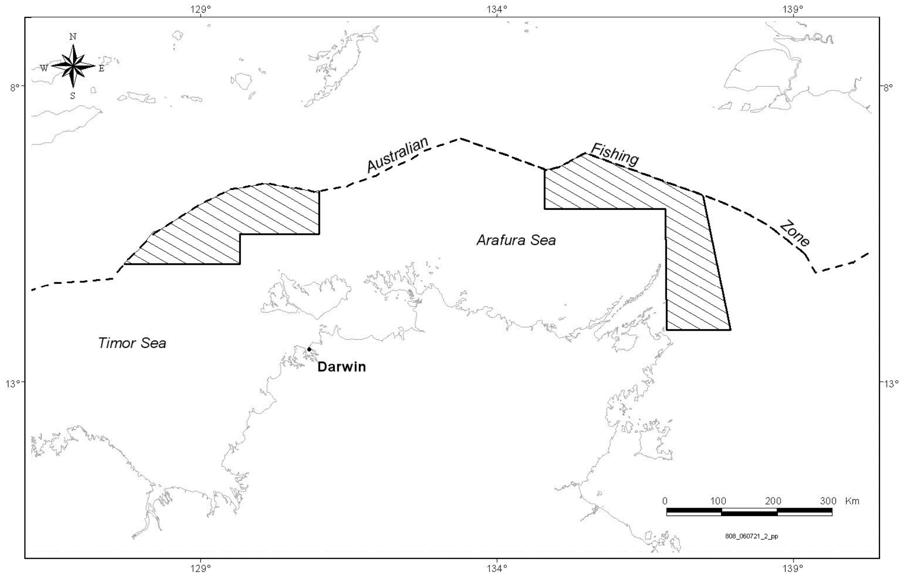


Figure 1.3.2. Expanded view of boxed area in Figure 1.3.1. Australian sampling sites are shown as shaded areas

1.4. Geomorphology and bathymetry of the study area

1.4.1. Arafura Sea

The Arafura Sea is a shallow sea (generally less than 65 m) extending from Australia's northern coastline to the Outer Banda Arc and the coast of Irian Jaya to the north; to Torres Strait in the east; and the Gulf of Carpentaria to the south; merging with the Timor Sea in the west (130°E) (Russell and Houston 1989). It is mainly composed of glauconitic sand and calcareous mud (Jongsma 1974). During the last glaciation, the Arafura Sea together with the Gulf of Carpentaria and the Torres Strait formed a land bridge connecting Australia to New Guinea.

1.4.2. Timor Sea

The Timor Sea consists of two components; the Timor Trench and the Sahul Shelf. The Timor Trench is a deep depression separating the Australian Continent and the Indonesian island of Timor. At its deepest point it is 3260 m (Van Andel Tjeerd 1967).

The Sahul Shelf is a broad, shallow platform 600-750 km at its widest point (Van Andel 1967), and is thought to be a recently submerged part of the Australian continental shelf (Heywood et al. 1997). Present water depth across the Sahul Shelf ranges from 50-200 m. Submerged carbonate banks, shoals and paleo-river channels are a characteristic feature of this region (DEWHA 2007a). During the peak of the last glaciation, sea levels were 100-140 m below present levels and the entire Sahul Shelf was exposed until 18,000 years ago (Heywood et al 1997). The offshore shoals and carbonate banks are thought to have once been islands along the paleo-coastline which were drowned during the rapid rise in sea level (Lavering 1993).

The origin of these submerged carbonate banks is thought to be related to hydrocarbon seepage and the associated microbial communities dependent upon this seepage; which in turn provided a food source for reef-building organisms (Glenn 2002). A full description of the role of hydrocarbon seepage in the formation of these hydrocarbon banks and their connection with productivity in these offshore areas is found in Section 1.4.3.

Dissecting these carbonate banks are deep paleo-river channels which can be up to 150 km long, 5 km in width and 240 m in depth (DEWHA 2007a). These channels play a significant role in transferring cool, nutrient enriched water between the Timor Trench and the Sahul Shelf by acting as a pathway for currents and tidal flow (DEWHA 2007a). Strong tidal currents found within these channels produce localised upwelling of cooler water as a result of topographic effects, particularly at channel entrances and around areas of high relief (DEWHA 2007b). These localised upwellings probably concentrate planktonic prey thereby attracting *Pristipomoides multidens* and other fish to this area. Similar findings were reported by Ralston et al. (1986), who observed from catch data that *P. filamentosus* occurred in higher density on the upcurrent side of an atoll than on the downcurrent side, while visual observations from a submersible revealed that *P. filamentosus* and *Etelis coruscans* were commonly found near underwater promontories. They hypothesised that this may be due to planktonic prey congregating in these areas as a result of vertical turbulence created when oceanic upcurrents hit underwater promontories of the atoll.

There appears to be a strong link between fish and the carbonate banks and shoals within the Timor Sea, with catches concentrated within the carbonate banks system and paleo-river channels (Figure 1.4.1.). This has been demonstrated by Lloyd and Puig (2009) who found highest commercial productivity (kg/ha) in the geomorphic unit classified as shelf and in the 110-120 m depth range. Commercial productivity (kg/ha) was calculated by dividing the commercial catch within a geomorphic unit by the area of the unit. Geomorphic units were adopted from those used in the National Bioregionalisation program. Bathymetric units were obtained by dividing the fishery into 10 m depth intervals and dividing the catch within a depth interval by the surface area of the interval to give commercial productivity in kg/ha. The commercial productivity for geomorphic units and bathymetry is shown in Figure 1.4.2. It appears that the structure supplied by the carbonate banks and shoals provide suitable habitat and protection for *P. multidens* and other lutjanids.

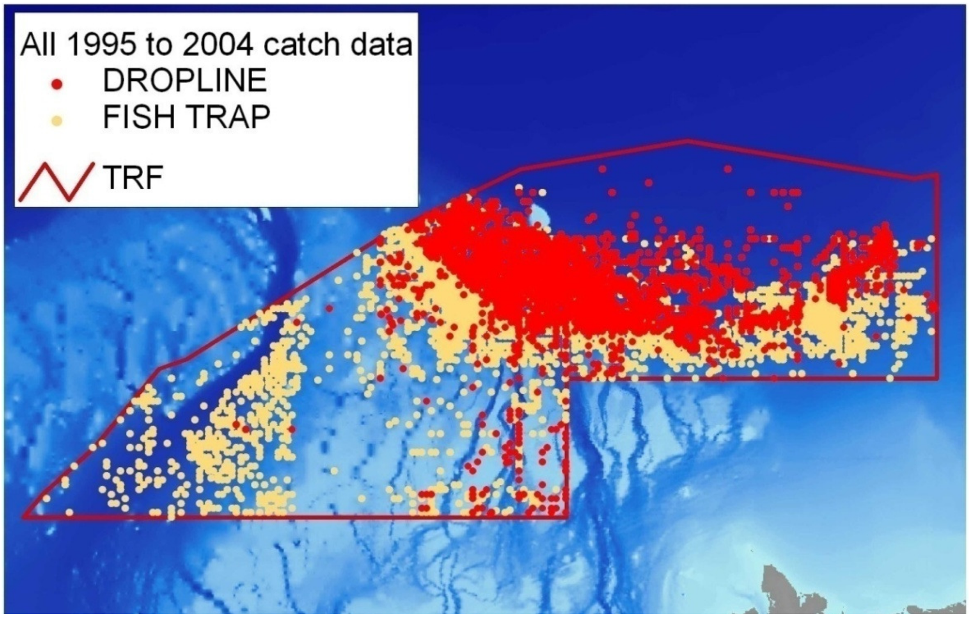


Figure1.4.1. Catch data from the Timor Reef Fishery superimposed upon the bathymetric map. The fishery is contained within the red bounded area (Map reproduced from Lloyd and Puig 2009)

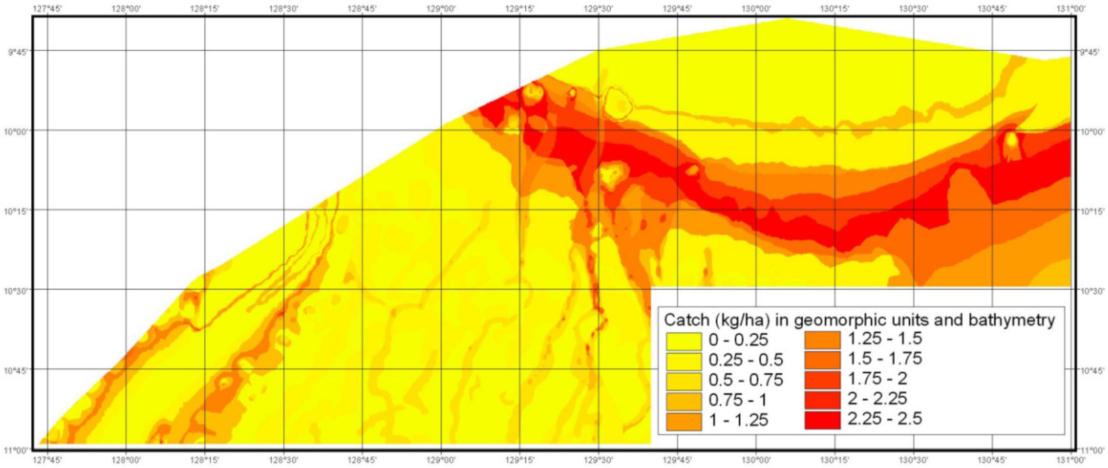


Figure 1.4.2. Commercial productivity (kg/ha) of the Timor Reef Fishery in geomorphic units and bathymetry (Map reproduced from Lloyd and Puig 2009)

1.4.3. Hydrocarbon seeps

O'Brien et al. (2002) propose that development of the carbonate banks and reefs in the Timor Sea was initiated by hydrocarbon seepage through the active migration along fault lines which occurred when the Eurasian and Australian crustal plates collided during the Pliocene period (<5 MaBP). When sea levels are low these gases escape directly to the atmosphere (Glenn 2002). However when sea level is high as it is today, some gases are trapped in the thermocline, but the rest rise through the water column where they are digested by small localised bacterial communities which utilised the hydrocarbons as a food source (O'Brien et al. 2002). This bacterium is a food source for zooplankton (such as foraminifera) and calcareous plants (such as *Halimeda*). When these marine organisms die their skeletal remains settle on the seafloor forming mounds around the mouth of the seeps. These are cemented together by biota such as coralline algae and chemical processes (CEE Consultants 2002). Over time this accumulation of calcareous material forms a steep sided cone which is colonised by coral spores and other reef building biota (Glenn 2002). This process creates bioherms or shoals, which can be millions of years old and have been subject to exposure and re-submergence during rises and falls in sea level (CEE Consultants 2002).

O' Brien et al. (2002) suggest that initial reef colonisation probably occurred during a period of low sea level which allowed sufficient sunlight to reach the seafloor. Rapid growth of the reef followed as ideal conditions for carbonate communities were provided by the rapid collision-related subsidence connected with the Timor Trough formation.

1.5. Oceanography

1.5.1. Indonesian Throughflow

In northern Australia, one of the most important influences in this region is the Indonesian Throughflow (ITF). This is a complex system of currents which links the Pacific and Indian Oceans through the Indonesian seas (Figure.1.5.1). It is responsible for the transfer of heat from the warmer Pacific Ocean to the cooler South Equatorial Current (SEC) in the Indian Ocean, thereby providing an important means of heat and water exchange between major ocean basins. Therefore it is not only an important factor regulating the climate in this region, but also has an important role in regulating global climate (Schneider 1998).

Gordon and Fine (1996) have found that the ITF is dominated by two components. One brings low saline, well-ventilated water from the North Pacific that flows through the Makassar Straits in the upper thermocline. The other component, which flows through the eastern Indonesian seas, brings more saline South Pacific water through the lower thermocline. The major exit passages into the Indian Ocean are the Lombok, Ombai and Timor Straights (CSIRO fact sheet No.64 2004). The majority of ITF flows into the SEC, which is the dominant westward current across the Indian Ocean. The Leeuwin Current, which is responsible for transporting warm, fresh water southwards down the coast, is supplied by a shallow component of the SEC that flows back towards the West Australian coast (CSIRO fact sheet No.64 2004). The ITF is driven by the pressure gradient between the Pacific and Indian Oceans (Wyrtki 1987). The strength of the ITF fluctuates seasonally, reaching a maximum during the south-east monsoon (SEM), between May and September. The ITF is weakest during the north-west monsoon (NWM), normally November to March (Tomczak and Godfrey 1994).

1.5.2. Influence of El Niño Southern Oscillation (ENSO) on ITF

The ITF is influenced by both monsoonal winds and ENSO, which varies on both seasonal and long term time-scales (Gordon and Fine 1996, Meyers 1996). Clarke and Liu (1994) postulate that during the *El Niño* phase, the ITF is weaker than normal as a result of anomalous westerlies along the equatorial Pacific which result in a fall in sea level in the western Pacific. Meyers (1996) found that ITF was a maximum during the *La Niña* period 1988-89 and minimum during the *El Niño* events of 1986-1987 and 1991-1994. Gordon and Fine (1996) also believe the strength of ITF changes in response to the phase of ENSO events, which in turn provides a feedback mechanism to ENSO by influencing the warm water pool across the Pacific. During the *El Niño* phase this pool of water moves southwards thereby lessening it's presence at the throughflow entrances. Godfrey (1996) suggests that complex feedback mechanisms probably exist between the monsoons, ENSO events and the physical dynamics within the Indonesian seas in relation to sea surface temperatures, winds and precipitation.

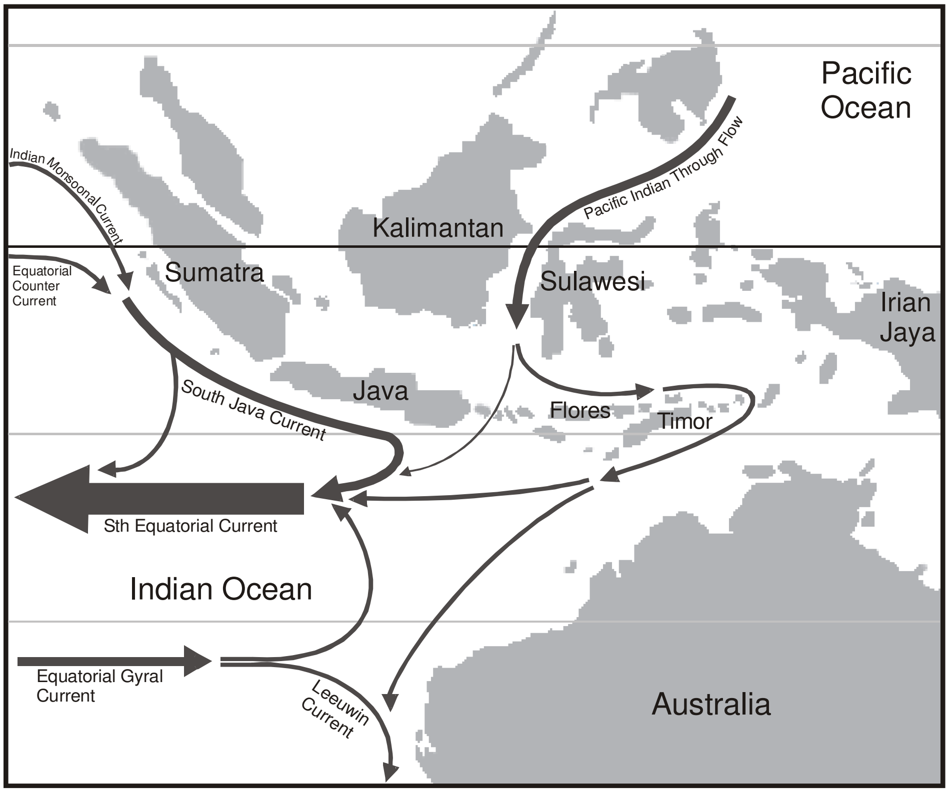


Figure 1.5.1. Pathway of the Indonesian Throughflow and associated current systems (modified CSIRO fact sheet No. 64)

1.5.3. Productivity drivers in the Timor Sea

Key factors that influence primary production are sunlight, nutrients and stability of the surface water (Duxbury and Duxbury 1984). In tropical regions waters are well-lit, but nutrient-poor, thereby limiting productivity (Duxbury and Duxbury 1984). Hence, physical processes, such as upwellings, provide an important mechanism for bringing deeper, nutrient-enriched waters into the euphotic zone where there is sufficient light for photosynthesis for phytoplankton (Gargett 1997).

Other mechanisms that affect productivity are local wind mixing of the surface layer and vertical mixing of the water column. However, phytoplankton blooms require a stable surface layer (Francis et al. 1998) and are affected by seasonal changes in surface winds. The depth of the upper mixed layer also affects phytoplankton production. While a well-mixed water column brings increased nutrients into the surface layers, it also results in decreased light intensity and a decrease in phytoplankton production (Gargett 1997). Moore and Marra (2002) found that phytoplankton blooms depend upon the availability of cold, nutrient enriched waters and mechanisms for mixing and uplifting these waters to the surface. Their observations in the Strait of Ombai (Indonesia) showed there was a correlation between phytoplankton blooms and monsoonal seasonality, with blooms peaking during the SEM when the thermocline is shallow (closer to the surface) and ceasing with the arrival of the NWM when the thermocline deepens. They also observed that ENSO events also influence bloom activity. During *El Niño* events the ITF weakens due to a lowering of sea level as a result of a decrease in the pressure gradient across the Pacific. This results in a shallowing of the thermocline and increase upwelling strength leading to enhanced phytoplankton production. During *La Niña* events the ITF strengthens as a result of higher sea level in the western Pacific, which deepens the thermocline and reduces upwelling strength (Susanto et al. 2001), thereby reducing phytoplankton production.

Phytoplankton blooms are also often concentrated at water mass boundaries or fronts due to increased upwelling of nutrients (Franks 1992, Yoder et al. 1994). These fronts can occur as a result of physical forces such as strong tidal flow over steep or complex bathymetry, or interaction with the topography (eg. islands or headlands) resulting in curvature of flow. This leads to strong vertical mixing (Moore and Marra 2002) bringing nutrients into the upper surface layers.

In summary there is an increase in upwelling during the SEM and *El Niño* events. This leads to an increase in phytoplankton production and productivity, which in turn is likely to affect lutjanids and other fish resources. It is during this period that nutrients are likely to be at their highest concentration, as a result of increased upwellings and a shallower thermocline. However, in addition to nutrients, plankton blooms also need a stable surface layer (Francis et al. 1998), which occurs during this period between the SEM and NWM. Therefore it is likely that the seasonal changes in oceanography provide a stimulus for spawning to ensure that larvae are produced during the period of highest food supply.

1.6. Global commercial fisheries targeting *Pristipomoides* species

There has been a long history of commercial fishing for lutjanids, dating back to the early part of the twentieth century in Hawaii (Haight et al. 1993), with Opakapaka (*Pristipomoides filamentosus*) being the main target species of the Hawaiian bottomfish fishery.

In other parts of the Pacific region there has been a steady increase in targeting deeper water lutjanids, primarily with the assistance of agencies such as South Pacific Commission (SPC). In 1974, the SPC began surveying the deep slope stocks of Vanuatu (Dalzell and Preston 1992), and extended the development of deep slope fishing to other South Pacific islands over the period 1974-1988 (Dalzell and Preston 1992).

In Fiji commercial fishing for deep-slope demersal fish began in 1979, but until 1982 all the catch was sold locally (Stone 2003). Deepwater fishing is concentrated on the continental slope, pinnacles and seamounts, with two distinct capture zones. In the 70-140 fathom depth range *Pristipomoides* spp., *Aphareus rutilans*, *Paracaesio kusakarii*, *Seriola rivoliana* and *Wattsia mosambica* dominate the catch, whereas *Etelis* spp., *Epinephelus* spp., and *Paracaesio stonei* are the target species in the 180-220 fathom zone (Stone 2003).

In Vanuatu, exploratory fishing for deep-bottom snapper began in 1976, but little development of this fishery occurred until after the establishment of an intensive training and development program in 1981 (Brouard and Grandperrin 1985). Species targeted are *Etelis carbunculus*, *E. coruscans*, *Pristipomoides multidens* and *P. flavipinnis* (Brouard and Grandperrin 1985).

In Tonga, the commercial bottomfish fishery for snapper began in 1980 as a result of development projects (Langi 1990). This fishery which targets deep water snapper and groupers is the largest commercial fishery in Tonga (Langi 1990). Species targeted are *Pristipomoides filamentosus* and *Etelis coruscans*, which are both exported, and *P. flavipinnis* and *E. carbunculus* which are important domestic species (Langi 1990).

In Western Samoa commercial harvesting of deep water slopes was initiated in 1974 with an FAO funded project which provided catamarans to harvest these waters. Prior to this, bottom fishing was limited to shallow reef slopes of less than 100 m using traditional methods (Su'a 1992). Target species are *Aphareus rutilans*, *Etelis carbunculus*, *E. coruscans*, *Paracaesio kusakarii*, *P. stoneii* and *Pristipomoides* spp. (Su'a 1992).

1.7. Fisheries targeting *Pristipomoides* species in Australian waters

The first report of commercial fishing targeting *Pristipomoides* species in Australian waters was during the period 1975-79 when Japanese droplining vessels fished the offshore areas of the Timor and Arafura Seas in what was then international waters. The total catch during this period was estimated at 500-1500 t annually (Stehouwer 1981). Fishing occurred mainly around Ashmore Reef and Troubadour Shoal in the Western Australian sector of the Timor Sea (Clarke 1984), with fishing operation ceasing due to the declaration of the Australian Fishing Zone in November 1979 (Lloyd 1993).

A feasibility study was undertaken from 1980-82 to investigate whether there was potential for a domestic offshore fishery targeting *Pristipomoides* species. This was carried out as a joint venture between an Australian and Japanese company. Fishing was concentrated in the western sector of the Timor Sea near Ashmore Reef, Vulcan and Barracouta Shoals in depths of 80-140 m (Clarke 1984). This study indicated the potential for a domestic fishery.

Commercial fishing by Australian operators targeting *P. multidens* and *P. typus* commenced in 1988 within the Northern Territory (Lloyd 1993) and in 1995 in the Kimberley area of Western Australia (Newman 2003). In both fisheries operators use either baited traps or vertical droplines to target these species (Figures 2.2.1. and 2.2.2 in Chapter 2).

Goldband snapper, which comprises the three species *P. multidens*, *P. typus* and *P. filamentosus*, accounts for 58% of the total catch in the NT Timor Reef Fishery, with *P. multiden*s being the most common of the three *Pristipomoides* species. The red snappers (*Lutjanus malabaricus*, *L. erythropterous*, *L. sebae*) accounts for a further 38% of the catch (Northern Territory Government 2009). A similar catch composition is reported for the Western Australian Northern Demersal Scale Fishery, with goldband snapper accounting for 45% of the total catch and the red snappers (*Lutjanus malabaricus*, *L. sebae*) for 27% (Fletcher and Santoro 2009).

1.8. Management of *Pristipomoides* stocks in Australian waters

1.8.1. Stock structure of Pristipomoides multidens

To assist in the formulation of management plans for the Western Australian and Northern Territory Fisheries targeting goldband snapper, a Fisheries Research and Development Corporation (FRDC) funded project was undertaken to investigate the stock structure of *P. multidens* (Lloyd 1996, Ovenden et al. 2002) using mitochondrial (mDNA) techniques. A subsequent study was undertaken by Newman et al. (2000c) using otolith microchemistry. Both studies were undertaken on fish from the same sites. The sampling sites for my study are the same sites as those sampled within the Northern Territory for these stock structure studies.

The genetic study showed no difference between Australian sampling sites in the Timor and Arafura Seas, but a significant difference in the Timor Sea between Kupang (West Timor) and the north-west Australian site less than 200 nautical miles on either side of the Timor Trench. Otolith microchemistry revealed significant differences in isotopic signature between all sites indicating that significant movement of fish between sites is unlikely. Therefore for the purposes of fisheries management, each site comprises a distinct stock of *P. multidens,* but the recruitment source for the stocks across north-western Australia may be from a common gene pool (Newman et al. 2000c).

It has been observed by Ovenden et al. (2002) that the ITF appears to be responsible for restriction of gene flow, resulting in genetically distinct populations of *P. multidens* on either side of the Timor Trench within the Timor Sea, a distance less than 200 nautical miles. The same study found genetic homogeneity between *P. multidens* samples taken from the Australia section of the Timor and Arafura Seas, which were separated by much greater distances than the genetically distinct samples within the Timor Sea.

These studies indicate that the adult populations of *P. multidens*, which is the component of the stock targeted commercially, are discrete between the sites and therefore separate management arrangements are appropriate for the two states, although the populations are linked genetically across northern Australia.

1.8.2. Current management for NT Timor Reef Fishery

The Timor Reef Fishery is managed through input controls to ensure that the landed catch of the target species does not exceed the estimated sustainable yield of 900 t. This is achieved by limiting the number of licences and the amount of fishing gear that can be used. Monitoring of the fishery is undertaken through the analysis of commercial logbooks and onboard observers (Northern Territory Government 2009).

1.9. Need

Although there has been significant development of deeper water fisheries in the Indo Pacific region over the last 30 years, in many cases these fisheries are very vulnerable, as they are restricted to certain depth ranges often occurring along narrow shelf slopes of islands and atolls (Brouard and Grandperrin 1985). The limited size of these resources means that the fisheries are relatively small-scale, but because of the high price of these fish, lutjanid fisheries provide substantial economic benefits for smaller countries (Shotton 2003). There is a growing awareness globally of the dramatic decline in world fisheries stocks (Pauly et al. 2002, 2003) and the need to ensure that fisheries are managed in an ecologically sustainable manner. Unfortunately attracting research funding for small-scale fisheries is very difficult given their specialised nature, hence extrapolation of population parameters from other areas and sometime other countries is the only recourse many scientists have in order to undertake stock assessment. Likewise management strategies are often applied based on what is effective for small inshore snappers.

Therefore there is an urgent need to examine how the demography of better studied lutjanids relates to other members of this group within different depth ranges and habitats.

1.9.1. Management outcomes from this study

This examination of lutjanid demography across depth ranges provides a framework for fisheries management when detailed information is not available, by allowing some idea of the risk involved in using proxy values. For some situations this may be a valid approach, but in other cases, the differences are likely to be significant. Also management strategies which may work well with shallow water lutjanids, may not be useful in other depth ranges where life history characteristics are very different.

1.10. Thesis objectives

In this thesis I will specifically examine:

- Whether there is a difference in demography between lutjanids inhabiting different depth ranges.
- How the demography of depth partitioned lutjanids relates to the environment which they inhabit.

- The pattern and magnitude of demographic variation in age, growth and reproduction of *Pristipomoides multidens* in northern Australia and compare these finding with lutjanids from other depth ranges reported in the literature.
- What implications these findings are likely to have with respect to lutjanid fisheries.

Chapter 2. Materials and Methods

Samples were collected over a two year period from 1999-2001 as part of a collaborative, Australian Centre for International Agricultural Research (ACIAR) funded project between the Northern Territory, the Commonwealth Scientific and Industrial Research Organisation (CSIRO), and Indonesia. This study covered a number of commercially important snapper species targeted by fishers in northern Australia and eastern Indonesia. I was responsible for the goldband snapper (*Pristipomoides multidens*) component of the project. This involved collection and processing of samples from Australian sites, and analysis of all goldband snapper data, both Indonesian and Australian. For the Indonesian samples, whole otoliths were sent to me for processing, but histological processing of gonads was undertaken in Indonesia and the slides sent to me for analysis.

In addition to this study, goldband snapper otoliths were collected since the inception of the trap and line fishery in the Timor Sea in 1990, together with samples from two trawl surveys (1990, 1992) and samples from Thai trawlers (1990) during the last year of its operation in Australian waters. This material has been incorporated into the data set and will also be used to provide a historical comparison to investigate changes in age structure.

A description of sample collection, sites and sampling gear is outlined in the following sections, however details of specific methods for age, growth and reproductive studies are found in the relevant chapters.

2.1 Sample collection

2.1.1. Joint Australian-Indonesian Project

Two thousand four hundred and thirty two fish samples were collected over a two-year period (1999-2001) from Australian commercial fishing vessels operating in the Timor and Arafura Seas (Chapter 1 Figure 1.3.2.). These samples were collected on a monthly basis; 20 samples per month from the Timor Sea and the same number from the Arafura Sea. Samples from the trap and line vessels (Timor Sea) were kept on ice and, where possible, fishers would collect samples from the last few days of their trip. The trawl fish samples (Arafura Sea) were frozen onboard. Sample collection details included: latitude, longitude, depth and collection date. Indonesia samples were collected from 6 sites: Bali (n=69), Kupang (n=301), Sape (n=204), Tual (n=145), Tanjung (n=74) and Probolingo (n=120) (Chapter 1 Figure 1.3.1). These samples were purchased from fish markets. As all samples were from commercial fisheries, sample sites were sometimes determined by where it would be logistically possible to sample regularly. While every effort was made to sample on a monthly basis in Indonesia, logistically this was very difficult and consequently sampling was often irregular.

Both fork length (FL) and standard length (SL) measurements (to the nearest mm) were taken for Australian samples. While Indonesian samples were predominantly measured as SL, some samples were measured as TL. To facilitate the comparison of results with the literature, it was decided to use FL rather than SL. A regression analysis was undertaken to determine the relationship between FL and SL for Australian samples. Indonesian samples were converted to FL using this equation ($FL=1.079SL+13.22$, $r^2=0.988$, $n=1505$).

All fish were weighed to nearest gram (g) total weight (TW). Sex and macroscopic gonad stage was recorded for Australian samples, however for Indonesian fish, sex was only recorded for samples from the Kupang sampling site. Both sagittal otoliths were removed for ageing studies (Chapter 3).

2.1.2. NT Fisheries Collection

From 1990-1998, *Priptipomoides multidens*, *P. typus*, *Lutjanus malabaricus*, *L. erythropterus* and *L. sebae* were collected on an opportunistic basis by myself and colleagues from the NT Fisheries Division. These samples were from commercial fisheries in the Timor and Arafura Seas. Where possible, fisheries officers collected the samples onboard as part of on-board monitoring of catches. If this was not possible, arrangements were made with vessel owners prior to a fishing trip for the collection of samples and the relevant collection details. All samples supplied by fishers included latitude, longitude, depth, and date of collection.

In addition to commercial monitoring, two fishery-independent trawl surveys were undertaken by the NT Fisheries Division in 1990 and 1992.

The total number of samples from the 1990-1998 collection (including trawl surveys) was 1014 *P. multidens*, 1102 *P. typus*, 517 *Lutjanus malabaricus*, 338 *L. erythropterus*, 335 *L. sebae*.

2.2 Sampling gear

As samples were collected from commercial fisheries, a number of different fishing gears were used. Australian samples from the Timor Sea were taken using traps and droplines, whereas samples from the Arafura Sea were taken by trawling. Indonesian samples were predominantly caught using bottom longline gear, although some were from trawlers. However because Indonesian samples were purchased from local markets, exact details of fishing gear were difficult to obtain.

Samples from the Australian sector of the Timor Sea were caught in an area dominated by offshore shoals, approximately 150 nautical miles north-west of Darwin at depths between 70-120 m. The Arafura Sea is considerably shallower than the Timor Sea and goldband snapper samples were caught in depths ranging from 50-70 m.

2.2.1. Description of traps

The majority of operators use “WA style traps”, weighing around 85 kg. The dimensions of the traps are predominately 1.0 m x 1.2 m x 0.8m. They are constructed of steel mesh (75 mm x 50 mm) and have one funnel (Figure 2.2.1). A trap door is located opposite the funnel entrance to allow easy removal of fish and for refilling the bait box. The bait box is located near the funnel entrance and is secured to the bottom of the trap. Pilchards are the most commonly used bait, although tuna, mackerel heads and trevally are also used.

Traps are deployed in lines and are set in such a way that the funnel entrance is set in the lee of the current, which makes it easier for fish to enter the trap. Traps are normally set at least 400 m apart, and have a soak time of 3-4 hours. Fishing commences at 4 am and finishes at 11 pm. Operators normally experience best catch rates during the spring tides as these tides are more effective in dispersing the odour of the bait further and more rapidly due to the strong tidal movement.

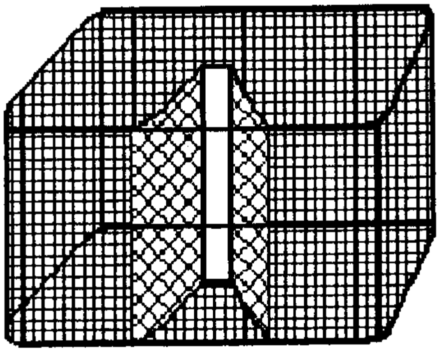


Figure 2.2.1. WA style fish trap used by majority of operators in the Timor Sea

2.2.2. Description of droplines

Droplines are deployed from the boat using hydraulic dropline machine. Each dropline consists of a single line with a 5 kg weight attached. The lower section of the line has 30-40 tuna circle hooks (size 11/0 to 13/0) each attached to the mainline with a short line (Figure 2.2.2). Squid is the preferred bait for dropline fishers.

Fishers search for schools of fish with a distinctive pattern indicative of goldband snapper on the echo-sounder. Once a school of fish is located, a signal is given to set the lines. Generally 2-6 lines are deployed at a time, and soak time can vary from 2-10 minutes.

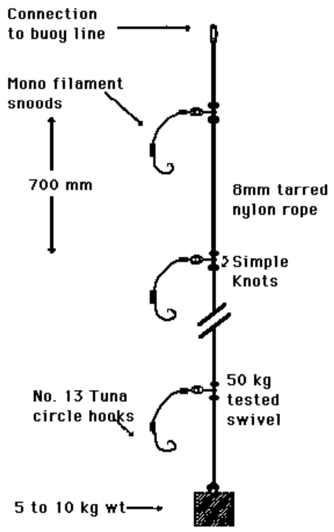


Figure 2.2.2. Lower section of the dropline rig used to capture goldband snapper

2.2.3. Description of commercial trawl net

Samples from the Arafura Sea were caught using a semi-pelagic trawl net. This net, designed by the vessel operator, was based on the "Julie Anne" trawl net, a semi-pelagic trawl net developed by NT Fisheries Division in conjunction with Industry to minimise seabed disturbance, without compromising commercial catch rates. This net is 9 inch mesh with a headline length of 42.2 m, with 74 floats (buoyancy of 2.8 kg) concentrated on wing ends and in the centre of the headline. Rubber bobbins surround the ground chain to allow it to roll over the bottom with minimum impact if they do contact with the seabed. The spread between trawl boards is about 78 m, and the distance of the net above the seabed is usually seven m. This net is designed specifically to catch red snappers (*Lutjanus malabaricus*, *L. erythropterus*) that school above the bottom. The optimal trawl speed is 3.6 knots, and fishing shots are usually of 3 hours duration.

2.2.4. Description of trawl survey sampling net

Trawl survey samples were collected using a standard Frank and Bryce net with a headline length of 26 m and stretched mesh sizes of 38-230 mm. The net had 30 m bridles and 30 m sweeps (Figure 2.2.3). Sampling sites were randomly selected in proportion to the size of the four management zones within the study region; encompassing both the Timor and Arafura Seas. Full details of sampling stations can be found in Ramm (1997).

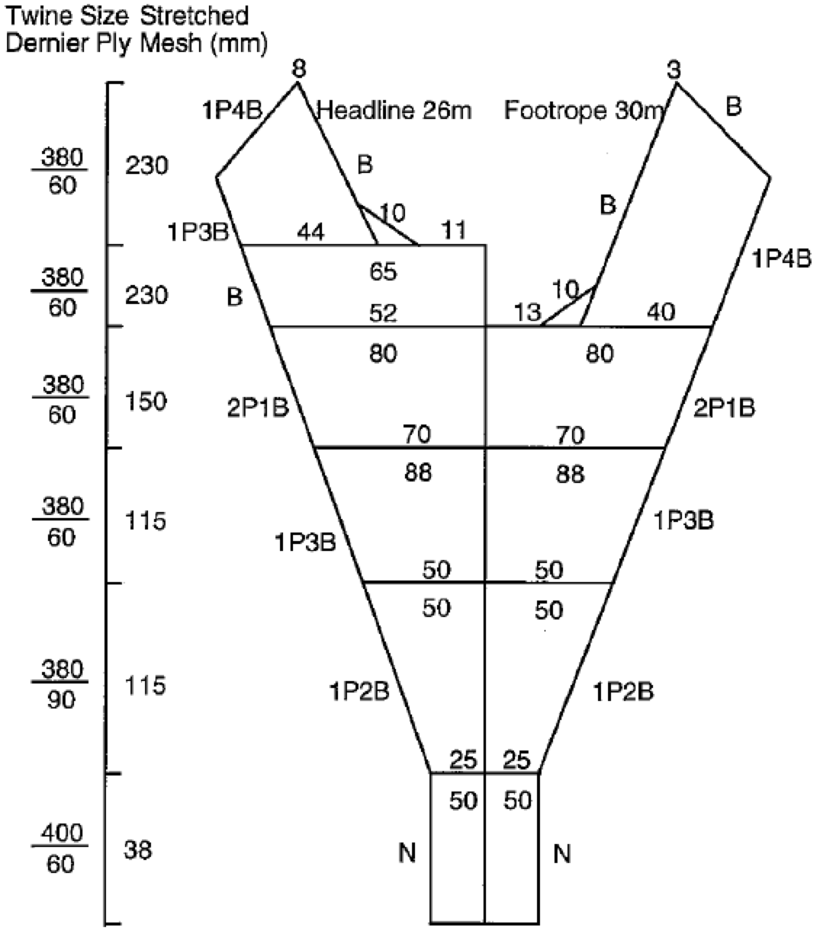


Figure 2.2.3. **Net plan for the standard Frank and Bryce trawl net used for trawl surveys undertaken during 1990 and 1992 (reproduced from Ramm 1997).**

Chapter 3. Investigation of differences in age and growth parameters within the lutjanid complex

3.1. Introduction

Age and growth information is an integral part of fisheries science. This was acknowledged by Pauly (1983) when he stated "It is largely with growth studies that fishery biology established itself as a field in its own by the end of the last century."

Age and growth studies provide information on population structure and effects of fishing on the stocks, assist in understanding life history events, and provide information on population responses to environmental changes (Jones 1992). For this reason there has been a large amount of research and controversy about the best way to measure fish growth and determine age.

While various methods have been employed to age fish and measure growth, Jones (1992) advocates for most fish, otoliths are the most reliable indicator of age. She outlines the advantages of otoliths over other calcified structures to be that they show the early life history of fish and there is no reabsorption under stress conditions. Therefore only otoliths were used for ageing in this study although researchers in earlier studies have used other hard parts for ageing lutjanids.

Much of what we know about lutjanids is based upon what has been observed for shallow water coral-reef fish studies. Most studies have shown that coral-reef fish consist of metapopulations, where sedentary adult populations are often segregated spatially and consequently may be exposed to diverse environmental, biological and ecological processes (Williams, 2003). This may result in populations exhibiting spatial differences in demographic parameters (Williams, 2003). In some cases species can show differences in growth even between reefs within close proximity (Newman et al. 1996b, Williams 2003).

In intermediate and deeper waters fish populations are influenced by different processes to those in shallow waters. By comparison, the environment is more uniform as large-scale current systems play an important role in these deeper waters offshore. Therefore it is possible that species living in these depth ranges have similar growth parameters across a broader range of areas.

3.1.1. Growth, natural mortality and environmental temperature

The topic of growth, metabolic rate, natural mortality and environmental temperature has been the subject of considerable controversy in recent years, with different theories evolving to explain the patterns seen in ectotherms within different habitats.

Pauly (1980) found a relationship between natural mortality, growth parameters (weight (W), growth rate (K)) and the mean water temperature for the 175 different fish stocks that he examined from both freshwater and marine environments. He suggested that the most likely explanation was due to differences in metabolic rates; where fish inhabiting warmer waters have higher metabolic requirements and therefore a greater exposure to predators as a result of the need to feed more frequently, than fish found in cooler waters. Therefore fish living in warmer water would be expected to have a higher growth rate (K), compared with those living in cooler water. Pauly (1984, 1998) refined this theory further by hypothesising that gill surface, which does not grow as fast as fish volume, provides a strong regulating mechanism for growth, metabolic rate and food consumption, which in turn has implications for natural mortality. Therefore fish with higher metabolic rate consume more oxygen, resulting in growth slowing at a smaller body size due to the limitations with gill surface area.

Gillooly et al. (2001) also found that temperature was involved in controlling the metabolic rate of an organism. They postulated that environmental temperature governs the metabolism of an organism's temperatures through the numerous individual biological reactions which are temperature-dependent. Therefore higher temperatures lead to an increase in individual reaction rates, which in turn results in higher metabolic rate.

Clarke and Fraser (2004) believe that this is too simplistic and that evolutionary trade-offs are involved. Although they note that metabolic rate increase with temperature they believe that this is due to the indirect effect of temperature on cellular metabolism. Studies by Arnott et al. (2006) also support the theory of evolutionary trade-offs in relation to growth and other life-history traits. Their study found faster growth rates in fish living in cooler environments than the same species living in warmer waters. This is the reverse of trend found by Pauly and others. Arnott et al. (2006) believe the reason for their finding is that there are advantages for fast growth in the colder areas as it enhances over-winter survival. However, fast growth and high metabolic rate incur a cost. Arnott et al. (2006) showed that this resulted in slower swimming speed as a greater metabolic allocation is required to digest larger rations and consequently greater exposure to predators, resulting in higher mortality rates. Therefore there is an evolutionary trade off between fast growth and the advantages it offers in cooler climates for over-winter survival and higher risks to predation through slower swimming performance.

Griffiths and Harrod (2007) also examined the role of environmental temperature and its effect on growth and natural mortality in fish. They revisited Pauly's (1980) original study and re-examined this work using additional data accumulated through FishBase 2004. Their results support Pauly's theory that mean mortality rates increase with temperature, but they also found that taxonomic groups and habitat had a significant effect on mortality rates suggesting that indirect effects dictated by ecological requirements also play a significant role.

Therefore although there is considerable controversy in this field, the majority of studies have found that metabolic rate increases with temperature, leading to an increase in growth with higher environmental temperatures, and an increase in natural mortality.

With an increase in depth there is a decrease in water temperature, therefore in keeping with the general observation that metabolic rate is related environmental temperature, it would be expected that lutjanids in deeper, cooler waters should show slower growth rates than those in shallower, warmer waters. My study examines this premise by looking at growth parameters of different lutjanid groups which inhabit the different depth ranges and therefore different temperature regimes. As many species within this Family are prized table fish, there has been a wide range of studies on a variety of species. However, the majority of research has been undertaken on the more accessible shallow water species, and the deeper water species targeted by the Hawaiian bottomfish fishery over the last 60 years, but there is a paucity of information on species in the intermediate depth range.

In this chapter I will focus on the genus *Pristipomoides*, which dominates this intermediate depth range, and compare similarities and differences from this group with shallow water and deep water genera documented in the literature. I will also incorporate age and growth information from a smaller study of lutjanids (*Lutjanus malabaricus*, *L. erythropterus*, *L. sebae*) which I collected in the same study area, but within a different depth range. By using *Pristipomoides multidens* as a case study I will investigate the biology with respect to age and growth of this species, and compare it to other members of the lutjanid complex in other depth ranges.

3.1.2. Objectives of this study

In this chapter I will specifically be examining:

- Do growth parameters and longevity change with respect to depth partitioning of genera?
- How parameter differences relate to the environment these species inhabit?
- Are there spatial variations between species occupying the same depth range with respect to age and growth parameters?

Age and growth parameters are key inputs in stock assessment models hence accurate determination of these parameters is critical for meaningful assessment. Many tropical fisheries are multi-species and cover wide depth ranges; therefore awareness of differences in fish growth is vital for appropriate fisheries management, particularly within multi-species fisheries.

3.2. Materials and Methods

For this study samples were collected from Australia and Indonesia as described in Chapter 2.

3.2.1. *Pristipomoides multidens* samples

Otoliths were collected from 2432 fish during a 2 year Australian-Indonesian collaborative study funded by ACIAR. This consisted of 1535 otoliths from the Australian sectors of the Timor and Arafura seas. The remaining 897 otoliths were collected by Indonesian collaborators from the other 6 sites in Indonesia: Kupang (n=301), Sape (n=204), Probolingo (n=120), Tual (n=145), Tanjung (n=74) and Bali (n=69). All Indonesian *P. multidens* otoliths were sent to Australia for processing.

3.2.2. Other lutjanid samples

In addition to *P. multidens* samples, I also collected a smaller number of other lutjanid otoliths; *Lutjanus malabaricus* (n=517), *L. erythropterus* (n=338), *L. sebae* (n=315), and *P. typus* (n=1102). These samples were collected at the same time as *P. multidens* samples from the two trawl surveys and the trap and line fishery. This material will be used to compare growth rates between species.

3.2.3. Otolith preparation

Upon removal otoliths were rinsed in tap water, air-dried and stored in paper seed packets. Both left and right otoliths were weighed separately to 0.0001 g on a Sartotius BA1105 electronic balance.

There are two collections in this study, which were processed several years apart. Hence, slightly different otolith preparation methods have been used for the two collections reflecting improvements in equipment over time.

3.2.3.1. NT Fisheries collection (1990-98)

If both otoliths were intact, the left otolith was set in epoxy resin and sectioned using a Gemmasta model GS6D lapidary saw which was modified for sectioning otoliths. Full details of saw modifications and otolith preparation are described in Bryce et al. (1998). Thin transverse sections of 400 microns were cut and the two sections with the best readability were placed on glass slides that had been coated with casting resin as an adhesive. A second coat of casting resin was applied over the sections before cover slips were applied. Slides were placed in an oven at 720 ºC for 14 hours to set the adhesive.

3.2.3.2. Joint Indonesian – Australian collection (1999-2001)

The Australian collection was prepared in the same way as the earlier NT Fisheries collection. However a Buehler Isomet low speed saw was purchased just prior to processing the Indonesian samples. This allowed Indonesian otolith sections to be cut to 270 microns, compared with 400 microns with the Gemmasta saw. The two most readable sections were chosen for mounting onto glass slides using the same method as described in section 3.2.3.1.

3.2.4. Age estimation

Otolith sections were viewed using transmitted light under a dissection microscope, attached to an OPTIMAS® image analysis system. This allowed greater enhancement of images. All otolith reading was done on-screen. Age estimation was undertaken by drawing a transect from the primordium to the proximal edge of the otolith, adjacent to the sulcal groove, and counting the number of dark increments along this transect.

The readability of each otolith was assigned on a scale of 1 to 5, with 5 deemed unreadable. Only otoliths with a readability of 3 or less were included in this study.

All estimates were made without knowledge of fish length to prevent bias. A reference collection of 65 *P. multidens* otoliths and 89 *L. malabaricus* otoliths were sent to the Central Ageing Facility (Victoria) for preparation and independent age assessment. This reference collection was used for the training of all readers.

3.2.5. Age precision estimate

To determine precision between readings we used an index of average percentage error (APE) developed by Beamish and Fournier (1981). Two independent readers double read the 1999-2001 Australian-Indonesian otolith collection, while the earlier (1990-92) NT Fisheries collection was read once by two independent readers. One reader read both collections.

3.2.6. Validation

Validation was only undertaken on *P. multidens* which were collected on a monthly basis over a two year period. The other lutjanid species were obtained on an opportunistic basis and there were not sufficient samples taken on a regular basis to be able to undertake validation. However, validation of *L. erythropterus* and *L. malabaricus* from the Timor and Arafura Seas has been undertaken by Fry et al. (2009). Their findings will be discussed in section 3.5.3.

Validation of *P. multidens* was undertaken using both marginal increment analysis (MIA) and edge analysis.

3.2.6.1. Marginal increment analysis

Marginal increment analysis was undertaken on otoliths sections using an OPTIMAS$^{®}$ image analysis system. MIA measurements were undertaken along the same axis that increment bands were counted. The distance from the last opaque zone to the outside edge of the otolith was measured, and is defined as the marginal increment (MI). Then the distance from the outside edge of last opaque zone to the outside edge of the previous opaque zone was measured. The appearance of the otolith edge was also noted as either opaque or translucent. All readings were done on-screen using OPTIMAS® image analysis software to undertake measurements.

Marginal increment ratio analysis (MIR) is used to determine the proportion of growth the marginal increment has undergone relative to the previous increment (PI), i.e.

$$MIR= MI/PI*100$$

As the majority (88%) of fish collected were in the 5-8 year age classes, the data was not separated by age class. Mean MIR was determined for each location, and plotted against month of capture.

3.2.6.2. Edge analysis

The collection of otolith sections used for MIA was sent to Dr Lou, a fish ageing consultant at James Cook University, to undertake edge analysis. Dr Lou has extensive experience in ageing tropical fish species and edge analysis. This provided an additional independent validation method.

To determine whether the margins of goldband snapper (*P. multidens*) were deposited annually, the otolith margins were assigned one of three classifications:

New margin where opaque material was visible on the otolith margin, although this opaque material does not have to be present around the entire margin.

Intermediate margin is seen as a continuous increment of translucent material visible on the outer margin of the opaque increment. This category is assigned when the marginal translucent increment is less than 2/3 complete.

Wide margin is assigned when the marginal translucent increment is more than 2/3 complete.

3.2.7. Relationship between otolith weight and age

Otolith weight has been found by Fletcher (1991), Worthington et al. (1995) and Choat et al. (1996) to be a good approximation of age as it increases in weight throughout the entire life of a fish and therefore has the potential to provide a fast and cheap method for ageing fish. Otoliths were prepared as described in Section 3.2.3. The relationship between otolith weight and age was examined using regression analysis with otolith weight as the dependent variable and age as the independent variable.

The regression slopes were compared between sexes for each location using analysis of covariance (ANCOVA). If there was no difference between sexes, then data were combined for the sexes and a regression analysis was undertaken on this combined data.

Using this age-otolith weight relationship, predicted age was estimated from otolith weight. This predicted age was a continuous variable, and was transformed to a discrete variable by rounding to the nearest integer.

To assess the differences between predicted ages and observed ages (i.e. age determined from sectioned otoliths), three indices of ageing error were used. These were: coefficient of variation (CV), bias and percent agreement (see Worthington et al. 1995). All three indices were assessed within each observed age class and across all age classes. The CV was calculated for each age class as the standard deviation of observed and predicted ages divided by their mean. Bias was obtained by subtracting estimated age from predicted age. When observed age and estimated age match, CV and bias are zero. Percentage agreement describes the percentage of ages that match the observed ages.

3.2.8. Von Bertalanffy growth model

The von Bertalanffy growth function (VBGF) was fitted to length at age data using nonlinear least squares estimation. Growth curves were determined for both sexes separately for Australian samples. A combined growth curve including juvenile samples was also determined. For Indonesian data samples were combined as there was insufficient number of fish from each site or data was from too few age classes to be representative.

The form of the VBGF used for length at age analysis was:

$$L_t= L_\infty(1-e^{-K(t- t0)})$$

Where:

L_t = length at age t

L_∞ = asymptotic length

K= a growth coefficient determining the rate at which L_∞ is reached

t_0 = the hypothetical age at fish length zero.

Due to the lack of juvenile fish, it was necessary to constrain t_0 to zero. The small number of juvenile fish occurred as a result of purchasing fish from the commercial fishery, which targets the adult population. Unfortunately the commercial fishery was the only option for obtaining samples.

3.2.9. Kimura's likelihood ratio test

Kimura's likelihood ratio test (1980) was used to compare VBGF curves to determine whether there were differences between sexes and locations, and which parameter was responsible for observed differences in the VBGF.

3.2.10. Mean length at age and growth rates

Mean fork lengths were determined for lutjanids at ages 5, 7 and 9 as these age classes had the greatest number of samples. Comparisons were made between Timor and Arafura seas and also between the Timor Sea and Kupang (Indonesia), for fish between the ages 5-9 years as this was the range of ages where data was well represented for both areas.

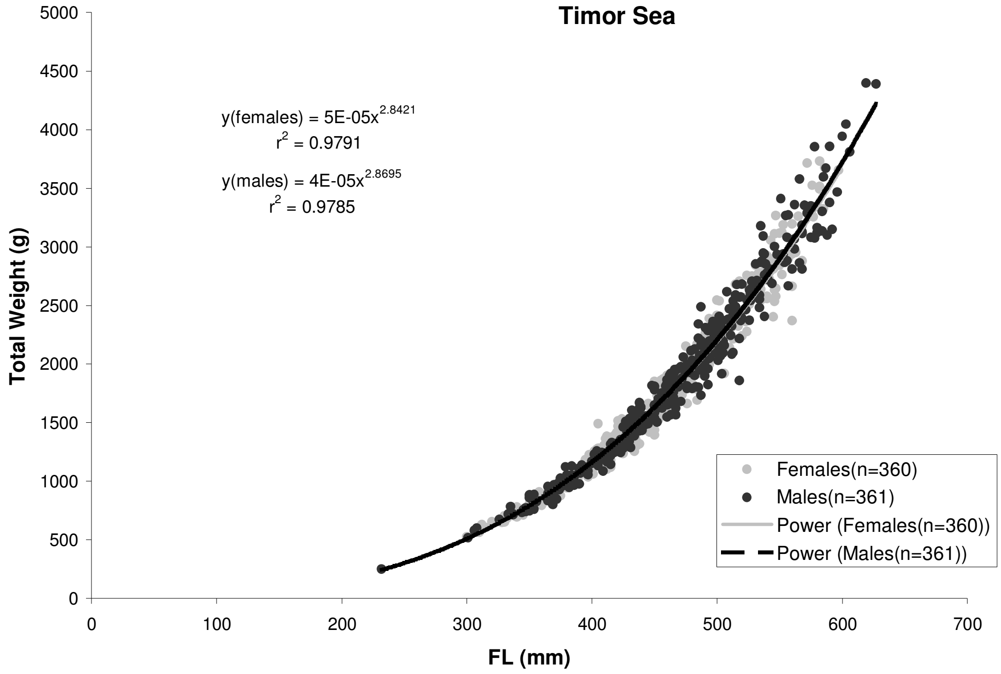
Growth rates were calculated by subtracting the mean fork length between successive years for fish in the 4 and 10 years age range to determine if there was a trend in growth rate with respect to depth.

Growth rates (mm/yr) were obtained for *P. multidens*, *L. malabaricus*, and *L. erythropterus*.

3.3. Results - *Pristipomoides multidens*

3.3.1. Length-weight relationships

Fork length-total weight relationships were examined for both sexes from the Timor and Arafura seas. This relationship between length (L) and weight (W) is described by the power function $W=aL^b$ (Figure 3.3.1). ANCOVA was undertaken on the $\log_e$ transformed data, and no difference was found between the sexes for either location: Timor Sea (ANCOVA, F1, 721=0.45, *P*=0.505), Arafura Sea (ANCOVA, F1, 755 = 2.88, *P*=0.0901) (Figure 3.3.2). Therefore sexes were combined and analysis of covariance was undertaken to determine if there was a difference in the fork length-total weight relationship between locations. A significant difference was detected between locations (ANCOVA, F1, 1479 =79.71, *P*<0.05) (Figure 3.3.3).



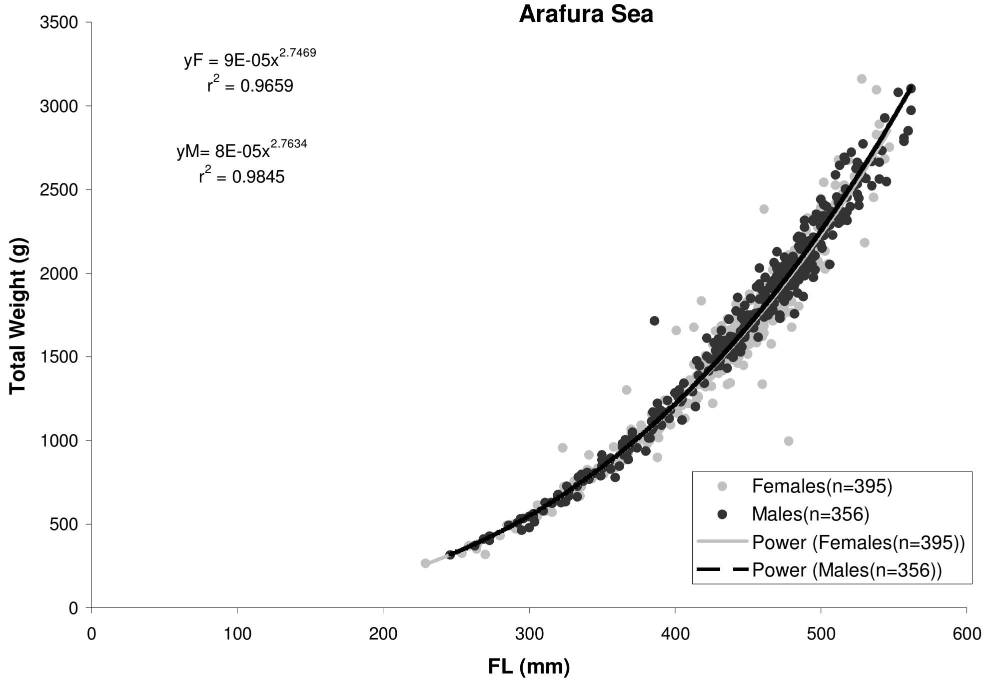
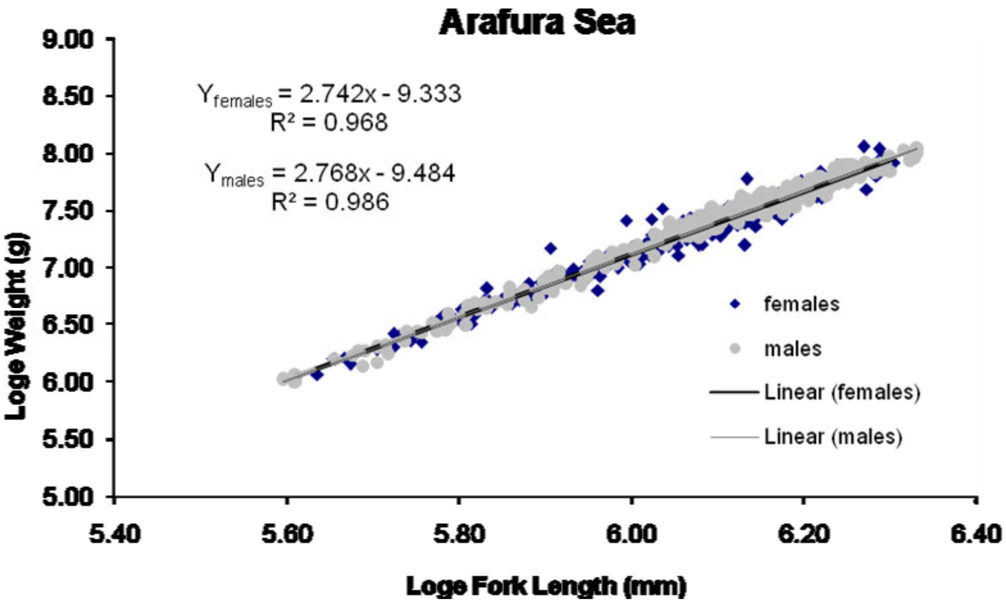


Figure 3.3.1. **Relationship between fork length (FL in mm) and total weight (g) for goldband snapper (*Pristipomoides multidens*) from the Timor and Arafura seas**



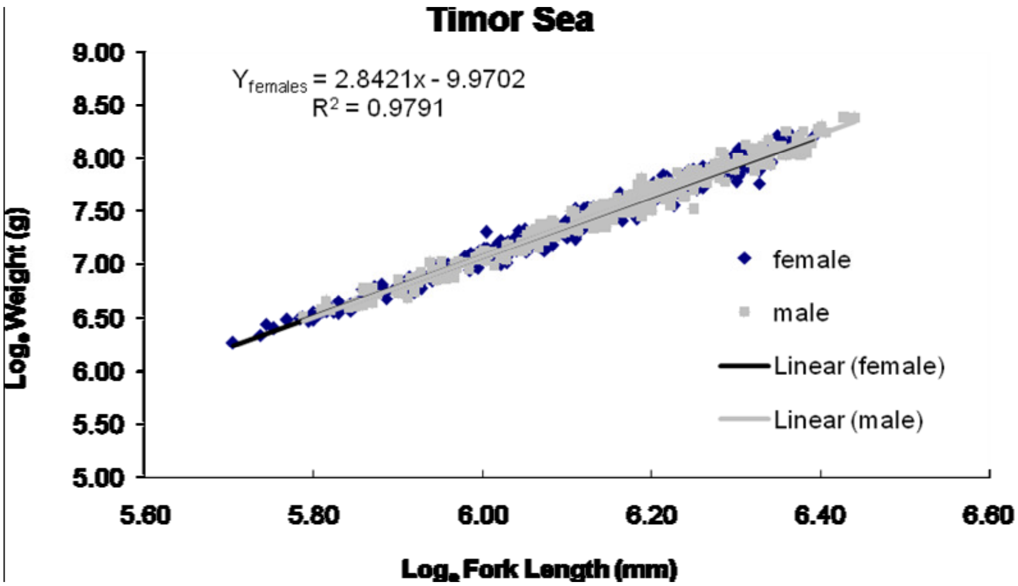


Figure 3.3.2. **Log$_e$ transformed length-weight relationship for goldband snapper (*Pristipomoides multidens*) from the Timor and Arafura Seas by sex**

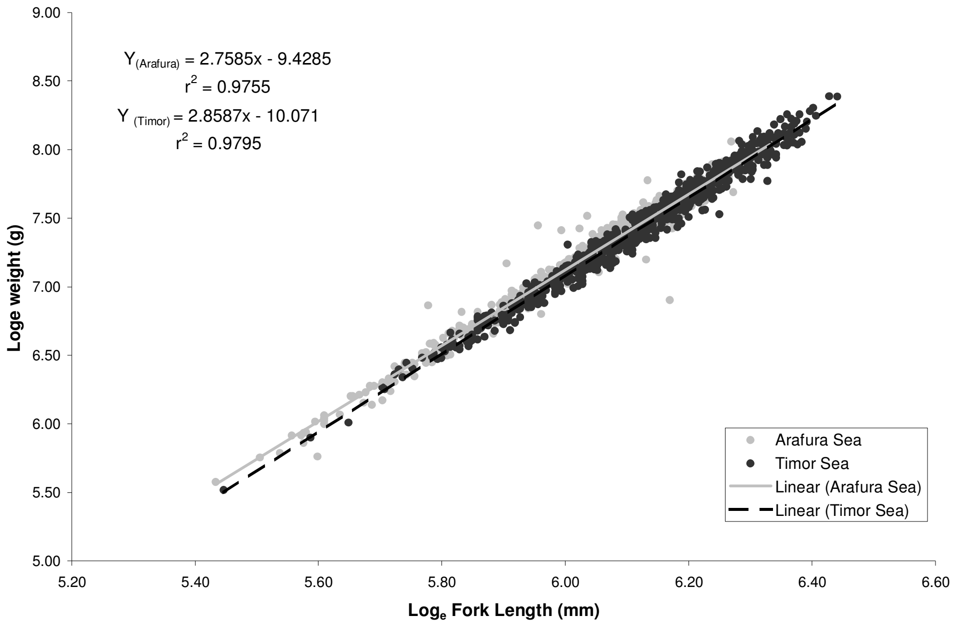


Figure 3.3.3. **Log$_e$ transformed length-weight relationship for goldband snapper (*Pristipomoides multidens*) from the Timor and Arafura Seas (sexes combined)**

3.3.2. Length frequency

Length-frequency analysis by sex was undertaken only for Australian samples, as the sex of fish was not routinely recorded for Indonesian samples. Fish from the Timor Sea ranged in size from 232-627 mm FL for males and 300-640 mm FL for females.

The size range of fish from the Arafura Sea was 246-562 mm FL for males and 229-528 mm FL for females (Figure 3.3.4.). There was no significant difference in length frequency between the sexes for the Timor Sea (Kolmogorov-Smirnov test: $D=0.054 < D_{0.05} = 0.101$), but length frequency distribution was significantly different between sexes for the Arafura Sea (Kolmogorov-Smirnov test: $D = 0.189 > D_{0.05} = 0.0987$).

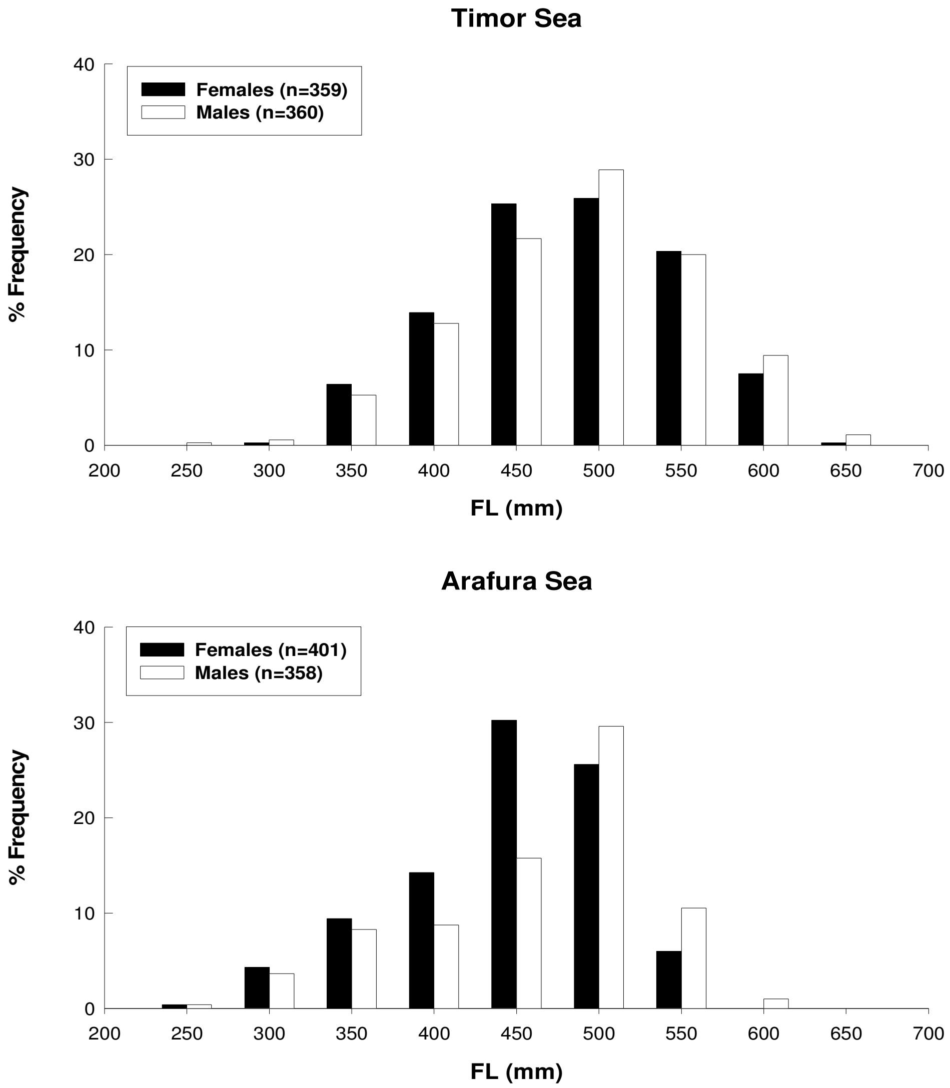


Figure 3.3.4. Length-frequency distribution by sex for goldband snapper (*Pristipomoides multidens*) from the Timor and Arafura Seas

Different capture methods were used between the Timor and Arafura seas, therefore to eliminate potential differences due to gear selectivity, length frequency was determined from samples obtained during a trawl survey from the 1990-92 NT collection, where the same fishing gear (trawl) was used for both locations. Results from this analysis showed no significant difference in length frequency distribution between the sexes. Timor Sea ($D=0.1403 < D_{0.05} = 0.2339$), Arafura Sea ($D=0.1620 < D_{0.05} = 0.1862$). When sexes were combined, there was no significant difference in length frequency distributions between locations ($D=0.1198 < D_{0.05} = 0.1483$, Figure 3.3.5).

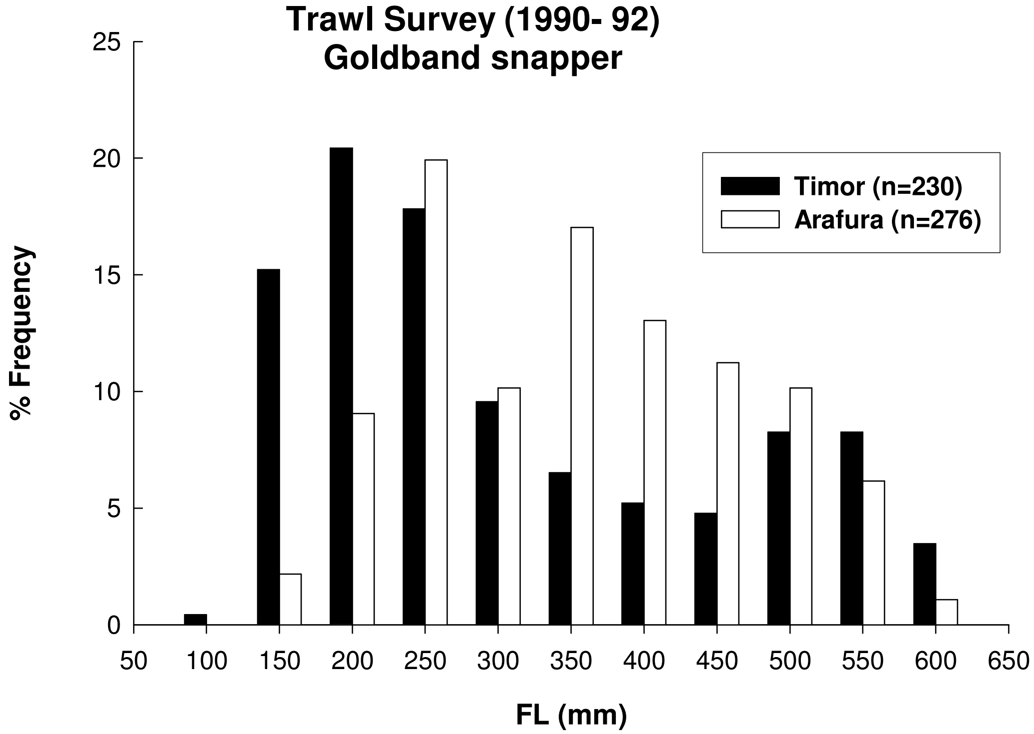


Figure 3.3.5. **Comparison of goldband snapper (*Pristipomoides multidens*) caught using the same sampling gear (trawl net) for both locations**

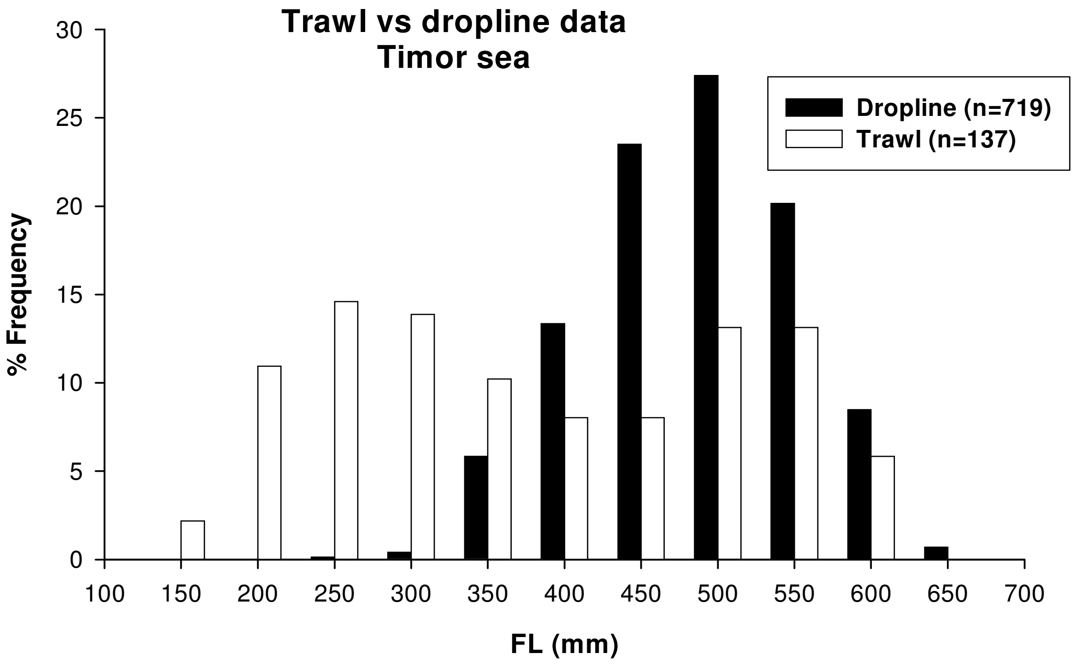


Figure 3.3.6. **Comparison of length frequency for *Pristipomoides multidens* using different sampling gears for the Timor Sea**

3.3.3. Age precision estimate

For the recent Australian-Indonesian study (1999-2001), Australian *P. multidens* otolith sections were double read by two readers. There was a 3.8% APE between the first and second reading of the same slides by reader one. Reader two had a 7.52% APE between the first and second reading of the same slides. The same procedure was used for the Indonesian samples, where reader one had a 1.25% APE, and reader two a 5.46% APE. Reader one had the lower APE and the most experience in reading tropical snapper otoliths, so these readings were used for the analysis. The better APE readings for the Indonesian samples were a result of obtaining a new saw resulting in clearer sections that were easier to read.

The earlier (1990-1992) NT Fisheries collection of *P. multidens* otoliths was read by two readers. Reader one was more experienced, having read the Australian-Indonesian collection. However both readers had a good APE between double readings of the same slide. Reader one's APE was 6.7% and reader two had APE of 9.6%. The between reader variability was 17.6%. Reader one had the lower APE, and more experience, so these readings were used for analysis.

3.3.4. Validation

3.3.4.1. Marginal increment analysis

In the Timor Sea there appears to be some seasonal trend in monthly mean MIR (Figure 3.3.7), suggesting annual periodicity of opaque and translucent zones. Minimum MIR values were observed in July 1999 and October 2000, suggesting that annual growth ring was put down over this period, but there are no clearly defined maximum values. However this period of increment deposition was consistent with the results for edge analysis for the Timor Sea (section 3.3.4.2) where increment deposition was observed between June and October. For the Arafura Sea there is no evidence of any seasonal trend.

3.3.4.2. Edge analysis

Due to difficulties in validation with the marginal increment analysis technique, edge analysis was also undertaken. As previously mentioned in Section 3.2.6.2, this work was undertaken on a consultancy basis by Dr Lou at James cook University (JCU), Townsville. Results from this work (Figure 3.3.8) indicate that there is annual periodicity of opaque and translucent zones for both the Timor and Arafura seas. New increment deposition occurred between June and October for the Timor Sea with 90 % of fish having a new opaque increment by September. The Arafura Sea showed similar results, with new increment deposition occurring between May-October, with 80% of fish having a new opaque margin by September. This winter-spring opaque zone formation was also observed by Newman and Dunk (2003) for *P. multidens* in the Kimberley region.

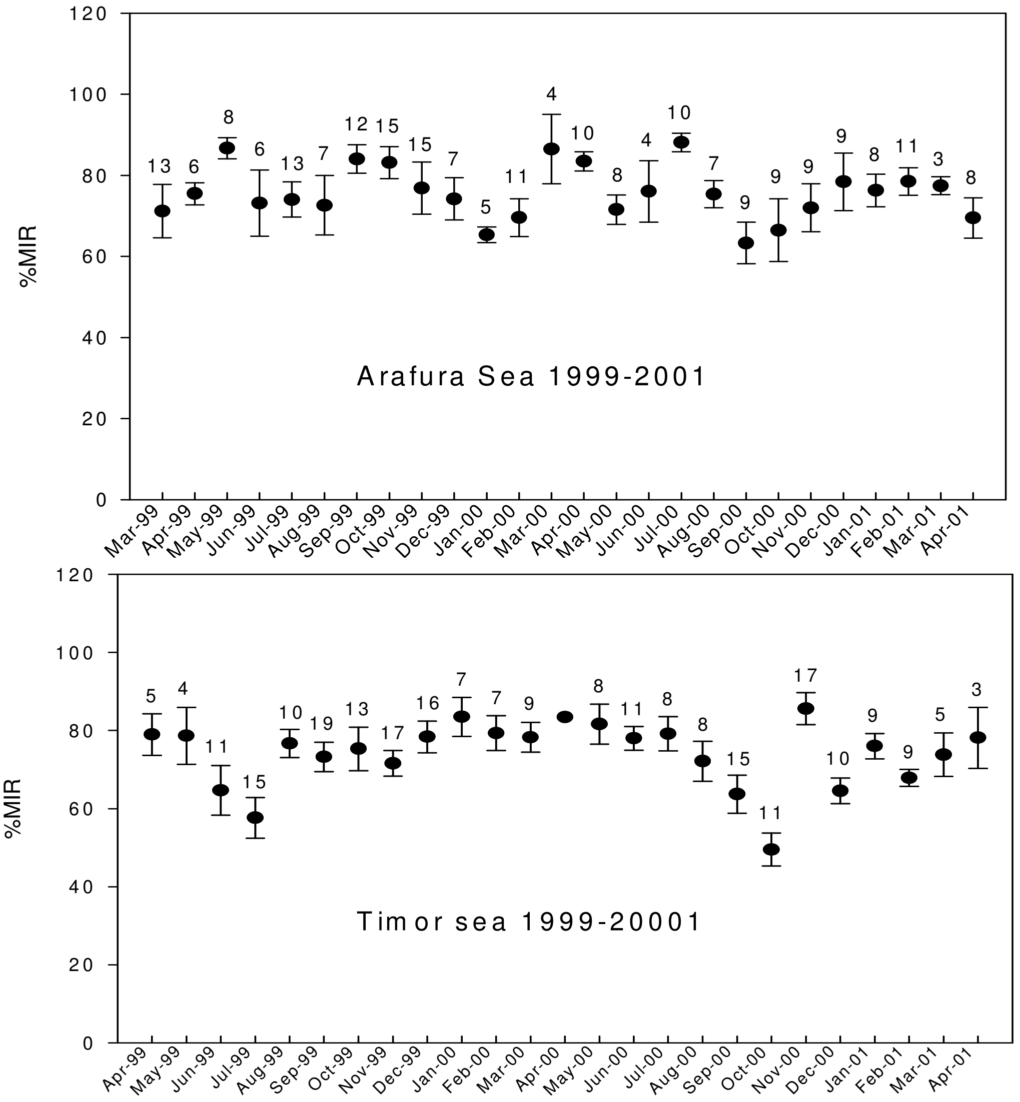


Figure 3.3.7. **Mean monthly increment ratio (MIR) ± standard error by location for *Pristipomoides multidens*. Samples size is shown above each data point**

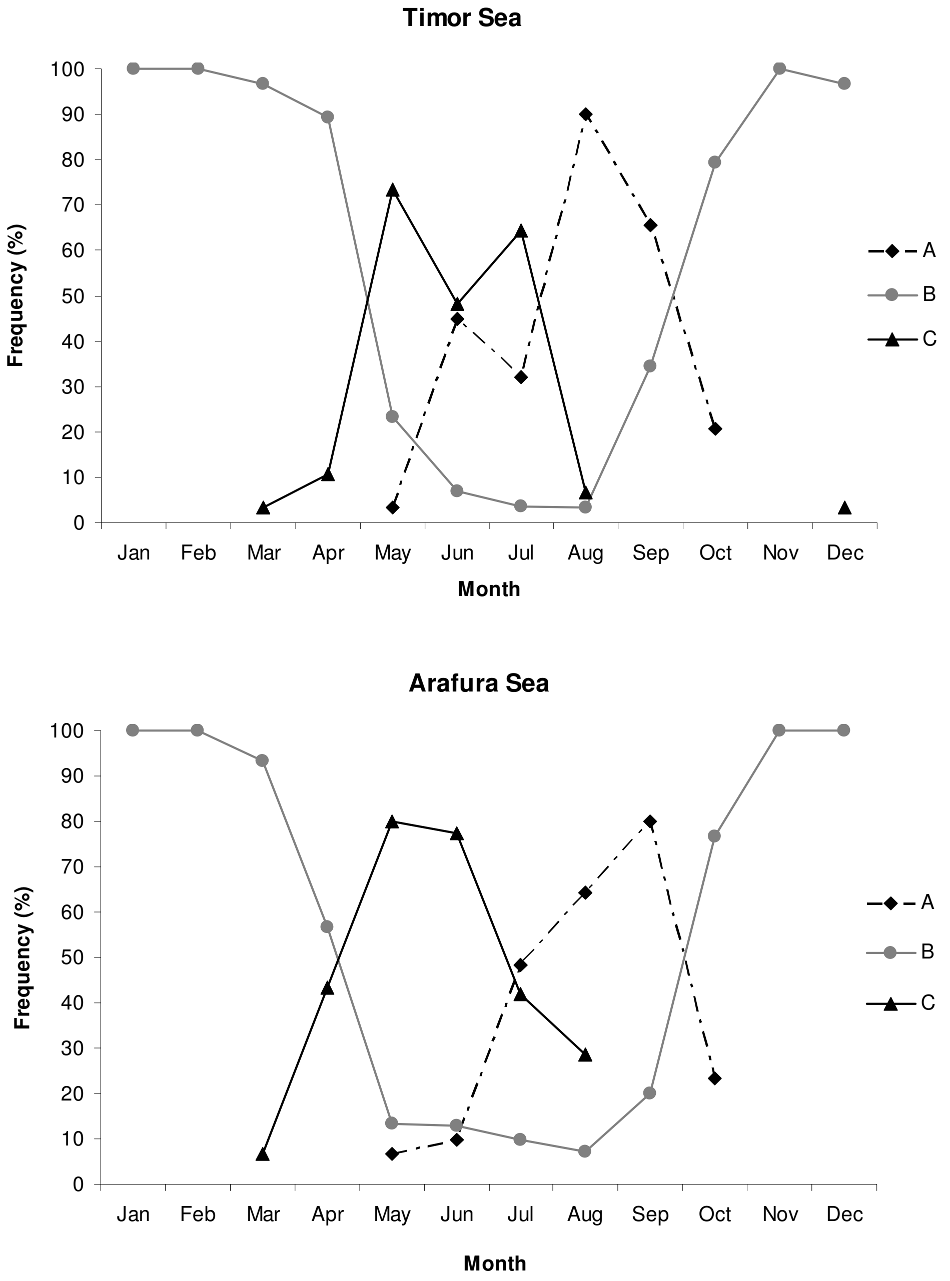


Figure 3.3.8. **Results of otolith marginal analysis for goldband snapper collected from Timor Sea and Arafura Seas in 2000. A) new margin, B) intermediate margin and C) wide margin**

3.3.5. Otolith weight vs age

Otoliths were prepared as described in Section 3.2.3. The relationship between otolith weight and age was examined using regression analysis with otolith weight as the dependent variable and age as the independent variable. The relationship between otolith weight and age was linear (Figures 3.3.9 and 3.3.10) with otolith weight accounting for 75% of the variation in age for females and 76% for males in the Arafura Sea, and 69% of the variation for females and 76% for males in the Timor Sea (Table 3.3.1).

The slopes of the regression lines between sexes were compared for each location using analysis of covariance (ANCOVA). Results show that the there was no difference between the sexes for the Timor Sea (ANCOVA, F_{1288}=2.053, P=0.153) therefore sexes were combined for this location and a relationship for combined sexes was used to predict age from otolith weight (section 3.3.4.). For the Arafura Sea, there was a significant difference between the sexes (ANCOVA, F_{1289}=5.928, P=0.0155), and therefore predicted age-weight analysis was undertaken separately for each sex for this location.

Table 3.3.1. Linear regression relationships for *Pristipomoides multidens* (otolith weight = b.age-a), where n=number of samples, r^2 is the coefficient of determination; F is the ratio of the mean squares due to the regression and the residual.

Sex and Location	**Relationship**	**n**	**r2**	**F**
Timor Sea males	y =0.128x-0.104	145	0.76	449
Timor Sea females	y=0.133x-0.168	146	0.69	324
Arafura Sea males	y=0.134x-0.139	143	0.76	464
Arafura Sea females	y =0.133x-0.155	147	0.75	413

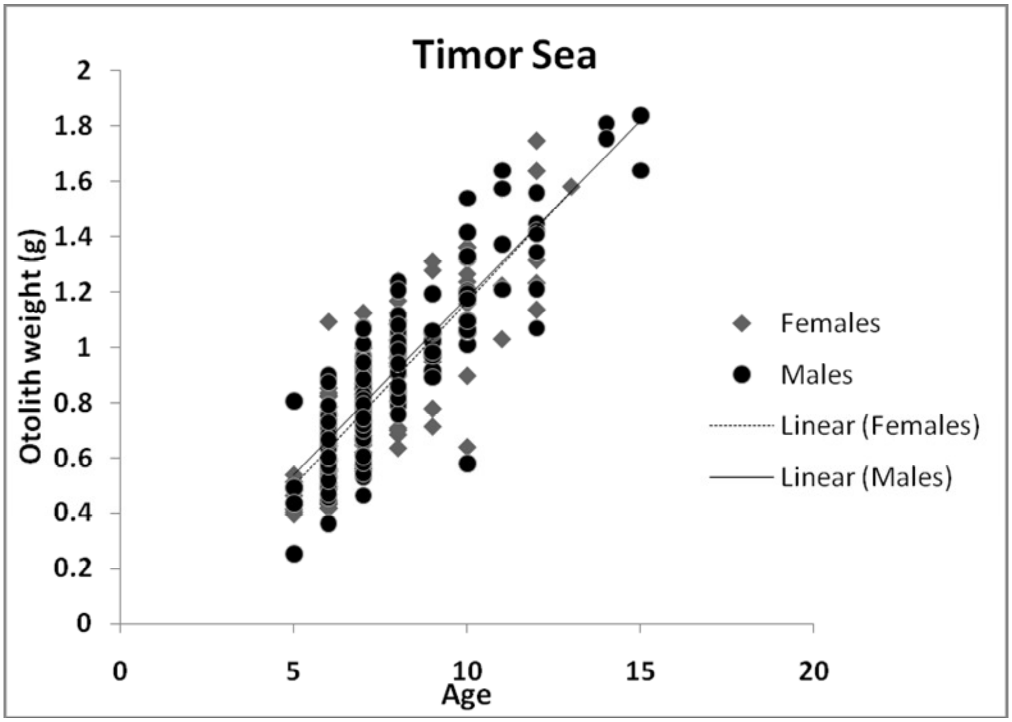


Figure 3.3.9. **Relationship between age and otolith weight (g) for *Pristipomoides multidens* from Timor Sea**

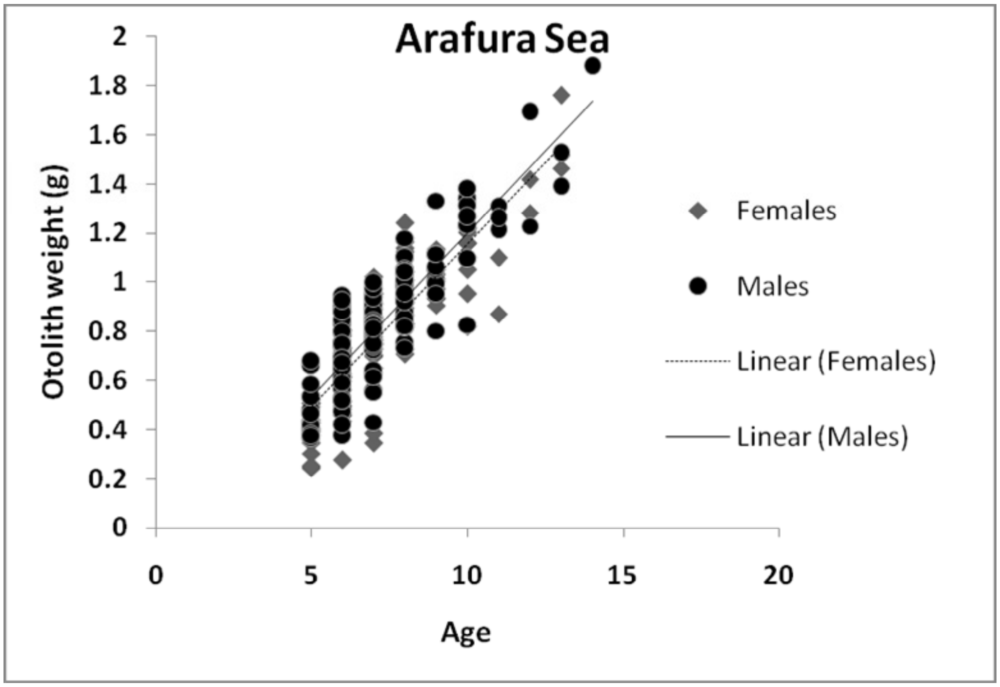


Figure 3.3.10. **Relationship between age and otolith weight (g) for *Pristipomoides multidens* from Arafura Sea**

3.3.5.1. Estimation of age from otolith weight

Using the age-otolith weight relationship determined in the previous section (Table 3.3.1), predicted age was estimated from otolith weight as described in section 3.2.7. This predicted age was a continuous variable, and was transformed to a discrete variable by rounding to the nearest integer.

As there was no significant difference between the sexes for the Timor Sea, sexes were combined. Separate analysis was undertaken for each sex for the Arafura Sea as there was a significant difference in the age-otolith weight relationship for each sex from this location. Results are shown in Tables 3.3.2 and 3.3.3.

Table 3.3.2. Assessment of the accuracy of predicted ages derived from otolith weight - age relationship for *Pristipomoides multidens* from the Timor Sea.

Observed age	**n**	**Range of Predicted ages**	**CV (%)**	**Bias (years)**	**Percentage agreement**
5	12	3-7	11	0.56	40
6	86	4-8	9.2	0.09	35
7	77	5-9	8.2	-0.12	35
8	53	6-11	7.2	-0.32	36
9	14	7-11	7.5	0.21	36
10	24	6-12	9.1	0.29	21
11	7	9-13	10.6	-0.57	0
12	13	9-14	7.6	0.43	31
13	1	13	0	0	100
14	2	14-15	2.4	-0.5	50
15	2	14-15	2.4	0.5	50

Table 3.3.3. Assessment of the accuracy of predicted ages derived from otolith weight age relationship for the female *Pristipomoides multidens* from the Arafura Sea.

Observed age	**n**	**Range of Predicted ages**	**CV (%)**	**Bias (years)**	**Percentage agreement**
5	19	3-6	15.3	0.51	42
6	34	4-8	15.6	-0.07	29
7	42	4-9	12.8	-0.23	55
8	25	7-10	12.1	-0.27	32
9	11	8-11	5.9	0.26	55
10	10	8-11	10.3	0.55	50
11	2	8-9	13.1	2.46	0
12	2	11-12	6.1	0.91	50
13	2	12-14	18.0	0.3	0

Table 3.3.4. Assessment of the accuracy of predicted ages derived from otolith weight age relationship for the male *Pristipomoides multidens* from the Arafura Sea.

Observed age	**n**	**Range of Predicted ages**	**CV (%)**	**Bias (years)**	**Percentage agreement**
5	19	4-6	14.9	0.45	32
6	32	4-8	21.9	-0.22	22
7	38	4-8	15.6	-0.03	18
8	29	7-10	11.8	-0.05	38
9	10	7-11	13.0	-0.12	67
10	8	7-11	14.6	0.10	38
11	3	10-11	4.0	0.55	33
12	2	10-14	22.5	0.07	0
13	2	11-12	6.7	1.10	0

For both locations the majority of fish are between 5 and 10 years. The CV for this age group ranged between 7.2-11% for the Timor Sea and 5.9-15.6% for females and 13.0-21.9% for males from the Arafura Sea. There was considerable overlap between age classes with most age groups having a range of 2 years either side of the observed age. The average percentage agreement was 33% for the Timor Sea and 35% for females and 27% for males from the Arfaura Sea. The large degree of overlap of predicted ages between age classes could be due to a number of factors including; errors when weighing otoliths, ageing errors, or spatial differences in otolith weight. Other studies have found spatial differences in the otolith weight-age relationship (Worthington et al. 1995, Pilling et al. 2003, Lou et al. 2005). This can be explained by the inter-relationship between the chemical composition of otoliths and the environment in which fish live. Water temperature, salinity and differences in water chemistry, all affect otolith composition and in turn, otolith density and weight. It is possible that differences in environmental conditions within the sample areas may contribute to differences in otolith weight. While my results do not indicate that otolith weight can be used as a proxy for age for *P. multidens*, further studies are needed on a smaller spatial scale to investigate this relationship further.

3.3.6. Von Bertalanffy growth model for Pristipomoides multidens

Results of the von Bertalanffy growth model for goldband snapper are presented in Table 3.3.5 and Figures 3.3.11.a-d. Due to the lack of juvenile fish t_0 was constrained to zero. There is little difference in growth parameters (Table 3.3.5) between locations for this species. The growth curves (Figures 3.3.11.a,b) show that for both sexes and both Australian locations, growth of goldband snapper is rapid for the first 10 years. Likewise Indonesian goldband snapper show similar growth patterns to Australian fish (Figures 3.3.11.c, d). Newman and Dunk (2003) obtained a similar growth curve for this species from the Kimberley region of Western Australia, although they obtained maximum ages of 30 years.

Kimura's (1980) Likelihood ratio test (Table 3.3.6) was applied to examine whether VBGF curves were significantly different between sexes for each location. Results show there was no significant difference for the VBGF curves between the sexes for the Timor Sea (χ^2=14.23, d.f.=3, P>0.05) and for *P. multidens* samples obtained from Indonesian waters (χ^2=4.42, d.f.=3, P>0.05). However there was a significant difference between the sexes in the Arafura Sea, χ^2=23.71, d.f.=3, P<0.05, with a significant difference (χ^2=10.7, d.f.=1, P<0.05) in $L\infty$ between the sexes and also a significant difference (χ^2=9.53, d.f.=1, P<0.05) in K values. When VBGF curves were compared for the Timor Sea and Indonesia (sexes combined), there was not a significant difference between the curves (Table 3.3.6).

The L_∞ values from this study are higher than those obtained by other researchers for this species, but similar to *Pristipomoides typus* (Table 3.4.7), and the K values are slightly lower than reported by other researchers (Table 3.4.7).

The von Bertalanffy curve is greatly influenced by the L_∞ and t_0 parameters at the extremities of the curve where data obtained from commercial fishery samples is usually poorly represented (Haddon 2001). Unfortunately due to the remoteness of the fishing grounds, it was not possible to get fishery-independent samples, therefore juvenile fish and older fish were poorly represented due to gear selectivity. I believe that this has artificially raised the value of L_∞, particularly in the Arafura Sea, where the largest fish observed was only 630 mm, therefore the values of L_∞ over 800 mm FL seem unlikely from this location. While L_∞values for the Timor Sea were slightly higher than values reported by other researchers for this species, it was close to the maximum FL observed for fish samples from the Timor Sea.

Table 3.3.5. Comparison of growth parameters derived from the von Bertalanffy growth function for *Pristipomoides multidens* from the Timor and Arafura Seas (Australia) and for Indonesia.

Site	**Sex**	**n**	**L_∞**	**K**	**FL Range**	**Age Range**
Timor Sea	Male	675	721.7	0.14	135-711	2-17
	Female	719	710.3	0.15	141-704	3-18
	Combined	1394	716.0	0.15	97-711	1-18
Arafura Sea	Male	738	871.0	0.10	120-630	2-15
	Female	706	713.6	0.13	135-584	1-14
	Combined	1572	787.6	0.11	97-630	1-15
Indonesia	Male	144	824.8	0.11	155-761	4-16
	Female	194	739.7	0.13	155-718	4-20
	Combined	338	824.5	0.10	155-761	4-20

Table 3.3.6. Comparison of VBGF parameters for *Pristipomoides multidens* from the Timor and Arafura Seas (Australia) and for Indonesia using likelihood ratio test (Kimura 1980). t_0 was constrained to zero.

Site	**Sex**	**L_∞**	**K**
Timor Sea	Male	710.3	0.15
	Female	721.7	0.14
		χ^2=2.21, P=0.137	χ^2=0.70, P=0.40
Arafura Sea	Male	713.6	0.13
	Female	871.0	0.10
		χ^2=10.7, **P=0.001**	χ^2=9.53, **P=0.002**
Indonesia	Male	739.7	0.13
	Female	824.8	0.11
		χ^2=0.62, P=0.43	χ^2=0.35, P=0.55
Timor Sea	F and M	863.5	0.10
Indonesia	F and M	824.5	0.10
		χ^2=0.48, P=0.49	χ^2=0.22, P=0.64

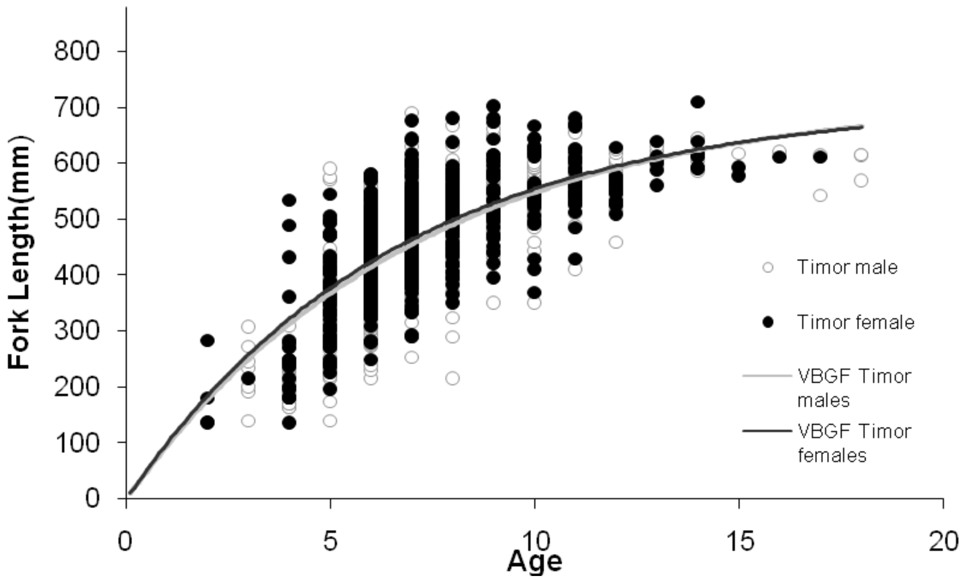


Figure 3.3.11a. Fork length at age and fitted VBGF curves for *Pristipomoides multidens* males and females for the Timor Sea

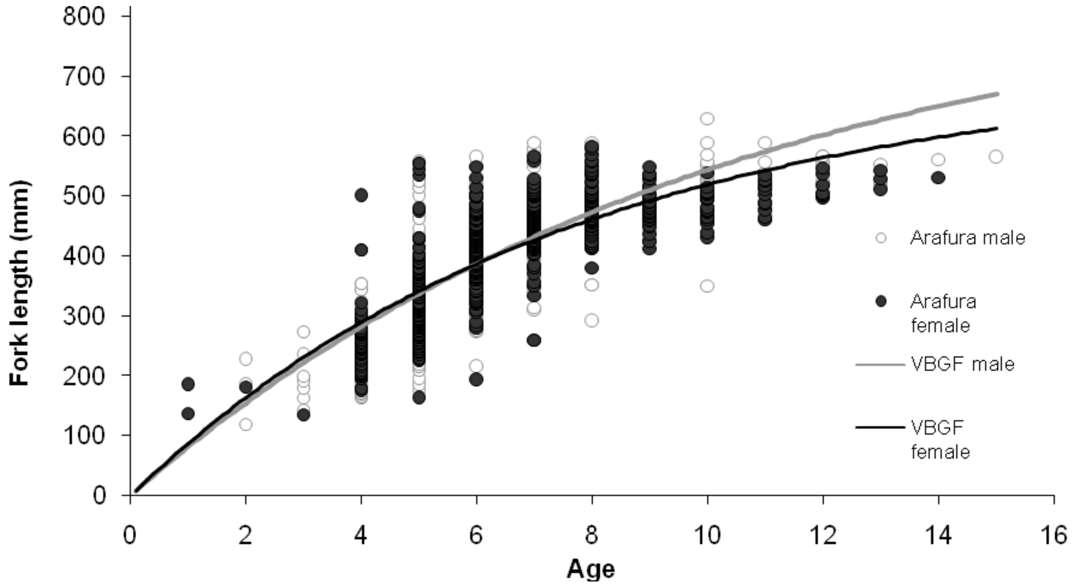


Figure 3.3.11b. Fork length at age and fitted VBGF curves for *Pristipomoides multidens* males and females for the Arafura Sea

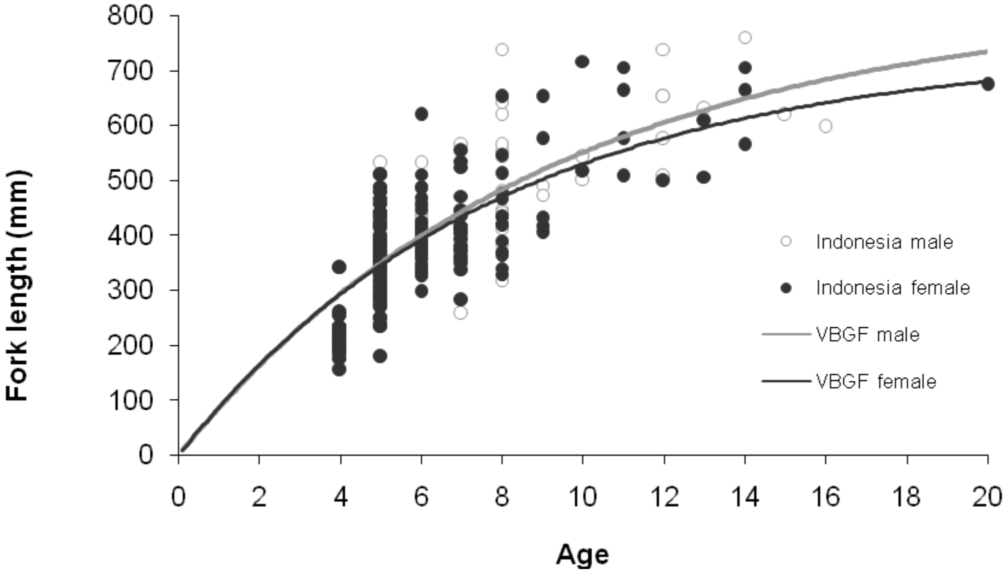


Figure 3.3.11c. Fork length at age and fitted VBGF curves for *Prisitipomoides multidens* males and females from Indonesian waters

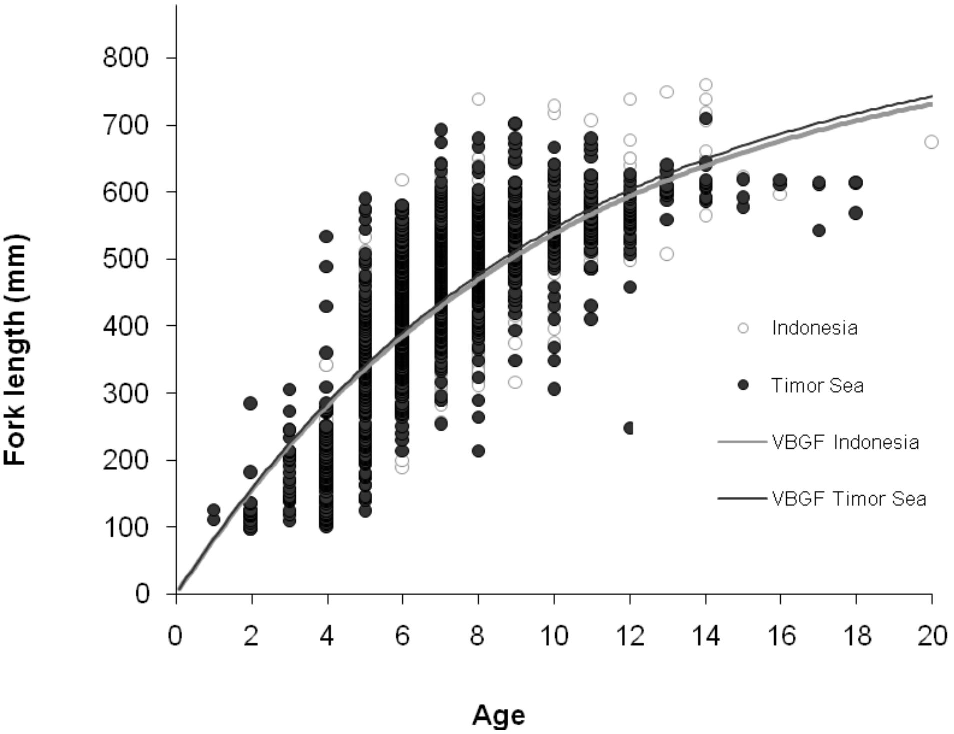


Figure 3.3.11d. Fork length at age and fitted VBGF curves for *Pristipomoides multidens* (sexes combined) from Australian and Indonesian waters

3.3.7. Comparison of mean length at age for Pristipomoides multidens

Comparison of mean length at ages 5, 7, 9 for *P. multidens* (Table 3.3.6) indicate that there is little difference in mean length at age between the sexes. However when sexes are combined and comparisons made between locations, it appears there is little difference in mean fork length for younger fish, but once fish reach 9 years the difference is pronounced, with fish in the Timor Sea having a substantially greater mean length than those from the Arafura Sea.

Table 3.3.7. Comparison of mean lengths at age *Pristipomoides multidens* from Arafura Sea (AS) and Timor Sea (TS).

Area	**Sex**	**L_5**	**s.e.**	**N**	**L_7**	**s.e.**	**N**	**L_9**	**s.e.**	**N**
AS	M	319	5.5	(161)	461	4.3	(138)	489	5.4	(30)
AS	F	320	5.0	(162)	450	3.4	(155)	479	5.3	(34)
TS	M	346	11	(61)	476	4.8	(168)	529	8.4	(49)
TS	F	355	10.6	(62)	475	5.2	(159)	545	11.3	(40)
AS	M and F	319	3.7	(323)	456	2.7	(291)	485	3.9	(640)
TS	M and F	350	7.6	(123)	476	3.5	(327)	536	6.9	(89)

3.3.8. Age frequency distributions Pristipomoides multidens

There was no significant difference between the age frequency distributions for the Timor and Arafura Seas (Kolmogorov-Smirnov test: $D=0.0560 < D_{0.05}=0.0702$) (Figure 3.3.12). For both sites the majority of fish are found in the 5-12 year age classes, with the peak age frequency being 6-8 years.

For both Australian and Indonesian sites, the dominant age classes are 6-8 years (Figure 3.3.13), and there is a significant difference in age frequency (Kolmogorov-Smirnov test: $D=0.1380 > D_{0.05}=0.0572$). However, there are a greater number of both older and younger fish in the Indonesian sample compared to Australian samples.

When this recent collection (1999-2001) is compared with the historical NT Fisheries collection (1990-92), there is no change in age frequency for the Timor Sea over this period of time (Kolmogorov-Smirnov test: $D=0.0372 < D_{0.05}=0.1072$) (Figure 3.3.14). The fishing method for both collections in the Timor Sea was trap and line. However in the Arafura Sea (Figure 3.3.15), there has been a significant change in age frequency over the nine year period between collections (Kolmogorov-Smirnov test: $D=0.4952 > D_{0.05}=0.0685$), with increased representation of older age classes (>6 years) in recent years.

When annual age-frequency is compared over a nine-year period (1990-98) from trap and line caught fish in the Timor Sea; it appears that the 5-8 year olds are the most abundant age classes (Figure 3.3.16). However due to the small sample size, trends between years cannot be inferred.

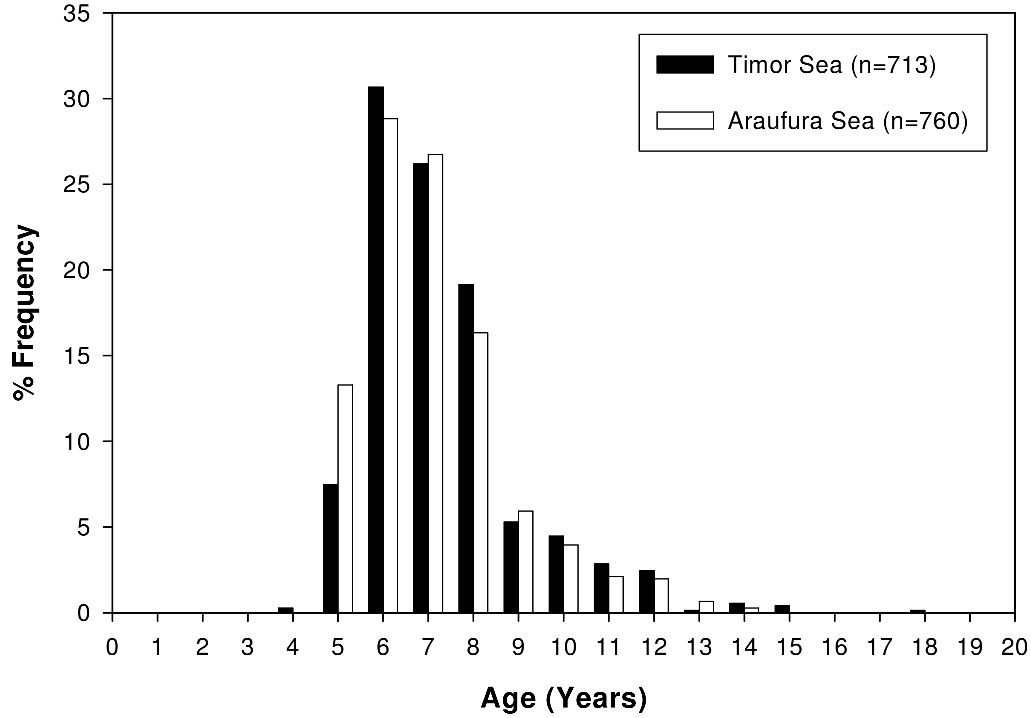


Figure 3.3.12. **Age-frequency for *Prisitpomoides multidens* for Timor and Arafura Seas**

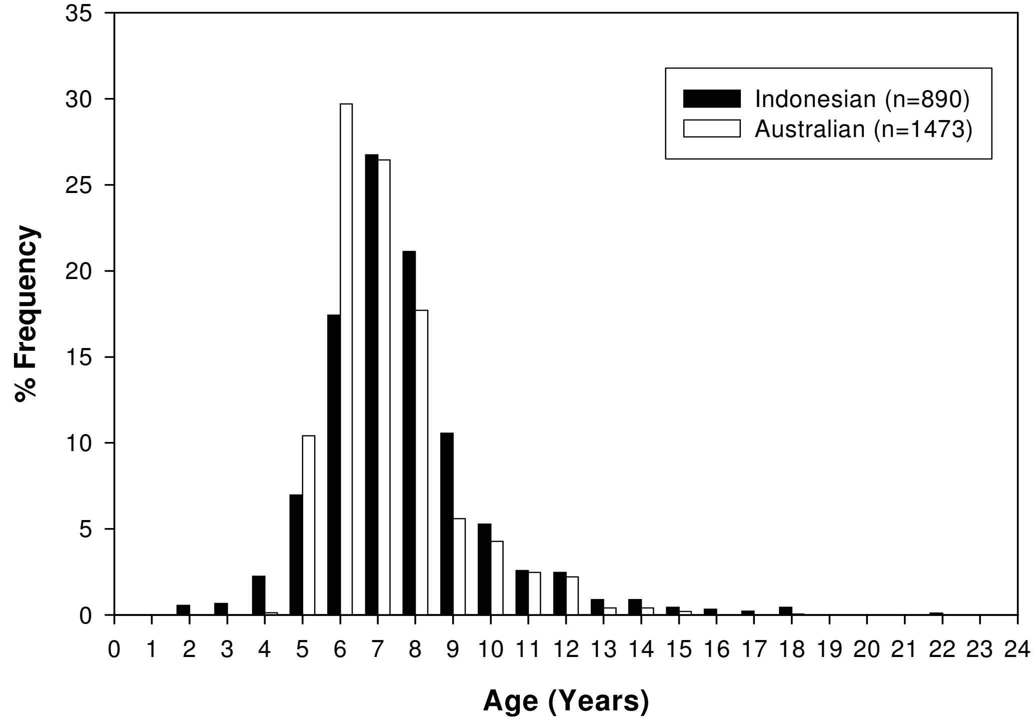


Figure 3.3.13. **Age-frequency for *Prisitpomoides multidens* of combined Australian and Indonesian samples**

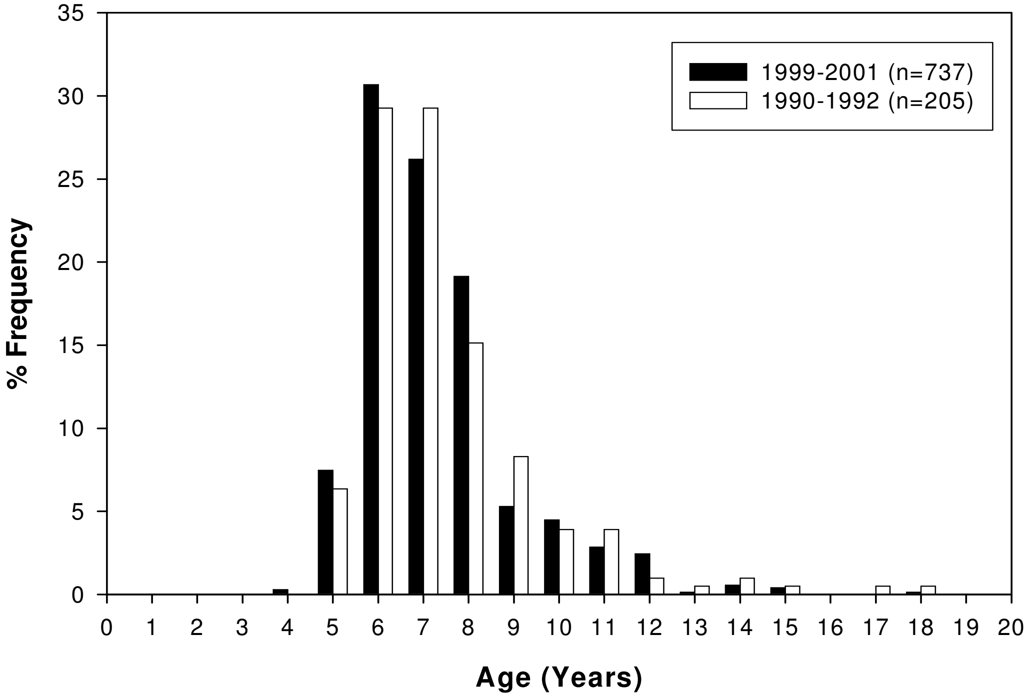


Figure 3.3.14. Age frequency comparison between historical NT Fisheries collection (1990-1992) and recent collection (1999-2001) for ***Pristipomoides multidens*** from the Timor Sea. The fishing method was trap and line

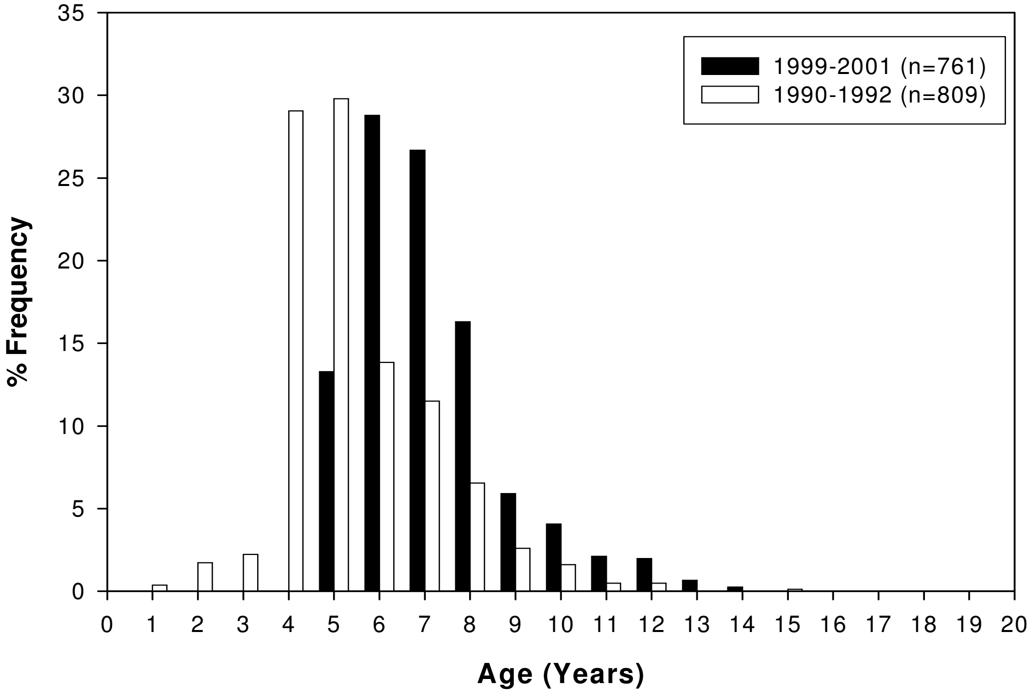


Figure 3.3.15. Age frequency comparison between historical NT Fisheries collection (1990-1992) and recent collection (1999-2001) for ***Pristipomoides multidens*** from the Arafura Sea. The fishing method was trawling

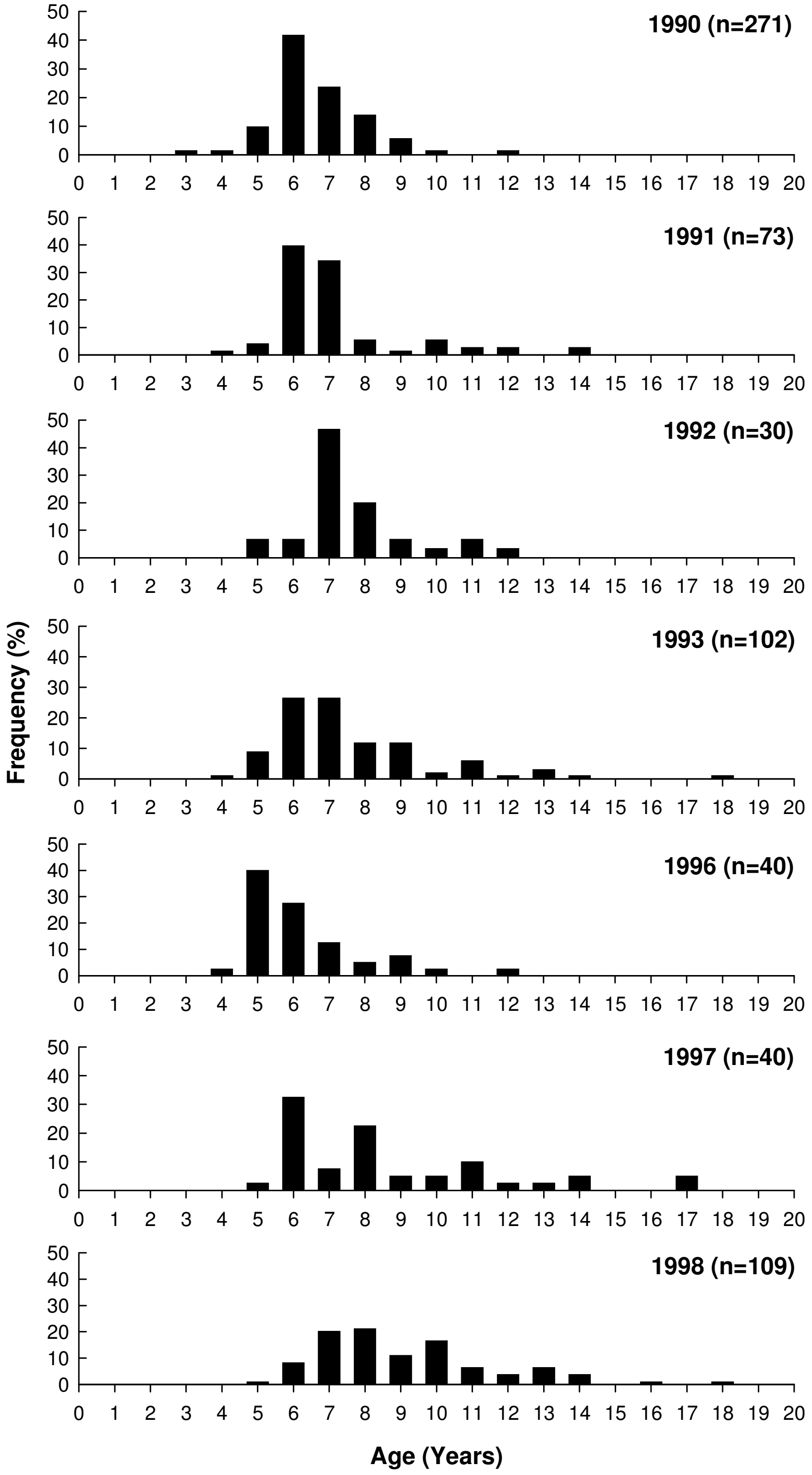


Figure 3.3.16. **Age-frequency distribution of goldband snapper (*Pristipomoides multidens*) from the Timor Sea (1990-1998)**

3.3.9. Mortality

Total instantaneous mortality (Z) for each location was estimated from the associated catch curves (Figures 3.3.17 and 3.3.18). These catch curves were obtained by plotting the log-transformed number of *P. multidens* in each age class, then fitting a linear regression to data which includes or exceeds the age at full recruitment to the fishery. The mode of the log-transformed catch-at age frequencies is assumed to be the age at full recruitment to the fishery. The slope of the catch curve is defined as the total instantaneous mortality (Z). Catch curves indicate that Z is estimated to be 0.59 for the Arafura Sea and 0.57 for the Timor Sea. Catch curves indicate that *P. multidens* is fully recruited to the fishery by 6 years.

Natural mortality (M) was estimated using Hoening (1983)

$M=\exp(1.46-1.01 \times \ln(t_{max}))$, where t_{max}=maximum age

This equation was derived for lightly fished stocks where the maximum age of the population is known. In the Timor Sea samples from the historical (1990) collection were from the early years of the fishery and therefore fit the criteria for use of the Hoening equation. The Arafura Sea samples were also taken in 1990. Although this was after a period of heavy trawling by foreign vessels in this area, therefore the maximum age for the Araura Sea is likely to be an underestimate of maximum age.

The oldest fish obtained for the Timor Sea was 18 years and for the Arafura Sea was 15 years. This gave M=0.18 for the Timor Sea and M=0.28 for the Arafura Sea.

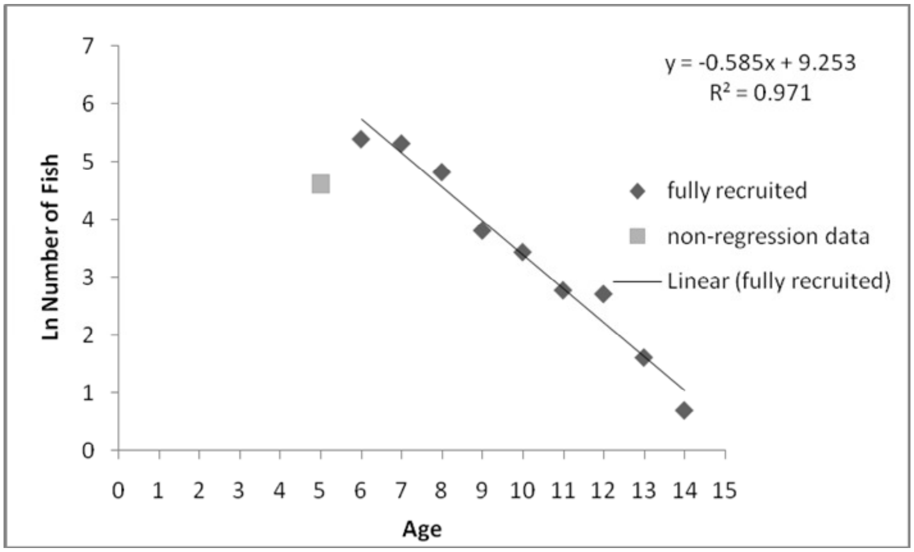


Figure 3.3.17. **Catch curve obtained from fitted regression to log transformed number of *Pristipomoides multidens* in each age class from the Arafura Sea. Only data from age classes which were fully recruited to the fishery were used for regression analysis**

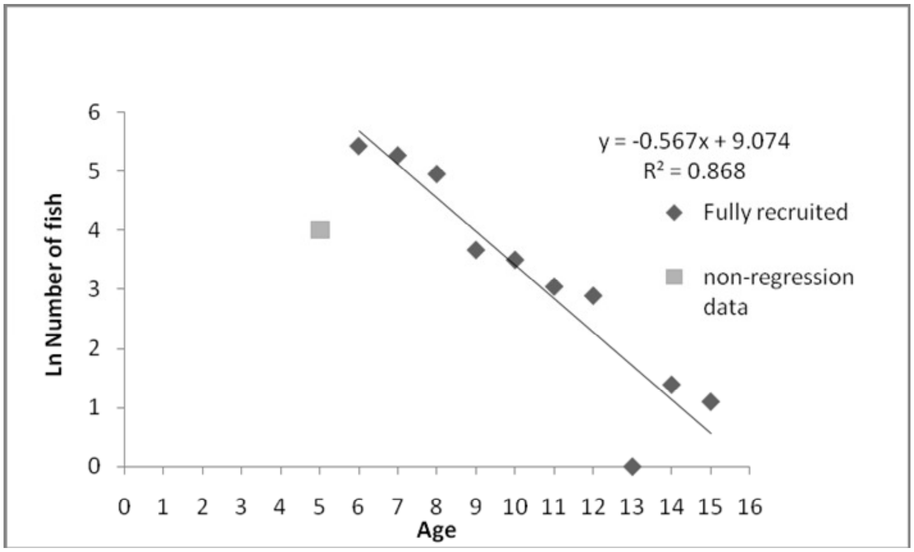


Figure 3.3.18. **Catch curve obtained from fitted regression to log transformed number of *Pristipomoides multidens* in each age class from the Timor Sea. Only data from age classes which were fully recruited to the fishery were used for regression analysis**

3.4. Results - Other lutjanids

3.4.1. Von Bertalanffy growth model for other lutjanids

Results from the von Bertalanffy growth model for *Lutjanus malabaricus*, *L. sebae*, *L. erythropterus* and *Pristipomoides typus* taken from the same locations as *P. multidens* are shown in Figures 3.4.1, 3.4.2, 3.4..3 and 3.4.4 and Table 3.4.1.

Kimura's (1980) likelihood ratio test (Table 3.4.2) was applied to examine whether VBGF curves were significantly different between sexes for each species. Results show that there is a difference between sexes for all four species examined, with both the L_∞ and K parameters exhibiting significant differences between the sexes.

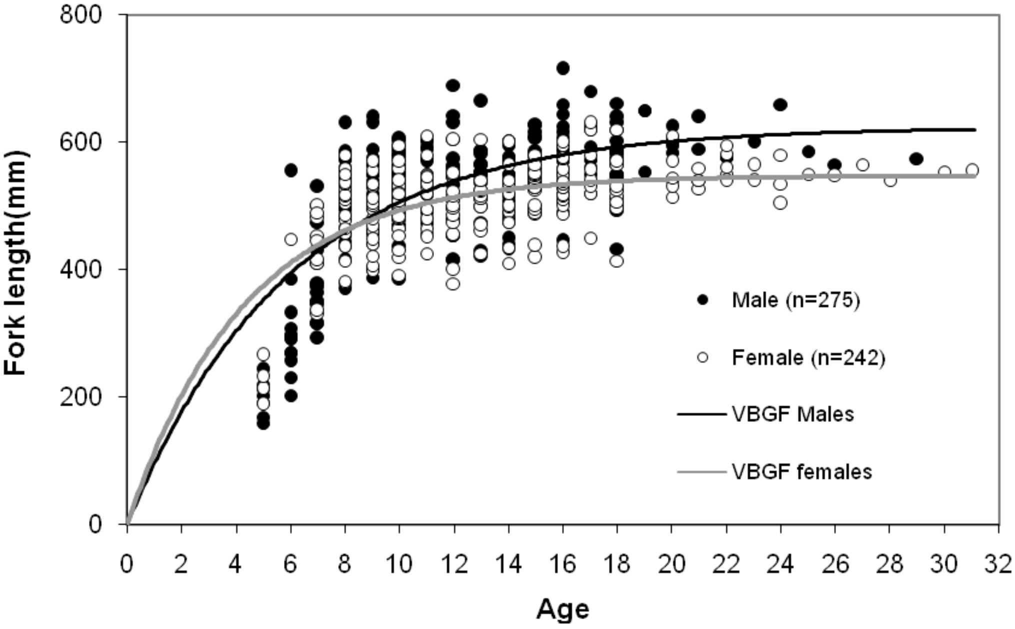


Figure 3.4.1. Fork length at age and fitted von Bertalanffy growth function for *Lutjanus malabaricus*

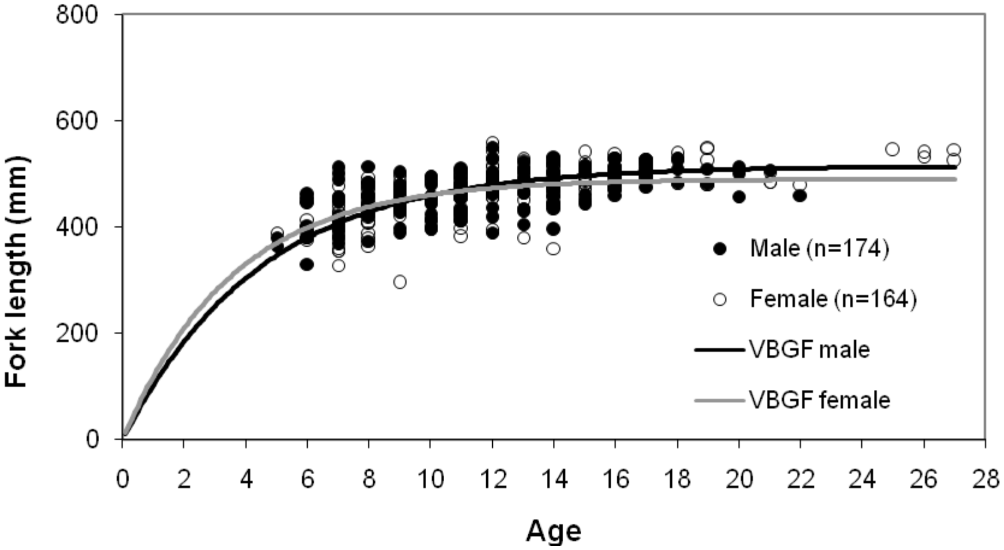


Figure 3.4.2. **Fork length at age and fitted von Bertalanffy growth function for *Lutjanus erythropterus***

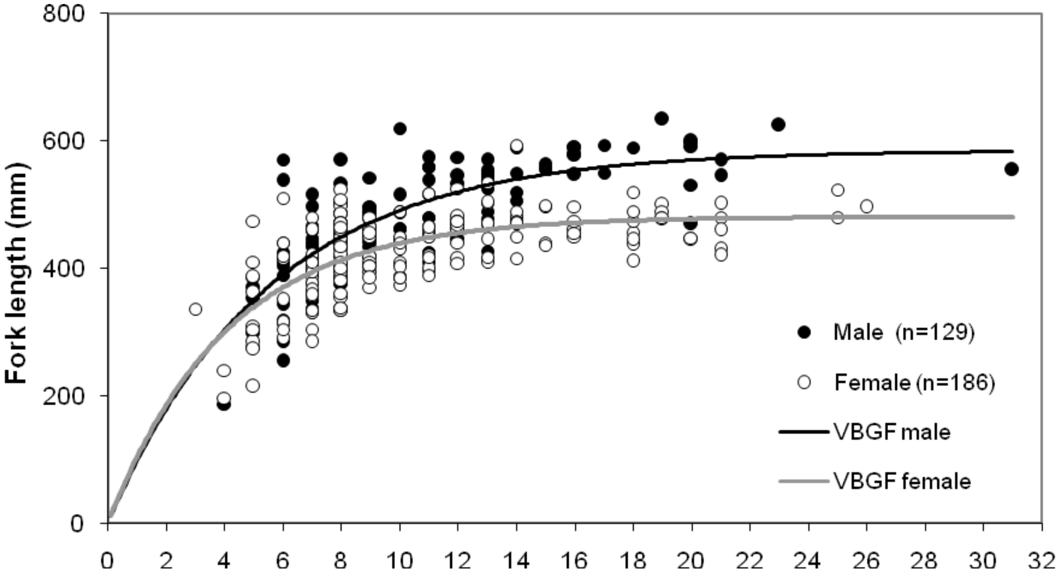


Figure 3.4.3. **Fork length at age and fitted von Bertalanffy growth function for *Lutjanus sebae***

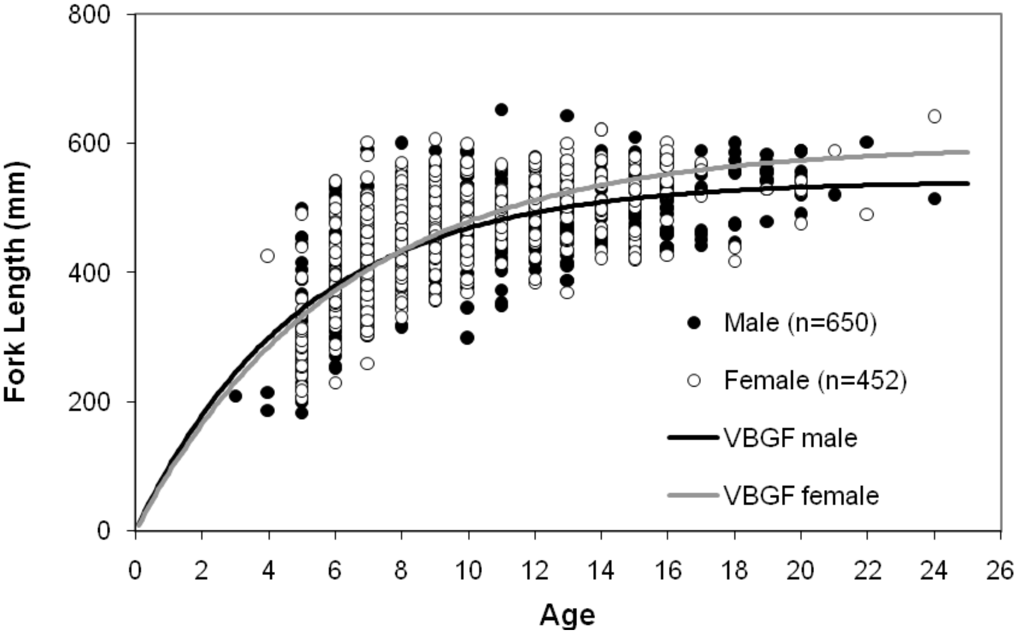


Figure 3.4.4. **Fork length at age and fitted von Bertalanffy growth function for *Pristipmoides typus***

Table 3.4.1. Comparison of growth parameters derived from von Bertalanffy growth function (VBGF) for other lutjanids from the Timor and Arafura Seas combined.

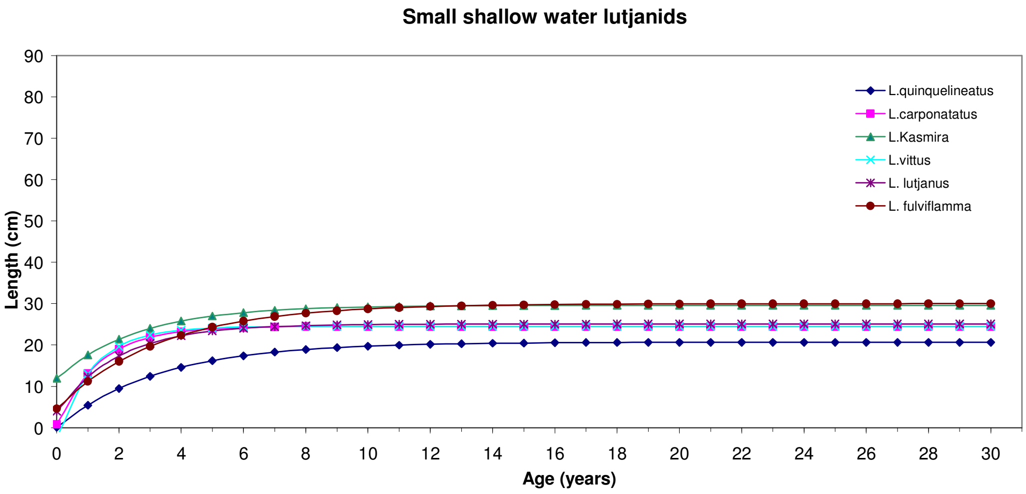
Species	**Sex**	**n**	**L∞**	**K**	**FL Range**	**Age Range**
Lutjanus malabaricus	Male	275	623.8	0.16	159-715	5-29
	Female	242	547.7	0.23	188-630	5-31
	Combined	517	585	0.19	125-715	5-31
L. erythropterus	Male	174	490.2	0.28	330-550	5-22
	Female	165	514.7	0.22	295-560	5-27
	Combined	402	503	0.25	365-560	5-27
L. sebae	Male	129	585.4	0.18	187-634	4-31
	Female	186	481.3	0.25	197-594	3-26
	Combined	389	540	0.18	105-634	3-31
Pristipomoides typus	Male	650	541.8	0.2	184-653	3-24
	Female	452	597.0	0.16	205-641	4-24
	Combined	1102	556	0.27	184-653	3-24

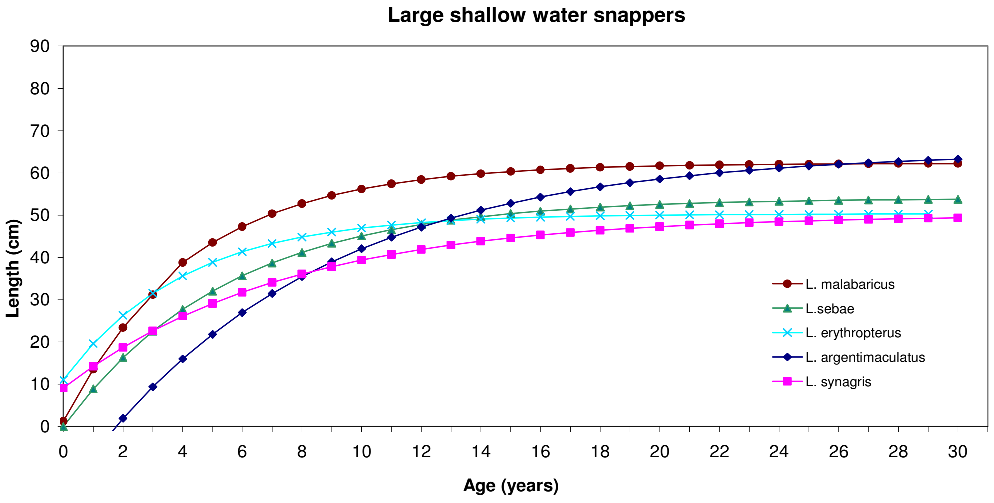
Table 3.4.2. Comparison of von Bertalanffy growth function parameters using likelihood ratio test (Kimura 1980).

Species	Sex	n	L_∞	K
Lutjanus malabaricus	Male	275	623.8	0.16
	Female	242	547.68	0.23
			χ^2=33.31, P=0.00	χ^2=15.4, P=0.00
Lutjanus erythropterus	Male	174	490.2	0.28
	Female	165	514.7	0.22
			χ^2=9.56, P=0.002	χ^2=8.94, P=0.003
Lutjanus sebae	Male	129	585.4	0.18
	Female	186	481.3	0.25
			χ^2=47.27, P=0.00	χ^2=10.48, P=0.001
Pristipomoides typus	Male	650	541.81	0.20
	Female	452	597.01	0.16
			χ^2=15.6, P=0.001	χ^2=11.7, P=0.001

3.4.2. General VBGF comparisons

To investigate whether growth changes with respect to depth, I examined VBG curves from genera within the different depth ranges. For species where I did not have data, curves are constructed from VBGF parameters in the literature, and were chosen only from papers where ages were obtained from otoliths and where the data was spread over a wide age range (Figure 3.4.5).


Small shallow water lutjanids


Large shallow water snappers

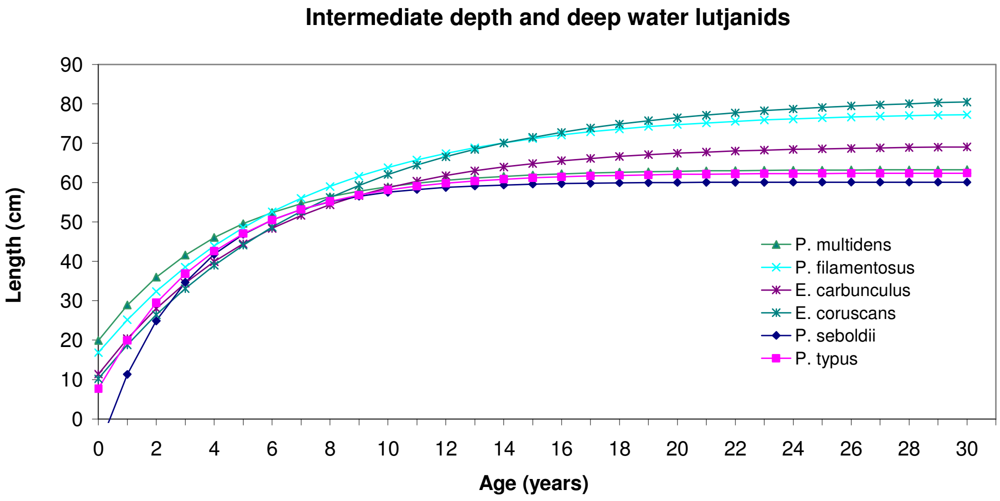

Intermediate depth and deep water lutjanids

Figure 3.4.5. **Comparison of generalised von Bertalanffy growth curves from the literature with respect to depth range. Growth curves have been constructed to age 30 years for the purposed of species comparison, but this does not indicate the maximum age of a species.**

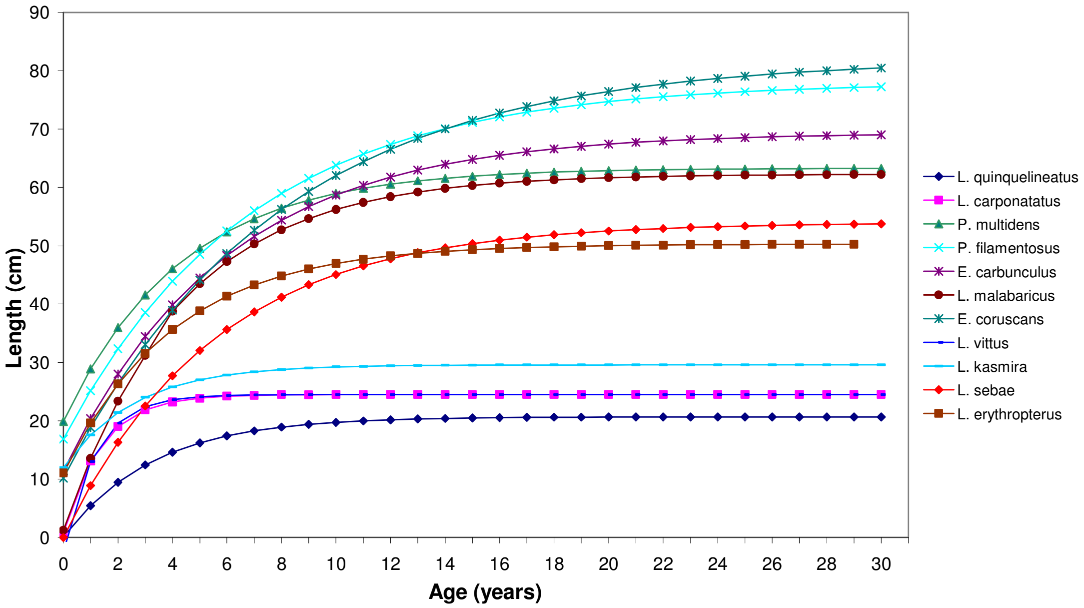


Figure 3.4.6. **Generalised von Bertalanffy growth curves from the literature for lutjanids within different depth ranges (see Table 3.4.3. for details). Growth curves have been constructed to age 30 years for the purposed of species comparison, but this does not indicate the maximum age of a species.**

Table 3.4.3. L_∞ and K values for species shown in Figure 3.4.6 with respect to depth range groupings.

Species	**L_∞**	**K**	**Location**	**Reference**
Small shallow water snappers				
Lutjanus quinquelineatus	20.7	0.306	Central GBR (Australia)	Newman et al.(1996a)
L. carponatatus	24.5	0.73	Palm Is GBR (Australia)	Krizer (2004)
L. vittus	24.5	0.853	Central GBR (Australia)	Newman (2000b)
L. kasmira	29.6	0.384	American Samoa	Ralston and Williams (1988a)
L. fulviflamma	30	0.3	New Caledonia	Loubens (1980a,b)
L. lutjanus	25.1	0.5	Malaysia	Ambak et al. (1985)
Large shallow water snappers				
Lutjanus malabaricus	62.3	0.225	NW Australia	Newman (2002)
L. sebae	54.0	0.18	Northern Australia	This study
L. erythropterus	58.5	0.39	GBR (Australia)	Newman et al. (2000a)
L. argentimaculatus	65.1	0.126	Qld (Australia)	Russell et al. (2003)
L. synagris	50.1	0.134	S Florida	Manooch and Mason (1984)

Species	**L_∞**	**K**	**Location**	**Reference**
Intermediate depth and deep water snappers				
Pristipomoides multidens	60.3	0.19	Kimberley (Australia)	Newman and Dunk (2003)
P. filamentosus	78	0.146	Hawaii	Ralston (1980)
P. seboldii	60.1	0.326	Hawaii	Williams and Lowe (1997)
P. typus	62.4	0.254	Northern Australia	Edwards (1985)
E. carbunculus	69.4	0.169	Hawaii	Ralston and Kawamoto (1987)
E. coruscans	82	0.128	Vanuatu	Brouard and Grandperrin (1984)

The VBGF curves in Figure 3.4.6 show a marked difference between small (L_∞ <40 cm) shallow water species and other lutjanids. It appears that for these small shallow water lutjanids (*L. kasmira*, *L. vittus*, *L. quinquelineatus, L. carponotatus*) growth is very rapid over the first five years, with asymptotic length occurring between 15 and 20 years. Recent studies have found that many of these species are long-lived. Maximum ages of 31 years have been reported for *L. quinquelineatus* (Newman et al. 1996a) and 18 years for *L. carponotatus* (Kritzer 2004). The larger shallow water species (*L. erythropterus, L. sebae, L, malabaricus, L. argentimaculatus*) exhibit VBG curves that are similar to species found in intermediate and deeper waters. Both the large shallow water and intermediate depth lutjanids experience the majority of growth occurs during the first 10 years, with asymptotic length occurring between 20 and 30 years. Maximum ages of 30-37 have been reported for these species (Table 3.4.7).

In the deeper water genera (*Etelis* spp.) the majority of growth occurs during the first 10-12 years with asymptotic length occurring at 30+ years. These species are longer lived than other lutjanids with maximum ages of 41 years reported for *E. carbunculus* (Brouard and Grandperrin 1984).

Therefore it appears that with increasing depth there is an increase in longevity and maximum size, and a decrease in growth rate, particularly in the early phase of life. Growth rates between species will be examined in more detail in Section 3.4.3.

3.4.3. Comparison of mean fork lengths at age and growth rates

A comparison of mean length at age was undertaken for *P. multidens, L. malabaricus* and *L. erythropterus* (Table 3.4.4). *Lutjanus sebae* was not included in this analysis as there was a large difference in growth rates between the sexes after 5 years. The results of this analysis show the mean lengths at age were greater in the Timor Sea than the Arafura Sea with the exception of mean length at 5 years for *L. malabaricus*.

Table 3.4.4. Comparison of *Pristipomoides multidens* mean length at ages 5, 7 and 9 years ± standard errors, sample number shown in brackets.

Location **Age**	***P. multidens***	**s.e.**	***L. malabaricus***	**s.e.**	***L. erythropterus***	**s.e.**
Arafura Sea						
5	319 (323)	3.7	212 (57)	3.1	378 (2)	10
7	456 (293)	2.7	376 (16)	16.3	414 (4)	5.2
9	485 (64)	3.9	484 (19)	14.2	426 (2)	17.5
Timor Sea						
5	350 (123)	7.6	180 (7)	10.1	385 (8)	7.5
7	476 (327)	3.5	426 (10)	43.4	415 (38)	5.8
9	536 (89)	6.9	528 (24)	10.4	457 (29)	5.8

To investigate this, growth rates were examined between the ages of 4-10 years for these species (Table 3.4.5.) to determine if there was a trend in growth rate with respect to depth. Unfortunately small sample sizes for all species except *P. multidens* made it difficult to compare growth rate at age between species. There appeared to be large fluctuations in growth between years for most species. Only *P. multidens*, which has larger sample sizes, showed a trend of decreasing growth with increasing age.

Table 3.4.5. Growth rate (mm/yr) comparisons between lutjanids. Number of samples is shown in brackets.

Age	***Pristipomoides multidens***	***Lutjanus malabaricus***	***Lutjanus erythropterus***
4	85.70 (210)	24.76 (14)	
5	88.57 (466)	67.10 (64)	17.19 (10)
6	49.37 (693)	119.25 (24)	13.89 (16)
7	48.88 (620)	106.53 (26)	27.44 (43)
8	15.42 (406)	4.39 (55)	6.75 (42)
9	15.42 (152)	11.24 (46)	40.15 (34)
10	17.65 (153)	13.72 (65)	20.00 (36)

Table 3.4.6. Comparison of upper 20% of the maximum ages of lutjanid species by location.

Species	Location	Fishing method	Mean 20% max Age	s.e.
Lutjanus malabaricus	Arafura Sea	Trawl	12.0 (5)	1.0
	Timor Sea	Trawl	15.1 (51)	0.36
	Timor Sea	Trap and dropline	20.3 (85)	0.37
L. sebae	Arafura Sea	Trawl	11.9 (24)	0.78
	Timor Sea	Trawl	14.9 (13)	0.99
	Timor Sea	Trap and dropline	17.8 (82)	0.43
L. erythropterus	Arafura Sea	Trawl	11.4 (36)	0.41
	Timor Sea	Trawl	13.0 (22)	0.51
	Timor Sea	Trap and dropline	18.3 (63)	0.37
Pristipomoides multidens	Arafura Sea	Trawl	9.0 (329)	0.08
	Timor Sea	Trap and dropline	10.6 (282)	0.11
P. typus	Arafura Sea	Trawl	10.2 (14)	0.67
	Timor Sea	Trap and dropline	16.2 (167)	0.16

The upper 20% of oldest fish for each species was analysed to compare mean maximum ages across species. Both location and capture method were taken into consideration (Table 3.4.6). Fish from the Timor Sea showed greater maximum observed age than those from the Arafura Sea and fish caught using trap and dropline method had greater maximum observed age than those caught by trawl in the Timor Sea.

When maximum observed age was compared between species*,* *L. malabaricus, L. erythropterus* and *L. sebae* all showed greater maximum observed age than *Pristipomoides* species.

3.5. Discussion

3.5.1. Age-frequency relationships

No significant difference was found in age frequency distributions of *Pristipomoides multidens* between the Timor and Arafura seas (Figure 3.3.12), however when age frequency is compared with the historical NT Fisheries collection (1990-92), there is a greater percentage of fish >5 years in the Arafura Sea collection compared with the historical collection (Figure 3.3.15). This may possibly be due to differences in fishing gear. The historical collection was taken with a Frank and Bryce trawl net (details are given in Chapter 2) with a 1 inch mesh net cod. This was a research cruise and the cod end had a smaller mesh than is normally used in commercial fishing gear in order to retain small fish and species which are not of commercial interest. Since this original collection was taken, there have also been developments in fishing gear with the development of the semi-pelagic trawl nets, such as the Julie-Anne trawl. The more recent collection was taken from a commercial vessel with this newer style trawl net which is designed to fish approximately seven metres from the sea-bed (to minimise habitat damage), whereas for the historical collection, the trawl nets fished across the sea-bed as was the practice at the time. Therefore these differences in fishing gear have probably contributed to the differences in size frequency rather than any a shift in age structure of the population.

3.5.2. Otolith weight versus age

Otolith weight was investigated to see if it could be used as a proxy for age and therefore provide a cheaper and more rapid assessment for ageing *P. multidens*. In both locations sampled, there was a large degree of overlap in otolith weights between age classes with most age groups having a range of 2 years either side of the observed age. The age percentage agreement between observed and predicted age was 39.4% for the Timor Sea and 37.5 % for the Arafura Sea. These results indicate that otolith weight would be a poor proxy for *P. multidens* age for these locations. These findings differ from studies undertaken by Newman and Dunk (2003) in Western Australia, who found a good correlation between otolith weight and age (r^2=0.94) for this species. However as Lou et al. (2005) has indicated, otolith-age relationships vary spatially and are dependent upon the environmental water conditions in which the fish live. Their study found variations in the relationship between otolith weight and age for *Plectropomus leopardus* between different sites. Worthington et al. (1995) also found spatial variations in the otolith weight-age relationship for the tropical damselfish *Pomacentrus moluccensis* and *P. wardi*. These studies concur with the spatial differences for *P. multidens* between Western Australian and Northern Territory sites and reinforce the need to determine the strength of the otolith weight-age relationship for each location even though the same species may show a good relationship between otolith weight and age elsewhere.

3.5.3. Validation

Marginal incremental ratio (MIR) analysis was investigated as a means of validating periodicity of zone formation for *P. multidens*. Although there was some suggestion of seasonality in the Timor Sea (Figure 3.3.7), it was inconclusive for validation purposes. The Arafura Sea MIR data showed no trends in seasonality.

Due to the difficulties in validating *P. multidens* using marginal increment analysis, edge analysis was undertaken. Results for this study showed annual periodicity of opaque and translucent zones for both the Timor and Arafura Seas (Figures 3.3.8). Opaque zones were laid down in greatest frequency from July-September and translucent zones between May and June, for samples taken from the Arafura Sea (Figure 3.3.8). For Timor Sea samples, opaque margins were most prevalent from June-September, and translucent margins between May-July (Figure 3.3.8).

Bomb radiocarbon analysis was undertaken by Kalish (2001) on *P. multidens* and *P. typus* from the Arafura Sea (NT), as a means of validating otoliths read by the author and also read by C. Green at the Central Ageing Unit. Kalish was unable to validate otoliths from the analysis of radiocarbon otolith cores. He concluded that the relatively low Δ 14C in the otolith core was either due to an overestimation of fish ages or the influence of the complex, and little understood oceanography, on the juvenile habitat. Age-at-length in this study is very similar to results obtained by Newman and Dunk (2003) for this species in the Kimberley region of Western Australia, and therefore it is more likely that oceanographic influences may be responsible for the relatively low Δ 14C in the otolith core.

Validation was not undertaken for *Lutjanus malabaricus, L. erythropterus* and *L. sebae* as samples were taken on an opportunistic basis. However validation of *Lutjanus malabaricus, L. erythropterus* from the same region of the Timor and Arafura Seas was undertaken Fry et al. (2009). They found that the formation of opaque growth increments in otoliths for these species occurred from April to September.

3.5.4. Age and Growth comparisons between lutjanids

Numerous studies (Pauly 1984, Pauly 1998, Gillooly et al. 2001, Griffiths and Harrod 2007) have found that metabolic rate increases with temperature, leading to an increase in growth with higher environmental temperature.

With increasing depth there is a decrease in water temperature and hence we would expect a decrease in the metabolic rate of fish, and if one accepts Pauly's theory, slower metabolic rate allows fish to reach a larger size before critical gill surface area to volume ratio is reached. Therefore it would be expected that fish would have slower growth and reach a larger size in deeper, cooler waters and conversely faster growth rate in the shallow water species, and also smaller maximum size. This is true for the shallow water species which do not migrate offshore upon maturity, such as *Lutjanus carponotatus, L. vitta, L. quinquelineatus* etc. where growth is very fast particularly in the first five years (Figure 3.4.5). Due to their accessibility and their sedentary nature, more studies have been conducted on these small shallow water species than the other lutjanid groups, and therefore the VBGF which they exhibit, with very fast growth in the juvenile phase is regarded by many as "typical reef fish growth". However this very fast juvenile growth may simply be an adaptation to the conditions in shallow waters where predation is high; particularly when juveniles leave the protection of reefs to forage. Hence it is advantageous to grow as quickly as possible through this vulnerable stage. In intermediate and deeper waters fishers target adult fish therefore juvenile fishing mortality is lower, and fishermen have reported anecdotally that there is a habitat separation for large and small *P. multidens* (Lloyd 1993), which may offer juvenile *P. multidens* some protection from predation by adult *P. multidens*. Therefore if mortality (both natural and fishing) is lower than for shallow water species, and productivity of deeper waters is poorer, then it is feasible that juvenile growth will be slower than at the equivalent stage for shallow water species, and as a consequence growth curves during this stage are very different.

Small shallow water lutjanids have high K and low L_∞ (Table 3.4.7.), exhibiting the characteristics Pauly attributes to "tropical fish". With improvements in ageing techniques, recent studies have found that many of these shallow water species are also relatively long-lived, e.g. *L. carponotatus*, which has a maximum age of 20 years (Newman et al. 2000b).

Many lutjanids, e.g. *L. malabaricus, L. erythropterus, L. sebae,* spend their juvenile phase in the shallow inshore waters and migrate offshore upon maturity (Williams et al. 2004). These species attain a higher L_∞ and have been categorised within this thesis as large shallow water snapper. In accordance with Pauly's theory it would be expected that these species would have a faster growth rate during their inshore juvenile phase compared to *Pristipomoides* spp., which spend their entire life in the intermediate depth range where temperatures are cooler. Unfortunately the very small number of juveniles in this study prevents this theory being tested. Growth rates *of L. malabaricus, L. erythropterus* and *P. multidens* were examined across cohorts 4-10 years (Table 3.4.5), but the small sample size of the three *Lutjanus* species prevented meaningful comparisons being made for growth rate at age between species. Only *P. multidens,* which had several hundred fish in each age class, showed a trend of decreasing growth rate with age. A large variation in fish growth within an age cohort is common in fish that are serial spawners, therefore a large sample size is needed to accommodate for variability within age classes.

Mean fork lengths at ages 5, 7 and 9 (cohorts with greatest sample numbers) were examined for large, shallow water lutjanid species and intermediate depth

Pristipomoides multidens (Table 3.4.4). For all species mean size at age was greater for the Timor Sea than the Arafura Sea. This is most likely related to depth differences and therefore different water temperature, as the Arafura Sea is shallower than the Timor Sea having a maximum depth of 60 m, compared to the Timor Sea with depths over 200 m. Samples from the Timor Sea were taken in the 100-150 m depth range, while samples from the Arafura Sea were caught in the 50-60 m depth range. An increase in fish size with depth has been reported by Brouard and Grandperrin (1985) for *Etelis carbunculus* and *P. filamentosus*. Findings from this study agree with these observations, and are consistent with Pauly's theory of an increase in size with decreasing temperature as a slower metabolic rate allows fish to reach a larger size before the critical gill surface area to volume ratio is reached.

Longevity was examined by comparing the upper (maximum) 20% of ages for *L. malabaricus*, *L. erythropterus* and *P. multidens*. Mean maximum ages were compared by location and capture method (Table 3.3.6). For all species longevity was greater in the Timor Sea than the Arafura Sea. This increase in longevity with depth is consistent with finding by Cailliet et al. (2001) for scorpaenids.

A gear selectivity factor was also observed (Table 3.4.6), as fish caught by trap and dropline were older than those caught by trawling. Examination of length frequency histograms for the Timor Sea by gear method (Figure 3.3.6) confirm that larger fish are caught by dropline method. This is probably due to competition, with larger, older fish being more aggressive and out competing smaller fish in the same school for baited hooks. Trawling is less selective with a more representative size range of fish taken.

When longevity was compared between species, *L. malabaricus, L. erythropterus* and *L. sebae* all showed greater longevity than the deeper water *Pristipomoides* species.

While the oldest fish in this study in NT waters was 18 years, few fish were observed older than 14 years, and a sharp decline in age classes after 8 years was observed (Figures 3.3.12, 3.3.14, 3.3.15 and 3.3.16). I do not believe that the lack of older fish in the NT study was due to the effect of overfishing as this fishery has been monitored since its inception, and age frequency shows no change over time (Figures 3.3.14). There may be a depth-related explanation for this observation. Cailliet et al. (2002) found that there is an increase in longevity with depth. The NT fishery is part of the Sahul Banks population and it is possible that the older fish are found in the deeper waters in the East Timorese section of the Sahul Banks. Newman and Dunk (2003) have reported a maximum age of 30 years for this species in the Kimberley region of Western Australia.

3.5.5. Comparison of von Bertalanffy growth function parameters between lutjanids

While fish growth has been linked to metabolic rate and water temperature, it is the VBGF which is commonly used to describe the major features of fish growth; i.e. K (growth rate) and asymptotic size (either length or weight). Examination of the VBGF curves (Figure 3.4.6) in relation to depth ranges shows that the small shallow water lutjanids which do not undertake offshore migration have a very different VBGF to the other lutjanid groups including the large, shallow water lutjanids. The VBGF growth parameters, and maximum ages (Table 3.4.7), also show that the large shallow water species have a greater similarity to lutjanids found in the intermediate depth ranges than the small shallow water species. In the intermediate depth range (100-200 m), which is dominated by the genus *Pristipmoides*, species have lower K and higher L_∞ compared with shallow water species. For most *Pristipomoides*, L_∞ ranges from 55 to 87 cm FL, and K values ranging from 0.10 to 0.36, with most authors reporting values between 0.20-0.28. In the deeper waters (>200 m), the *Etelis* species dominate e.g. *E. carbunculus* and *E. coruscans*. These species have low K (0.1-0.3) and high L_∞ (80-120 cm) compared with other members of the lutjanid complex. Maximum ages are similar to those reported for the intermediate species.

In addition to differences in metabolic rate due to temperature, variations in growth with respect to depth may be a result of adaptations to the differences in environmental conditions in which the different genera are found.

Many shallow water lutjanids, e.g. *L. vitta* (Davis and West 1992), and *L. quinquelineatus* (Newman et al. 1996a) grow at different rates after maturity (usually 3-4 years old), when the males grow significantly faster than females. Such differences do not appear to be the case for intermediate depth species such as *P. multidens,* where there appears to be no difference in length-at-age between sexes (this study, Newman and Dunk 2003).

There appears to be more variation in VBGF parameters for shallow water species than for the other depth ranges, especially for K values. For example, for *L. vitta*, K values can range from 0.22-0.98; likewise *L. carponotatus* exhibits K values ranging from 0.37-0.77 (Table 3.4.7). By comparison, species inhabiting intermediate depths and deep water have remarkably consistent VBGF parameters (Table 3.4.7), despite large regional and latitudinal differences. Several authors have found variation in growth parameters for shallow water reef fish on very small spatial scales. Newman et al. (1996b) found that for *L. quinquelineatus* on the Great Barrier Reef (GBR), growth varied between reefs within close proximity. Williams (2003) also found differences in growth between adjoining reefs on the GBR for *Lethrinus miniatus*. He examined what might be the driving factor for this and concluded that it was most likely to be related to food availability although a number of other localised factors could also be responsible.

In deeper waters, such as those found in the Timor Sea, conditions are influenced by the ITF, with the deep paleo-river channels found in this region providing an important means of transferring nutrient–enriched water from the Timor Trench (section 1.4.2). Therefore conditions are likely to be more uniform over a larger spatial scale than those found in inshore reefs inhabited by small-shallow water lutjanids.

3.5.6. Comparison of VBG parameters between regions

As the lutjanid complex is widely spread throughout tropical waters, VBGF parameters are available for species in different areas, allowing a regional comparison. Within Australia, *Lutjanus malabricus* and *L. sebae* have been studied from the Pilbara and Kimberley areas of Western Australia, through Northern Territory (NT) waters of the Arafura and Timor Seas to the Great Barrier Reef (GBR) of Queensland.

Examination of VBG parameters for these species within the Australia region (Table 4.4.7.) shows marked difference in L_∞ between species found in east coast waters, with those from the NT and Western Australia. For example, McPherson and Squire (1990), Newman et al. (2000a) have reported L_∞ for *L. malabaricus* as ranging from 72.8 cm FL to 105 cm FL in Queensland waters. Newman and Dunk (2002) have reported L_∞ of 56-68.6 cm FL for this species from Western Australia and Lloyd (this study) has found similar values for *L. malabaricus* in NT waters with L_∞ of 58.8-62.4cm FL. Large differences in L_∞ values have also been reported for *L. sebae* with McPherson and Squire (1990), Newman et al. (2000a) reporting L_∞ values for *L. sebae* ranging from 72.0 cm SL to 102 cm FL in Queensland, whereas Newman and Dunk (2002) have found for the same species taken from Western Australia to have L_∞ ranging from 48.2-62.8 cm FL. Lloyd (this study) has found similar values to Newman and Dunk (2002), with L_∞ 48.1-58.5 cm FL for *L. sebae* in NT waters.

3.5.7. Mortality

Total instantaneous mortality (Z) was determined from catch curves and was similar for both locations; Z was estimated to be 0.59 for the Arafura Sea and 0.57 for the Timor Sea.

Natural mortality (M) was estimated using Hoening (1983) equation, and was estimated to be 0.18 for the Timor Sea, and 0.28 for the Arafura Sea. However the M value for the Arafura Sea is likely to be an over-estimation of natural mortality, as the samples for the Arafura Sea were taken in 1990, immediately after a period of heavy trawling by foreign vessels in this area.

These regional differences may be the result of differences in natural mortality for different regions or genetic differences between different populations. Genetic studies of *L. malabaricus* undertaken by Elliot (1996) indicated that samples from east coast of Queensland were significantly different from samples taken from the Gulf of Carpentaria and the North West Shelf, suggesting that there is little gene flow through the Torres Strait.

Gear selectivity factors could also contribute to the observed differences in natural morality between the east coast and other areas. Samples taken by McPherson and Squire (1990) and Newman et al. (2000a) were obtained using line methods, whereas samples obtained by Lloyd (this study) and Newman and Dunk (2002) were from the commercial fisheries using trap and dropline methods.

3.6. Conclusion

In conclusion, there appear to be differences in demography within the lutjanid complex with respect to depth. Small, shallow water species show very different patterns compared with other lutjanids. There appear to be more variation in small, shallow water lutjanids across local scales, compared with deeper water lutjanids, which show similar growth patterns for separate stocks in different habitats and different regions.

With increasing depth there is an increase in size and longevity within species groups. Fish from the shallower Arafura Sea exhibited a smaller mean size at age than the same species in the Timor Sea. These observations are consistent with the theory of Pauly (1984, 1998) and others (Griffiths and Harrod 2007, Gillooley et al. 2001) that with decreasing temperature there is a decrease in metabolic rate.

Gear selectivity also seems to confound results, as fish caught by trap and dropline methods are larger and older than fish caught by trawling in the same location. This may be due to older larger fish being more aggressive than smaller fish towards baited gear or perhaps larger fish were able to evade trawl gear. This in turn may have an effect on L_∞ as the VBGF is highly influenced by samples at the extremities of the sample range. Therefore a lack of older fish in the Arafura Sea may account for the observed L_∞ which is considerably larger than that for the Timor Sea for *P. multidens*.

Table 3.4.7. Age and growth parameters for members of the lutjanid complex from the literature. Figures in **bold** were derived from equations in Froese and Binohlan (2000).

Species	**L_∞ (cm)**	**K**	**t_0**	**Sex**	**$L_{maturity}$ (cm)**	**$A_{maturity}$ (years)**	**A_{max} (years)**	**M**	**Comments**	**Location**	**Source**
Small shallow water											
Lutjanus adetii	26.5	0.145	-8.077	M and F	**17.04**		24	0.24	Otoliths	Central GBR (Aust)	Newman et al (1996a)
L. carponotatus	24.6	0.77	-0.049	F	19	1.9	18		Otoliths	Palm Is GBR (Aust)	Krizer (2004)
	26.4	0.69	-0.049	M	**16.8**	**1.4**	16		Otoliths	Palm Is GBR (Aust)	Krizer (2004)
	28.4	0.453	0.001	F	**18.2**	**2.3**	17	0.2	Otoliths	Central GBR (Aust)	Newman et al (2000b)
	34.4	0.371	-0.03	M	**21.8**	**2.7**	18	0.2	Otoliths	Central GBR (Aust)	Newman et al (2000b)
	31.3	0.449	-0.02	M and F	**19.9**	**2.3**	20	0.2	Otoliths	Central GBR (Aust)	Newman et al (2000b)
L. fulviflamma	30	0.3	-0.55	M and F	21.5	3.5	23	**0.96**	Otoliths	New Caledonia	Loubens (1980a, b)
L. kasmira	24.8	0.38	**0.46**	Unknown	**14.9**	**2**	8	**1.11**	Otoliths	New Caledonia	Loubens (1980a, b)

*t_0 constrained to zero

Species	**L_∞ (cm)**	**K**	**t_0**	**Sex**	**$L_{maturity}$ (cm)**	**$A_{maturity}$ (years)**	**A_{max} (years)**	**M**	**Comments**	**Location**	**Source**
Small shallow water											
L. kasmira	29.6	0.384	-1.35	Unknown	**18.9**	**1.31**	**4.6**		Otoliths	American Samoa	Ralston and Williams (1988a)
	39.6	0.212	-0.75	Unknown	**24.9**	**3.9**	**13.1**		Otoliths	American Samoa	Ralston and Williams (1988a)
	40	0.212	-0.75	Unknown	**25.2**	**3.9**	**13.1**		Otoliths	N. Marianas	Ralston and Williams (1988a)
L. lutjanus	24.7	0.7	**-0.23**	Unknown	15.1	1	**4**	1.32	Unknown	Ticao Pass Philippines	Corpuz et al. 1985
	25.1	0.497	**-0.35**	Unknown	**16.2**	**1.7**	**6**	**1.26**	Unknown	Malaysia	Ambak et al. (1985)
L. quinquelineatus	20.7	0.306	-2.59	M and F	**13.5**	**0.86**	31		Otoliths	Central GBR (Aust)	Newman et al (1996a)
	20.5	0.37	**-0.495**	M	13.3	2.5	22	**1.46**	Otoliths	New Caledonia	Loubens (1980a ,b)
	20.5	0.37	**-0.495**	F	13.4	2.5	20	**1.46**	Otoliths	New Caledonia	Loubens (1980a, b)
L. vitta	42.2	0.22	-0.56	M	**26.4**	**3.9**	8	0.59	Urahyles	NW Shelf (Aust)	Davis and West (1992)
	32.5	0.37	-0.23	F	**20.7**	**2.5**	7		Urahyles	NW Shelf (Aust)	Davis and West (1992)
	24.2	0.818	-0.1	F	**15.6**	**1.7**	12	0.34	Otoliths	Central GBR (Aust)	Newman et al (2000b)

*t_0 constrained to zero

Species	**L_∞ (cm)**	**K**	**t_0**	**Sex**	**$L_{maturity}$ (cm)**	**$A_{maturity}$ (years)**	**A_{max} (years)**	**M**	**Comments**	**Location**	**Source**
Small shallow water											
L. vitta	24.4	0.983	-0.08	M	**15.7**	**1**	9	0.34	Otoliths	Central GBR (Aust)	Newman et al (2000b)
	24.5	0.853	0.109	M and F	**15.8**	**1.3**	12	0.34	Otoliths	Central GBR (Aust)	Newman et al (2000b)
	33.1	0.32	-0.498	M	**21.0**	**2.7**	12	**0.9**	Otoliths	New Caledonia	Loubens (1980a ,b)
	28	0.3	**-0.56**	F	17.6	**2.7**	12	**1.02**	Otoliths	New Caledonia	Loubens (1980a ,b)
Large shallow water											
Aprion virescens	66	0.31		Unknown	**40.4**	**3.05**	**10.3**		Otoliths	New Caledonia	Loubens (1980a ,b)
	95	0.29		M	**57.1**	**3.17**	**10.7**		ELEFAN	Seychelles	Mees (1992)
	108	0.14		F	63	**6.3**	**20.5**		ELEFAN	Seychelles	Mees (1992)
	79	0.13		Unknown	47.9	7.2	19		ELEFAN	Seychelles	Pilling et al. (2000)
L. argentimaculatus	65.1	0.126	1.761	M	44.9	**11.0**	37	0.16	Otoliths	N.Australia	Russell et al. (2003)
	68.1	0.126	2.893	F	51.2	**14**	37	0.16	Otoliths	N.Australia	Russell et al. (2003)
L. erythropterus	93.3	0.09	-1.416	Unknown	**49**	**6.9**	32	0.49	Otoliths	N. Australia	Sheaves (1995)
	105	0.187	-0.642	Unknown	**62.8**	3	**16**	0.25	Otoliths	E.Malaysia	Ambak et al. (1985)
	73.8	0.17	-0.781	Unknown	**44.9**	**4**	**18**	**0.51**	Otoliths	New Caledonia	Loubens (1980a ,b)

*t_0 constrained to zero

Species	L_∞ (cm)	K	t_0	Sex	$L_{maturity}$ (cm)	$A_{maturity}$ (years)	A_{max} (years)	M	Comments	Location	Source
	60	0.41	0.21	M	**36.9**	**2.5**	**7**	**0.73**	Otoliths	GBR (Aust)	McPherson and Squire (1990)
Large shallow water											
L. erythropterus	60	0.44	0.21	F	**36.9**	**2.3**	**7**	**0.73**	Otoliths	GBR (Aust)	McPherson and Squire (1990)
	65.6	0.3	**-0.447**	Unknown	**40.2**	**2.7**	**6**	**0.63**	Otoliths	N.Australia	Milton et al. (1995)
	58.5	0.39	0.177	Unknown	**38.4**	**2.6**	32	0.15	Otoliths	GBR (Aust)	Newman et al. (2000a)
L. gibbus	45.8	0.17	**-0.89**	Unknown	**28.6**	**4.9**	**16.1**	**0.71**	Otoliths	New Caledonia	Loubens , G. (1980)
	47.6	0.31	**-0.472**	Unknown	**29.7**	**2.7**	**10**	**0.87**	Otoliths	PNG	Munroe and Williams (1985)
L. griseus	69.7	0.18	0.49	M	**42.6**	**5.7**	24	**0.55**	Otoliths	Florida	Burton (2001)
	76.8	0.16	0.16	F	**46.6**	**6**	24	**0.51**	Otoliths	Florida	Burton (2001)
	71.6	0.17	-0.001	M and F	**43.7**	**5.5**	24	0.43	Otoliths	NE. Florida	Burton (2001)
	62.5	0.13	-1.33	M and F	**38.4**	**6**	15	0.38	Otoliths	S. Florida	Burton (2001)
	89	0.10	-0.316	Unknown	**53.7**	**8.8**	21	0.22	Otoliths	E.Florida	Manooch and Matherson (1983)
	53.8	0.24	-0.616	F	34.1	**3.6**	7	**0.73**	Otoliths	SE Cuba	Baez Hilago et al (1980 and 1982)

*t_0 constrained to zero

Species	**L_∞ (cm)**	**K**	**t_0**	**Sex**	**$L_{maturity}$ (cm)**	**$A_{maturity}$ (years)**	**A_{max} (years)**	**M**	**Comments**	**Location**	**Source**
	53.8	0.24	-0.616	M	25.7	2	7	**0.73**	Otoliths	SE Cuba	Baez Hilago et al (1980 and 1982)
Large shallow water											
	52.8	0.15	-1.84	Unknown	**32.7**	**4.6**	**20**	**0.74**	Otoliths	Cuba	Salahange (1984)
L. johnii	66.7	0.13	**-1.06**	Unknown	**40.8**	**6.2**	**23**	**0.63**	Length based	Philippines	Pinto (1986)
	72.4	0.37	**-0.345**	Unknown	39.1	2	8	**0.62**	Unknown	Indonesia	Badrudin (1985)
	96.1	0.116	**-1.084**	Unknown	29.4	**2**	9	**0.5**	Scales	Andaman Sea India	Druzhinin (1970)
L. malabaricus	56	0.262	-0.09	F	**34.6**	**3.6**	26	0.11	Otoliths	NW Australia	Newman (2002)
	68.6	0.18	-0.33	M	**41.9**	**4.9**	31	0.11	Otoliths	NW Australia	Newman (2002)
	62.3	0.225	-0.09	M and F	**38.2**	**4.1**	31	0.11	Otoliths	NW Australia	Newman (2002)
	60	0.31	**-0.382**	Unknown	**36.9**	**2**	**10**	0.42	Otoliths	Vanuata	Brouard and Grandperrin (1984)
	86.6	0.168	0.418	Unknown	**52.3**	5.9	10	**0.53**	Vertebrae	Arafura Sea,Aust	Edwards (1985)
	72.8	0.287	0.239	Unknown	**44.4**	**3.5**	20	0.13	Otoliths	GBR, Aust.	Newman et al.(2000a)
	99.3	0.19	**-0.641**	M	**59.6**	**4.2**	**16**	**0.44**	Otoliths	GBR, Aust.	McPherson et al. (1985)
	105.4	0.25	**-0.474**	F	**63.0**	**3.2**	**12**	**0.43**	Otoliths	GBR, Aust.	McPherson et al. (1985)

*t_0 constrained to zero

Species	**L_∞ (cm)**	**K**	**t_0**	**Sex**	**$L_{maturity}$ (cm)**	**$A_{maturity}$ (years)**	**A_{max} (years)**	**M**	**Comments**	**Location**	**Source**
	83.8	0.23	-0.13	F	**50.7**	**3.9**	7	0.23	Otoliths	GBR, Aust.	McPherson and Squire (1990)
Large shallow water											
L. malabaricus	98.7	0.18	-0.13	M	**59.2**	**5.0**	7	**0.45**	Otoliths	GBR, Aust.	McPherson and Squire (1990)
	86.1	0.252	-0.08	F	21.1	2	10	0.32	Unknown	NW Shelf, Aust	Chen et al. (1984)
	86.1	0.252	-0.085	M	21.1	2	10	0.32	Unknown	NW Shelf, Aust	Chen, et al. (1984)
	96.36	0.12	1.29	Unknown	**57.9**	**5**	8	0.48	Vertebrae	Arafura Sea, Aust	Lai and Liu (1979)
	93.72	0.126	1.34	Unknown	**56.4**	**4.5**	8	**0.49**	Vertebrae	NW Shelf	Lai and Liu (1979)
L. sebae	48.2	0.271	0.065	F	**30.0**	**3.7**	12		Otoliths	Kimberley, NW Aust	Newman and Dunk (2002)
	62.8	0.151	-0.6	M	**38.6**	**5.7**	19		Otoliths	Kimberley, NW Aust	Newman and Dunk (2002)
	86.1	0.21	**-0.601**	F	**52.0**	**3.8**	**14**	**0.49**	Otoliths	GBR, Aust.	McPherson et al. (1985)
	108.8	0.14	**-0.858**	M	**64.9**	**5.6**	**21**	**0.42**	Otoliths	GBR, Aust.	McPherson et al. (1985)
	79.2	0.139	-0.92		**48.1**	**5.8**	19.0		Otoliths	GBR, Aust.	Newman et al. (2000a)
	88.7	0.18	-0.32	F	**53.5**	**4.8**	16.0		Otoliths	GBR, Aust.	McPherson and Squire (1990)

*t_0 constrained to zero

Species	**L_∞ (cm)**	**K**	**t_0**	**Sex**	**$L_{maturity}$ (cm)**	**$A_{maturity}$ (years)**	**A_{max} (years)**	**M**	**Comments**	**Location**	**Source**
	102	0.15	-0.32	M	**61.1**	**5.8**	19		Otoliths	GBR, Aust.	McPherson and Squire (1990)
Large shallow water											
L. sebae	79.8	0.18	-0.4	Unknown	**48.4**	**4.8**	15.8		Otoliths	Arafura Sea, Aust	Liu and Yeh (1991)
	81.7	0.13	-1.09	Unknown	**49.9**	5	10	**0.54**	Unknown	NW Aust	Yeh et al. (1986)
L. synagris	50.4	0.38	**-0.376**	Unknown	**31.3**	**2.2**	10	**0.73**	Otoliths	Alamba, USA	
	50.1	0.134	-1.49	Unknown	31.1	**5.7**	10	0.27	Otoliths	S Florida	Manooch and Mason (1984)
	48.8	0.25	-1.05	Unknown	**30.4**	2	12	**0.79**	Otoliths	N Cuba	
L. synagris	70.8	0.22	-0.55	M	**43.2**	1	4	0.47	Otoliths	Trinidad	Manickchand-Dass (1988)
	60.3	0.2	-0.68	F	**37.1**	2	4	0.43	Otoliths	Trinidad	Manickchand-Dass (1988)
Intermediate depth											
Pristipomoides multidens	59 (SL)	0.22	-0.07	Unknown	**35.5**	4	14	0.31	Vertebrae	Timor Sea, Aust	Edwards (1985)
	59.5	0.19	-0.36	M	**30.1**	3	30	0.1-0.14	Otoliths	Kimberley Aust	Newman and Dunk (2003)

*t_0 constrained to zero

Species	**L_∞ (cm)**	**K**	**t_0**	**Sex**	**$L_{maturity}$ (cm)**	**$A_{maturity}$ (years)**	**A_{max} (years)**	**M**	**Comments**	**Location**	**Source**
	60.3	0.19	0.002	F	**37.1**	5	27	0.1-0.14	Otoliths	Kimberley Aust	Newman and Dunk (2003)
Intermediate depth											
Pristipomoides multidens	59.8	0.19	-0.173	M and F	**6.5**		30	0.1-0.14	Otoliths	Kimberley Aust	Newman and Dunk (2003)
	72.2	0.14	*0	M				0.18	Otoliths	Timor Sea, Aust	Lloyd (this study)
	71.0	0.15	*0	F				0.18	Otoliths	Timor Sea, Aust	Lloyd (this study)
	71.6	0.15	*0	M and F				0.18	Otoliths	Timor Sea, Aust	Lloyd (this study)
	87.1	0.1	*0	M				0.28	Otoliths	Arafura Sea, Aust	Lloyd (this study)
	71.4	0.13	*0	F				0.28	Otoliths	Arafura Sea, Aust	Lloyd (this study)
	78.7	0.1	*0	M and F				0.28	Otoliths	Arafura Sea, Aust	Lloyd (this study)
	65	0.28		Unknown	**35.5**	3		0.42	Otoliths	Vanuatu	Brouard and Grandperrin (1984)
	61	0.35		Unknown	**33.5**	2		**0.46**	Daily rings	Vanuatu	Brouard and Grandperrin (1984)
	73.6	0.188	-0.22	Unknown	**39.6**	4	16		Daily rings	PNG	Richards (1987)

*t_0 constrained to zero

Species	**L_∞ (cm)**	**K**	**t_0**	**Sex**	**$L_{maturity}$ (cm)**	**$A_{maturity}$ (years)**	**A_{max} (years)**	**M**	**Comments**	**Location**	**Source**
P. filamentosus	81.7	0.29		Unknown	**43.5**	3		0.53	Length freq	Seychelles	Mees (1993)
	75.8	0.24	-0.26	Unknown	**40.7**	3	12	**0.46**	Length freq	Seychelles	Mees and Rousseau (1997)
Intermediate depth											
P. filamentosus	78	0.146	-1.67	Unknown	**41.8**	4	19	0.25	Daily rings	Hawaii	Ralston and Miyamoto (1983)
	80.5	0.164	-0.84	Unknown	**43**	4	17	**0.44**	Daily rings	Hawaii	Ralston (1980)
P. seboldii	60.1	0.36								Hawaii	Williams and Lowe (1997)
P. typus	62.4	0.254							Vertebrae	Nth Australia	Edwards, R.C. (1985)
	54.2	0.2	*0	M					Otoliths	Nth Australia	Lloyd (this study)
	99.7	0.16	*0	F					Otoliths	Nth Australia	Lloyd (this study)
Deep water											
Etelis carbunculus	63.9	0.36	-0.51	Unknown	**34.9**	2	8				Uchida et al. (1982)
	94	0.07	-1.792	Unknown	**49.4**	9	41	0.08		Vanuatu	Brouard and Grandperrin (1984)
	82.1	0.151	-1.06	Unknown	**43.7**	4	19			Main Hawaii Is	Ralston and Kawamoto (1987)

*t_0 constrained to zero

Species	L_∞ (cm)	K	t_0	Sex	$L_{maturity}$ (cm)	$A_{maturity}$ (years)	A_{max} (years)	M	Comments	Location	Source
	69.4	0.169	-1.06	Unknown	**37.6**	4	17			NWHI	Ralston and Kawamoto (1987)
	69.1	0.175	-0.51	Unknown	**37.5**	4	17			Hawaii	Polovina. and Ralston (1986)
Deep water											
Etelis carbunculus	71.8	0.19	4.03	Unknown	**38.8**	8	20	0.52	Daily rings	Hawaii	Smith and Kostlan (1991)
	68	0.126	2.35	Unknown	**36.9**	9		0.21	Daily rings	French Polynesia	Smith and Kostlan (1991)
	127	0.129	1.14	Unknown	**64.7**	7	25	0.28	Daily rings	Vanuatu	Smith and Kostlan (1991)
E. coruscans	92.1	0.273	1.6	Unknown	**48.5**	4	13	**0.4**	Daily rings	Hawaii	Williams and Lowe (1997)
	82	0.128	-1.79	Unknown	**43.7**	4	22	**0.12**		Vanuatu	Brouard and Grandperrin (1984)
	109	0.123	-1.19	Unknown	**56.4**	5	23	0.36		NWHI	Ralston and Williams (1988b)
	89.4	0.143	-0.51	Unknown	**47.2**	5	20			Main Hawaii Is	Ralston and Kawamoto (1987)
	97.6	0.166	-0.51	Unknown	**51.07**	4	18			Hawaii	Polovina and Ralston (1986)
	99.3	0.13		Unknown	**51.7**	6	23	**0.38**		Tonga	Langi and Langi (1987)

*t_0 constrained to zero

Species	L_∞ (cm)	K	t_0	Sex	$L_{maturity}$ (cm)	$A_{maturity}$ (years)	A_{max} (years)	M	Comments	Location	Source

*t_0 constrained to zero

Chapter 4. Comparison of reproductive traits within the lutjanid complex

4.1. Introduction

An understanding of reproduction and subsequently how much biomass is contributed through recruitment is an important part of fisheries stock assessment. The relationship between recruitment and spawning stock is complex and our understanding of the dynamics of this relationship has evolved over the past 30 years; from the focus on fecundity (Bagenal 1973, Nikolsky et al. 1973) to the belief that the larval stage was the main driver of population regulation (Heath 1992 as cited by Rothschild 2000). In more recent times, there has been a shift in theory away from the notion that one life-history phase is the key contributor to the recruitment-stock relationship, to the view that all life-history phases are important and environmental factors are the population regulator that influences fish life-history stages and the density-dependent processes that occur within each stage (Rothschild 2000).

An understanding the dynamics of the recruitment-spawning stock relationship is required for fisheries management to develop strategies aimed at preserving spawning stock and avoiding recruitment over-fishing. Therefore it is essential for fisheries management to determine basic reproductive information such as: length at maturity, spawning season, and where possible, egg production of the spawning stock.

While stock levels can vary independently from fishing mortality levels, fishing mortality can put additional pressure on stressed stocks. That is, during times of increased productivity, fishing has minimal effect on the stocks, but when productivity is in decline, the effects of fishing intensify the pressure on a population (Rothschild 2000). Therefore it is important to understand the link between reproductive output and environmental drivers.

4.1.1. *Early Life-history stage of Pristipomoides multidens*

Very little is known about the spawning and larval phases of *P. multidens*. As a member of the subfamily Etelinae, it is probable that *P. multidens* spawning characteristics are similar to *P. sieboldii and P. filamentosus*, the only two eteline species where spawning mode is known. These species spawn pelagic eggs (Leis and Lee 1994) and larvae are predominately found in oceanic waters, seaward from the edge of the continental shelf and oceanic islands (Leis 1987).

Due to the difficulty in obtaining samples from the early life-history stages of *P. multidens* and other lutjanids, this study has not examined the stock-recruitment relationships, but has concentrated on exploring how environmental factors may influence the reproductive life-history strategy of the lutjanid group.

4.1.2. *Early life-history of the lutjanid group*

In the literature it has been noted that lutjanids are gonochoristic (Allen 1985, Grimes 1987), with no evidence of protogynous hermaphroditism. Lutjanids are batch spawners with individual fish spawning multiple batches of ova during the spawning season. Evidence for this has been presented in numerous studies, which found ova diameters showing polymodal frequency distribution, distinct variations in gonadosomatic indices, ova in different stages of development within the ovary, and low reproductive investment, where ripe ovaries accounted for a very small percentage of body weight (Min et al. 1977, Kikkawa 1984, Grimes and Huntsman 1980, Everson, 1984).

Lutjanids are also largely monomorphic, with sexual dimorphism only reported in two *Pristipomoides* species (Kami 1973).

4.1.3. Spawning patterns

Allen (1985) reported two distinct spawning patterns amongst the Lutjanidae family: (1) restricted summer spawning period and (2) protracted spawning with peaks in activity in spring and autumn. It is believed that these different strategies relate to whether the environmental conditions are relatively stable all year round and suitable for spawning, or whether spawning is timed to utilise maximum productivity which occurs during the summer months (Grimes 1987, Cushing 1975, Lambert and Ware 1984). However there are different theories to explain why species follow one pattern and not the other. Grimes (1987) relates this to whether lutjanids are found in continental or island habitat, while Cushing (1975) believes these differences relate to whether fish are found in low latitudes or high latitudes. While Lambert and Ware (1984) have proposed that the spawning is timed to optimise the best conditions for larva.

While most authors agree that spawning of reef fish is influenced by environmental cues such as water temperature, tides, photoperiod, rainfall, lunar cycle, there is some debate as to whether this is controlled by larval requirements (Qasim 1956, Parrish et al. 1981, Bakun et al. 1982, Lambert and Ware 1984, Sherman et al. 1984, Checkley et al. 1988 as cited by Robertson 1991) or whether juvenile or adult biological requirements play a significant role in this process (Robertson 1991). Robertson (1991) believes that this question is a complex one and that the role of the adult's requirements is not widely addressed. He stated that "there is no reason to assume that the season that is best for spawning is also best for larval survivorship, and there is evidence to the contrary for some species." He explored the idea that spawning maybe timed to avoid predation on adults or to minimise the amount of time adults require for parental care. He also pointed out that because of adult biological constraints it might be preferable to spawn continuously in small batches, as long as there is an overall minimal gain for the effort.

In regard to spawning amongst the Lutjanidae, it is feasible that differences in environmental cues play an important role in the nature of reproduction. Stability of the environment increases with depth, while illumination and temperature decrease. Therefore in intermediate (100-200 m) and deeper waters (200 m+), lunar cycles and photoperiod should have limited influence on spawning, while oceanography may play a more important role. It is hypothesised that in deeper water, large-scale current systems, such as the ITF provide seasonal triggers for reproduction. As previously outlined in section 1.5.3, these currents are responsible for seasonal upwellings, which supply an injection of nutrients from deeper waters into the euphotic zone. Productivity is also increased through regular, but less predictable, wind induced vertical mixing and tidal fronts. This seasonal infusion of nutrients may supply the stimulus for spawning among lutjanids in intermediate and deep waters by providing an increase in food supply for larvae and juveniles. While large-scale current systems provides a degree of seasonality in these deeper waters, it is not as distinct as the environmental cues found in shallow waters; such as increasing water temperature, photoperiod or high rainfall which have been shown to provide spawning triggers in shallow water species such as *L. argentimaculatus* (Russell et al. 2003, Doi and Singhagraiwan 1993). Therefore it is expected that lutjanids in intermediate and deep waters would show a more extended spawning season, while shallow water species would respond to distinct environmental cues by exhibiting a shorter more discrete spawning season.

4.1.4. Reproductive study aims

In this chapter I will present a detailed study on the reproductive biology of *Pritipomoides multidens* and compare reproductive trends for this species with shallow and deep water lutjanids cited in the literature. I will also examine possible triggers for *P. multidens* spawning by linking what is known about the environmental conditions in area where *P. multidens* is found in higher commercial concentrations in the Timor Sea. I will examine the literature for studies linking environmental factors to reproductive trends and compare how environmental conditions within the different depth ranges may produce different reproductive strategies within the shallow, intermediate and deep water lutjanids.

Specifically, this chapter will:

Examine if there are differences in spawning patterns between the lutjanid groups in relation to depth partitioning of genera.

Examine the possible environmental triggers for spawning of *P. multidens* in the study area. I compare these findings with environmental triggers for shallow-water lutjanids from published literature to determine if environmental cues for lutjanid spawning differ within or between depth ranges.

Determine the length at maturity for *P. multidens* in the Timor and Arafura Seas and if there is a difference between the two locations: How do my findings compare with studies from other locations for this species? Do environmental conditions modify length at maturity?

4.2. Materials and Methods

4.2.1. Sample collection

The same fish were used for reproductive studies as were used for growth studies. These were collected over a two-year period from 1999-2001 from commercial fisheries. Details on sites and collection methods are described in Chapter 3. Fish purchased from the Timor Sea were kept on ice, however those purchased from a trawler in the Arafura Sea had been frozen onboard, which affected the quality of the specimens for histological processing, but still allowed identification of histological stages. The majority of Indonesian samples had also been frozen. These were processed in Indonesia and sent to me as histological slides.

All fish were measured to the nearest mm, and both fork length (FL) and standard length (SL) were taken. Total weight was recorded to the nearest gram (g). The sex and macroscopic stage (Table 4.2.1) was noted and gonads were removed and weighed to the nearest 0.1 g. Large gonads were cut longitudinally to ensure completed penetration of fixative. Gonads were fixed in Formaldehyde-acetic acid-calcium chloride (FAACC) fixative for 1 week before being transferred to 70% alcohol for storage.

Histological processing was undertaken only on females with intact gonads and gonads that were identified macroscopically as stage 2 or higher. This was to reduce processing costs. A small section approximately 2-4 mm thick was taken from the middle of each ovary and embedded in Paraplast^{TM}. Sections were cut at 3-5 μm and stained with haematoxylin and eosin.

4.2.2. Histological staging

As lutjanids are batch spawners, oocytes in different stages of development are observed within one ovary. While West (1990) has outlined a number of different options for determining histological stage in this situation, he notes that, "In most studies, ovaries are classified by the most advanced type of oocyte present". This criterion has been used in this study based on histological examination (Figure 4.2.1). The histological description of oocyte developmental stages has been based on that developed by West (1990) and Marshall et al. (1993). An additional stage (resting) has been included, based upon criteria used by Mackie and Lewis (2001), Samoilys and Roelofs (2002). Oocyte developmental stages are presented in Figure 4.2.1.

Table 4.2.1. Histological staging scheme used for *Pristipomoides multidens*.

Stage		A Histological Description	B Macroscopic staging
I	Immature	Chromatin nucleolar	
		Small oocytes. Nucleus contains a single large nucleolus.	Ovary small, translucent, pink, uniform appearance. No eggs visible.
II	Early Developing	Perinuclear stage	
		The nucleus increase in size and numerous nucleoli found at periphery of nucleus.	Ovary usually pink, uniform appearance. No eggs visible
R	Mature Resting	Resting stage	
		This stage refers to mature fish that have undergone ovulation. Gonads contain predominantly chromatin nucleolar and perinucleolar stage oocytes. Gonad walls are generally thicker in resting than in immature fish. Brown bodies may be seen and the lamellae are generally less compact.	Difficult to distinguish macroscopically
III	Developing	Yolk vesicle formation	
		Yolk vesicles appear as round spherical structures in the cytoplasm. The nucleus remains round and lightly stained. Lamp brush chromosomes are often visible in the nucleus. Thin zona radiata is present at this stage.	Slight speckled or granular appearance. First indication of yolked eggs that are just visible externally and when cut.

Stage		A Histological Description	B Macroscopic staging
IV	Developed	Yolk granular stage	
		Oocytes increase in size. This stage is characterised by the appearance of numerous pink-staining yolk granules in cytoplasm. In yolk granule stage, the nucleus becomes less distinct.	Individual eggs clearly visible both externally and when cut.
V	Ripe	Nuclear migration and yolk fusion	
		Nucleus migrates to the periphery of the oocyte. The nuclear membrane dissolves and merges with the surrounding cytoplasm. Large irregular shaped yolk masses form as yolk granules coalesce. The oocyte is large and irregular in shape.	Translucent speckled appearance. Ripe eggs visible, usually still in ovarian tissue.
VI	Running ripe	(Pre-)Ovulation	
		Hydration of oocytes. All yolk granules fused into yolk masses and separated from the cell membrane. Appearance of large oil globules in the yolk masses.	Large areas of translucent ripe eggs in ovary, although these are not always visible. Eggs ovulated from ovarian tissue and free in lumen. In some fish ripe eggs in lumen only visible after cutting.
VII	Spent	Spent	
		Disintegration of the zona radiata. Yolk begins to liquefy around periphery and is reabsorbed. Granulosa collapses and oocyte become irregular shaped.	Difficult to distinguish macroscopically.

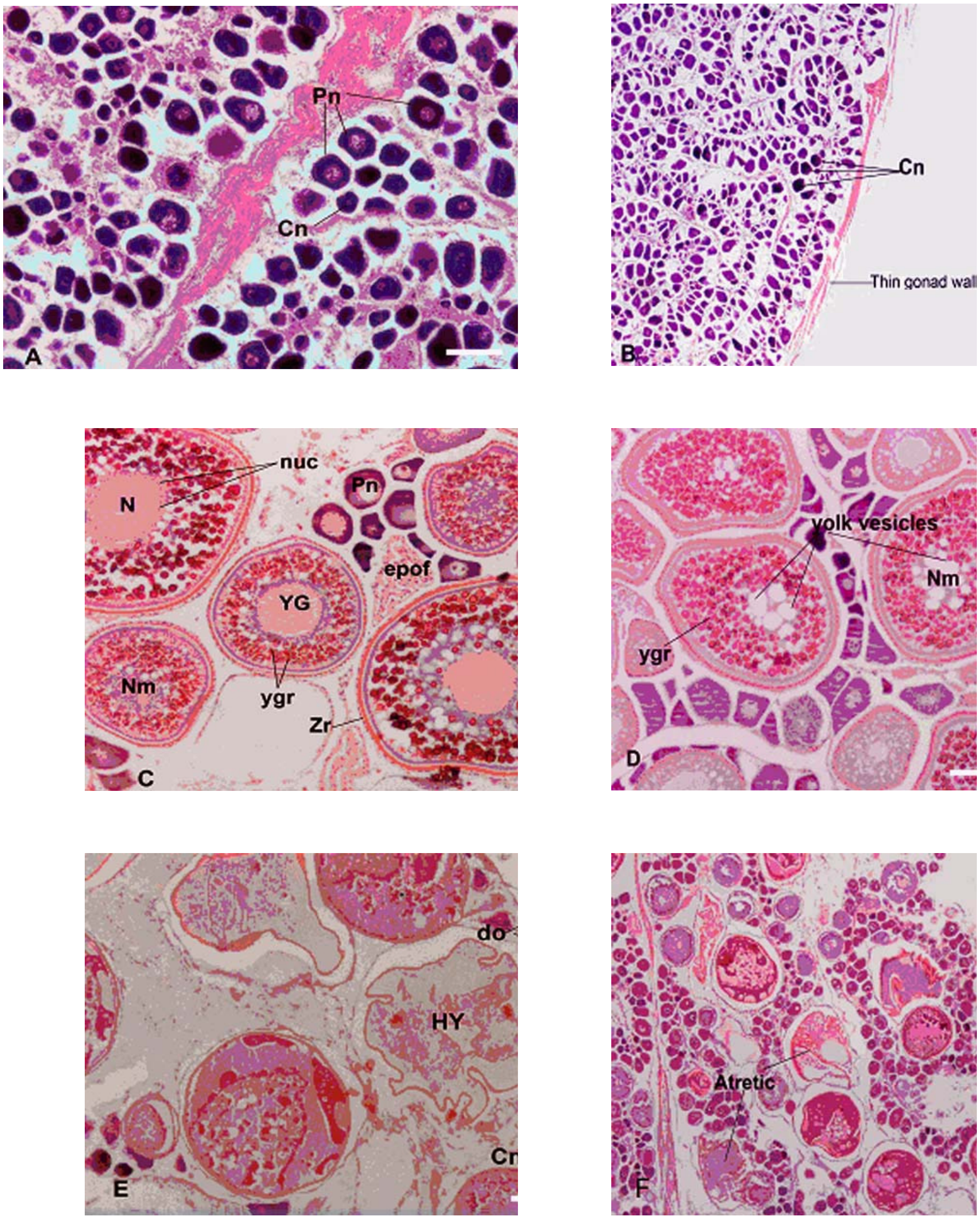


Figure 4.2 1. **Histological stages of *Pristipomoides multidens*: (A) resting stage (B) perinuclear stage (C) yolk granular stage (D) nuclear migration and yolk fusion stage (E) pre-ovulation stage (F) spent. White scale bar 0.1 mm. Symbols in Appendix I**

4.2.3 Analyses

Length at maturity (Lm) was defined as the length at which 50% of the female fish were mature. This was determined using a logistic GLM program which models all the unbinned data. This program was developed by John McKinlay (WA Department of Fisheries), further details are found in Appendix II.

The gonadosomatic index (GSI) was determined using the following formula:

G.S.I = gonad weight/total weight*100

In analysis of trends in mean monthly GSI, only fish that were above the length at maturity were used.

The spawning season was determined by examining trends in mean monthly GSI, percentage frequency of histological stages and comparison of month frequency of histological stages.

Sex ratios were compared between locations for Australian sites and analysed for variation from the expected 1:1 sex ratio using a Pearson’s $\chi 2$ goodness of fit test, corrected for type I error by G_{adj} (by the continuity correction). Sex ratio was not determined for Indonesian data, as it was not routinely taken.

4.3. Results

4.3.1. Spawning season

Histological staging was undertaken on female fish in all three locations (Figures 4.3.1 and 4.3.2). For both the Timor and Arafura Seas, there was a high proportion of resting stage females during the middle months of the year. Conversely the lowest proportion of 'ripe' stages (IV, V, VI) were observed during this period (Figure 4.3.1). For

Indonesian samples the highest proportion of resting stage occurred from May-November, and like the Australian sites the lowest proportion of 'ripe' stages occurred during this period (Figure 4.3.2).

Examination of monthly mean GSI (Figure 4.3.4) showed a rise in GSI in the later part of the year (September in the Arafura Sea, October in the Timor Sea), reaching a peak in December, and remained elevated (with some fluctuations), until March in the Timor Sea and April in the Arafura Sea. Then GSI dropped and remained low during the middle months for both locations. Indonesia results suggest a later spawning period compared to Australia sites, with a rise in GSI beginning in December and peaking in February, then declining after April. Both the Timor Sea and Indonesia do not show a very distinct pattern for mean GSI, compared with the Arafura Sea. For male fish the trend in mean GSI (Figure 4.3.5) is not as clear as it is for females. In the Timor Sea males show a slightly elevated mean GSI from Nov-Jan. In the Arafura Sea, mean GSI fluctuates throughout most of the year, but during the months May-August, mean GSI values are at a minimum. With the Indonesian samples, mean GSI values fluctuate throughout the year, but because there are no samples for October and November, it is difficult to comment on trends.

The spawning season was determined by examining trends in monthly mean Gonadosomatic Index (GSI) throughout the year for both male and female fish and histological staging of the female gonads (Figures 4.3.4 and 4.3.5).

When mean GSI and % of ripe fish (stages IV, V, VI) was plotted against month (Figure 4.3.6), a similar trend emerged for all three locations. A high mean GSI corresponded to a high proportion of ripe fish and vice versa. There is also a difference in mean GSI values for fish from the Arafura Sea compared with fish from the Timor

Sea and Indonesia, with the Arafura Sea having mean GSI values almost double that of other sites. The Arafura Sea also has a much higher proportion of ripe fish compared with other areas, as shown from the monthly frequency of histological stages (Figure 4.3.3).

Results from histological staging, monthly mean GSI and % mature females all indicate that spawning appears to occur through most of the year for *P. multidens* in northern Australian waters, except for a short period during the Southern Hemisphere winter when spawning activity is minimal. Indonesian female fish show a rise in December with a peak in February, and a decline after April. Neither GSI nor % mature exhibited as great a decline as Australian sites (Figure 4.3.6). Examination of female histological stages for Australian sites, indicated that the largest percentage of resting stage fish occurred during the winter months when ripe stages were at a minimum (Figure 4.3.3). There is a positive relationship between mean GSI and percentage of mature fish (Figure 4.3.6), with the greatest percentage of mature fish observed at maximum mean GSI, and the smallest percentage at minimum mean monthly GSI. Indonesian data showed more variation. A similar pattern was observed with histological stages (Figure 4.3.3), but slightly later than Australia, with highest percentage of resting stage fish and minimum ripe fish occurring from August to November.

4.3.2. Length at maturity

The length at which 50% of the female fish were mature (L_{50}) was 382 mm FL in the Timor Sea (Figure 4.3.7), and the smallest mature female was 300 mm FL. In the Arafura Sea, L50 was 313 mm FL (Figure 4.3.7) and the smallest mature fish observed from this sample was 308 mm FL. There was insufficient immature fish to run the model for the Indonesian data, however the smallest mature female was 285 mm FL.

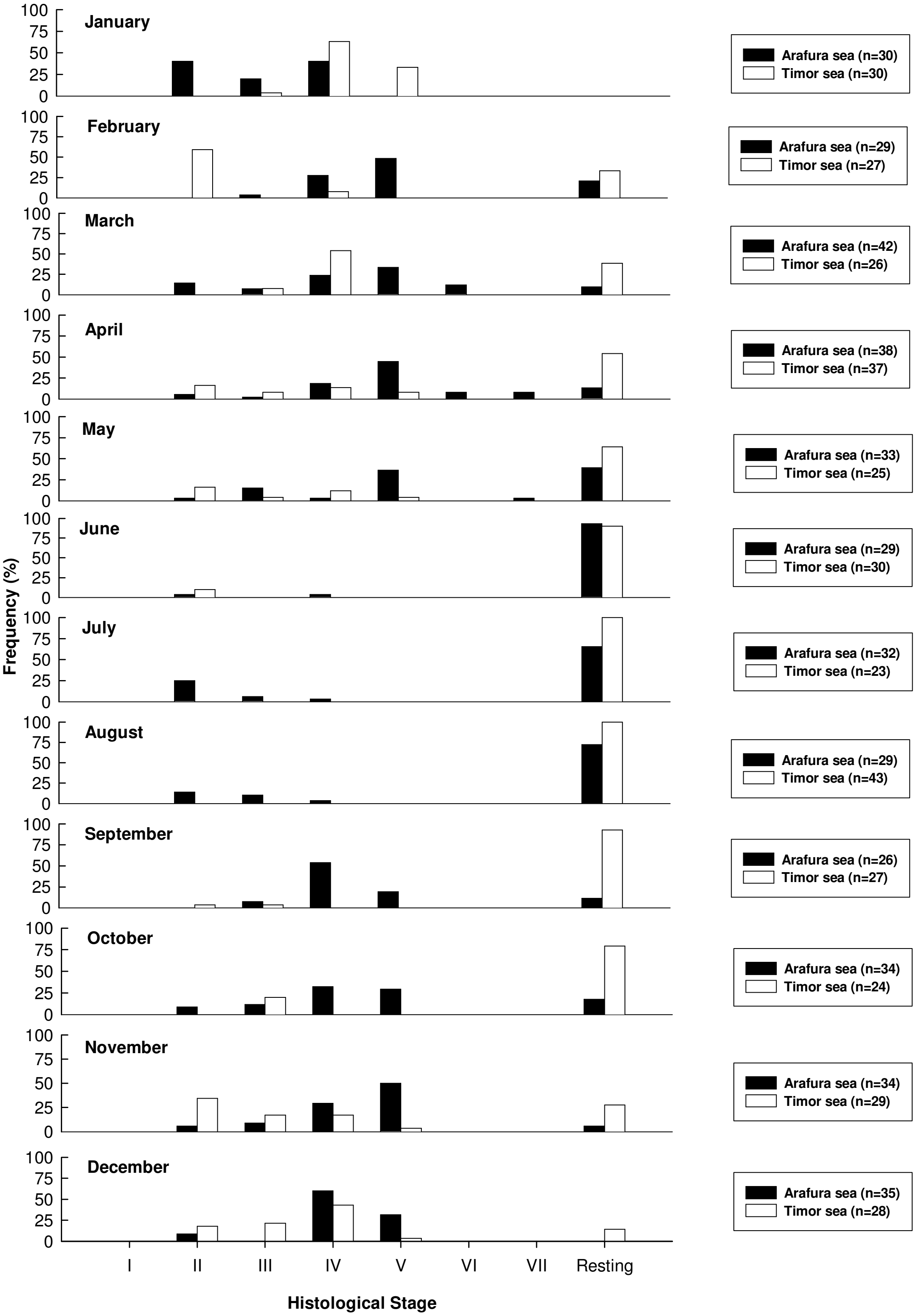


Figure 4.3.1. **Percentage frequency of histological stages observed each month through the year for female *Pristipomoides multidens* from the Timor and Arafura Seas**

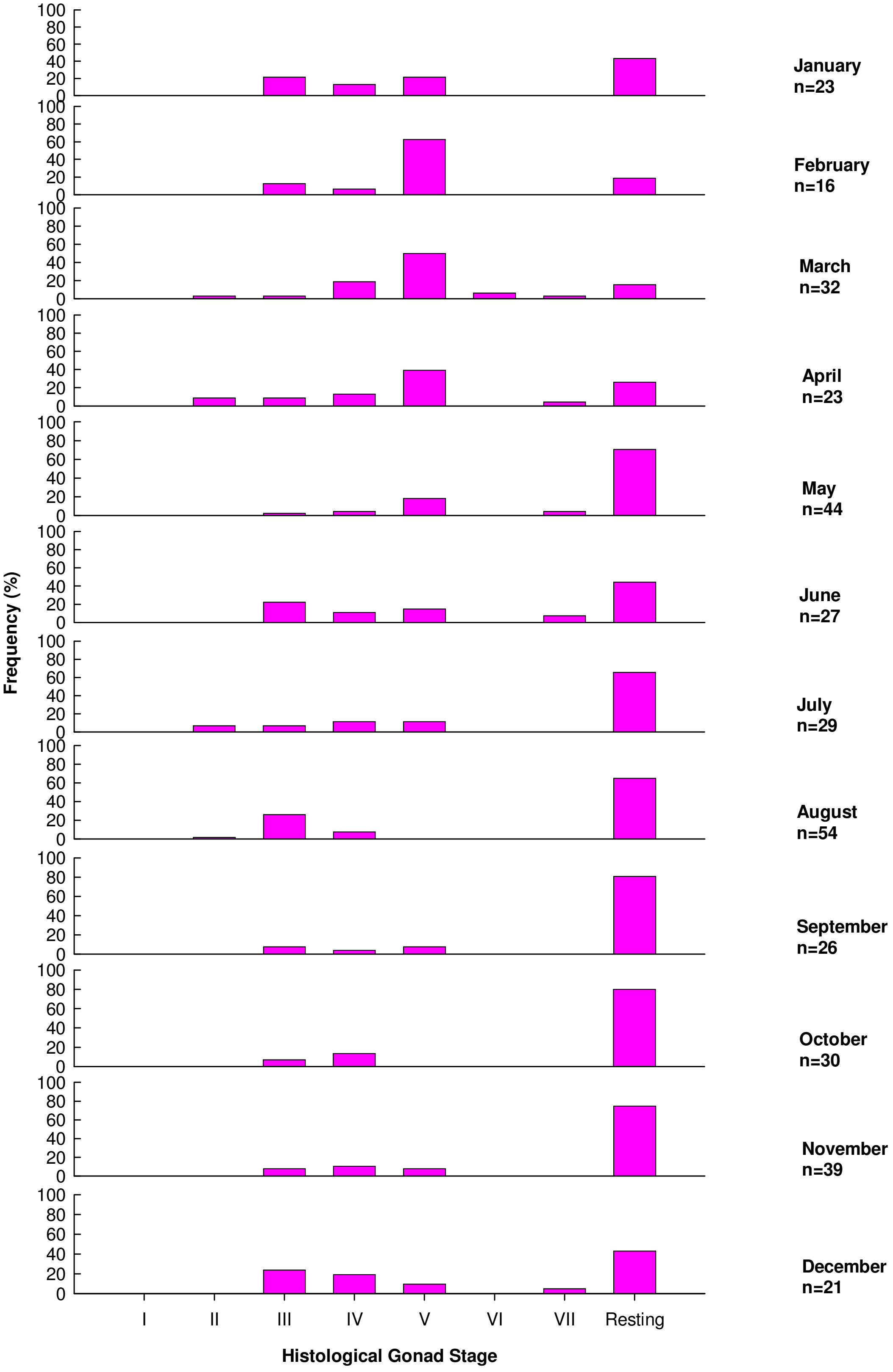


Figure 4.3.2. **Percentage frequency of histological stages observed each month through the year for female *Pristipomoides multidens* from Indonesia**

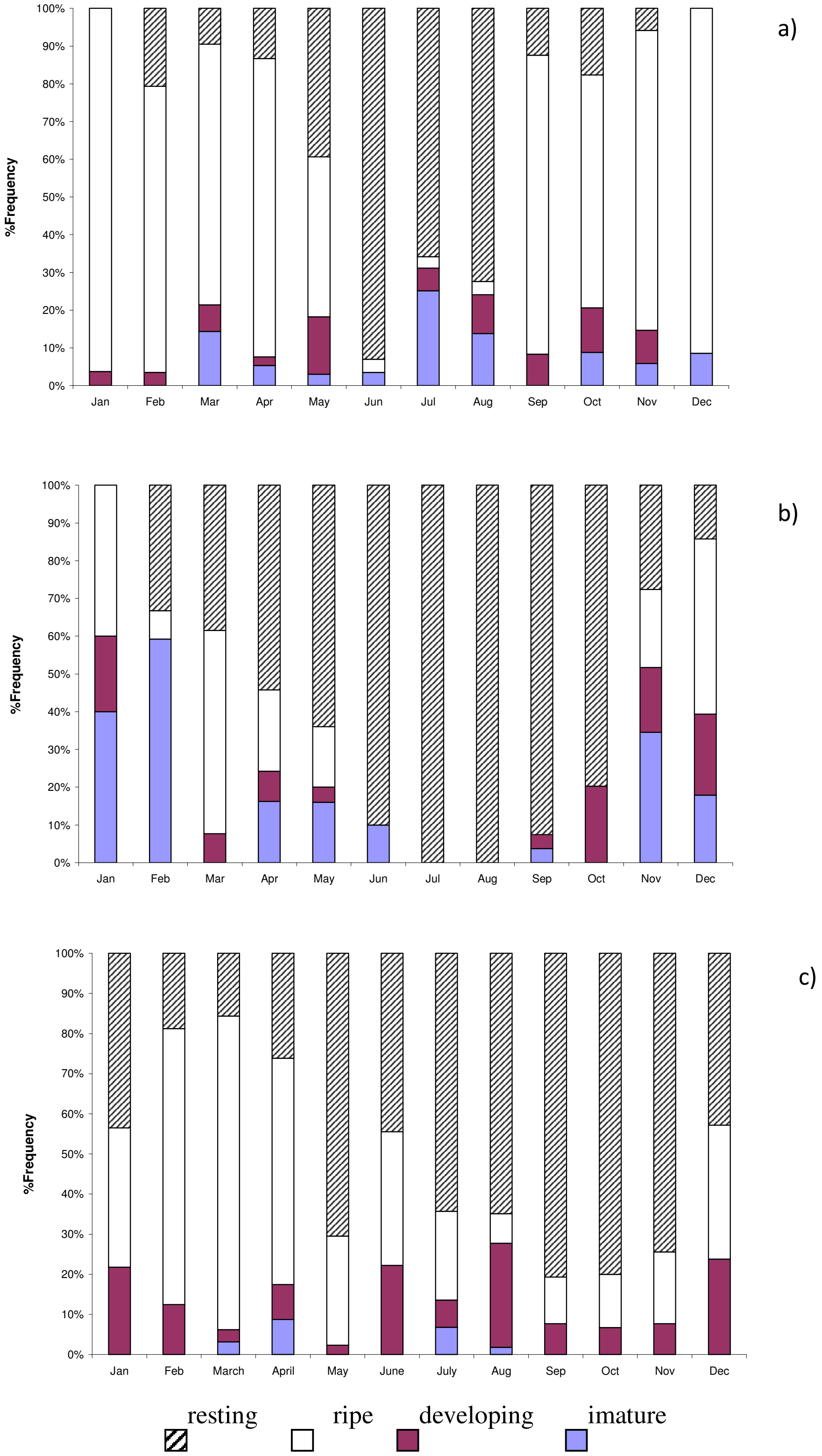
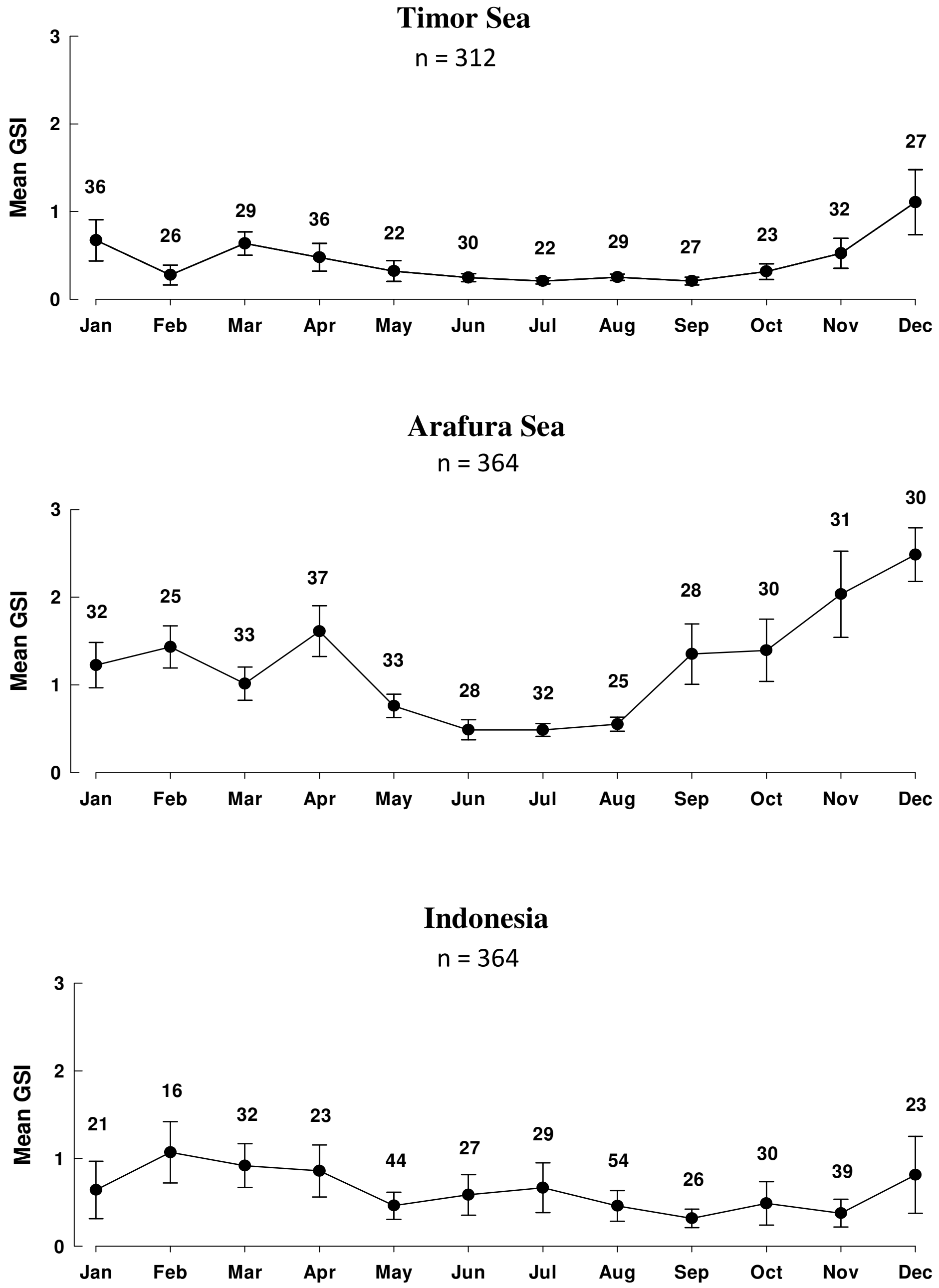


Figure 4.3.3. **Monthly frequency of histological stages of *Pristipomoides multidens* from the three locations: a) Arafura Sea, b) Timor Sea and c) Indonesia**



Timor Sea
n = 312

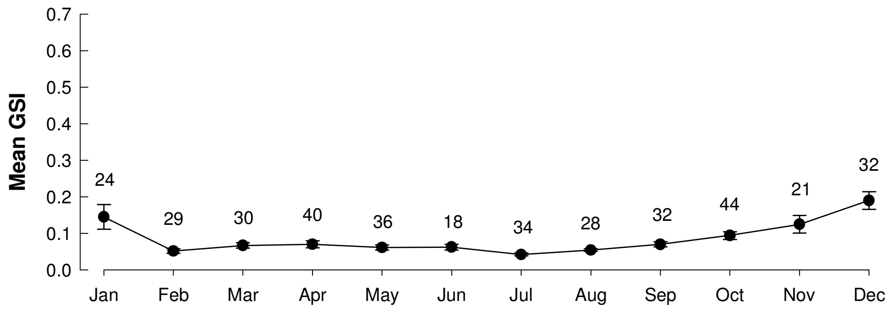
Arafura Sea
n = 364

Indonesia
n = 364

Figure 4.3.4. **Monthly mean Gonadosomatic Index (GSI) ± standard errors for female *Pristipomoides multidens* collected from sample locations**

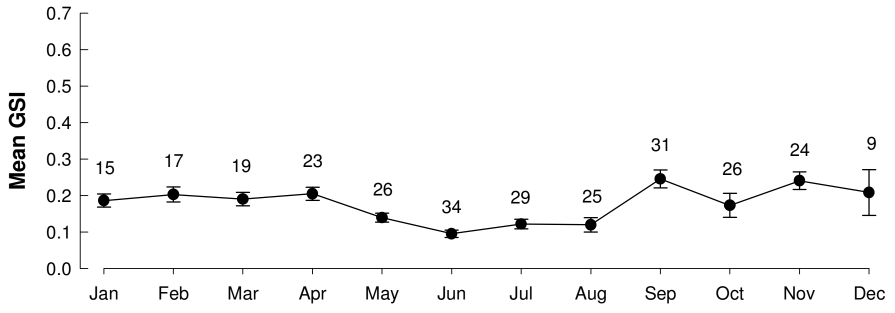
Timor Sea

n = 368



Arafura Sea

n = 278



Indonesia

n = 80

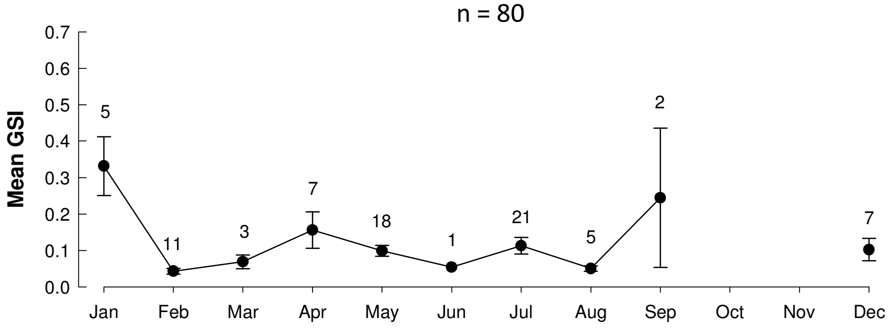


Figure 4.3.5. **Monthly mean Gonadosomatic Index (GSI) ± standard errors for male *Pristipomoides multidens* collected from sample locations**

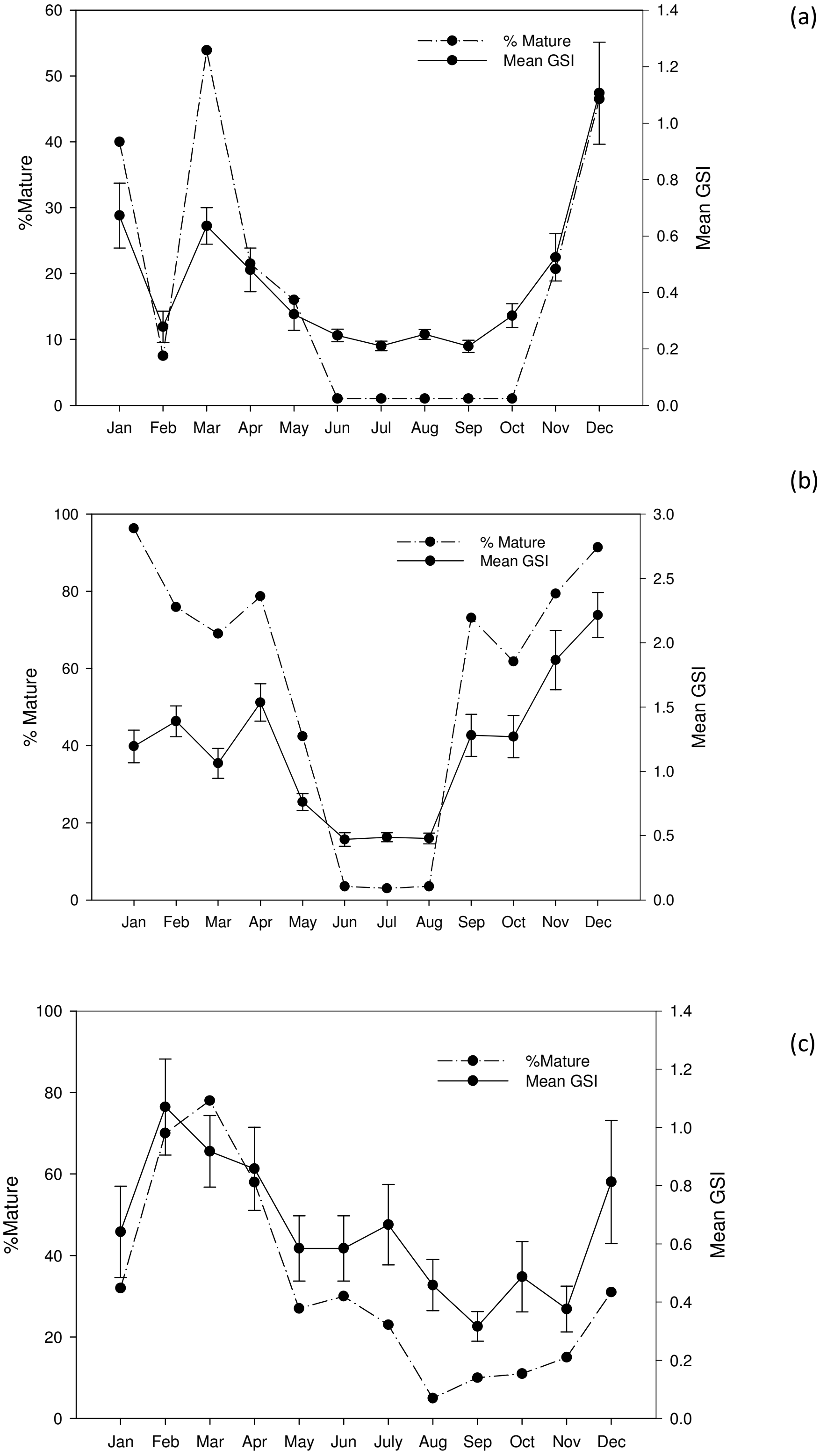
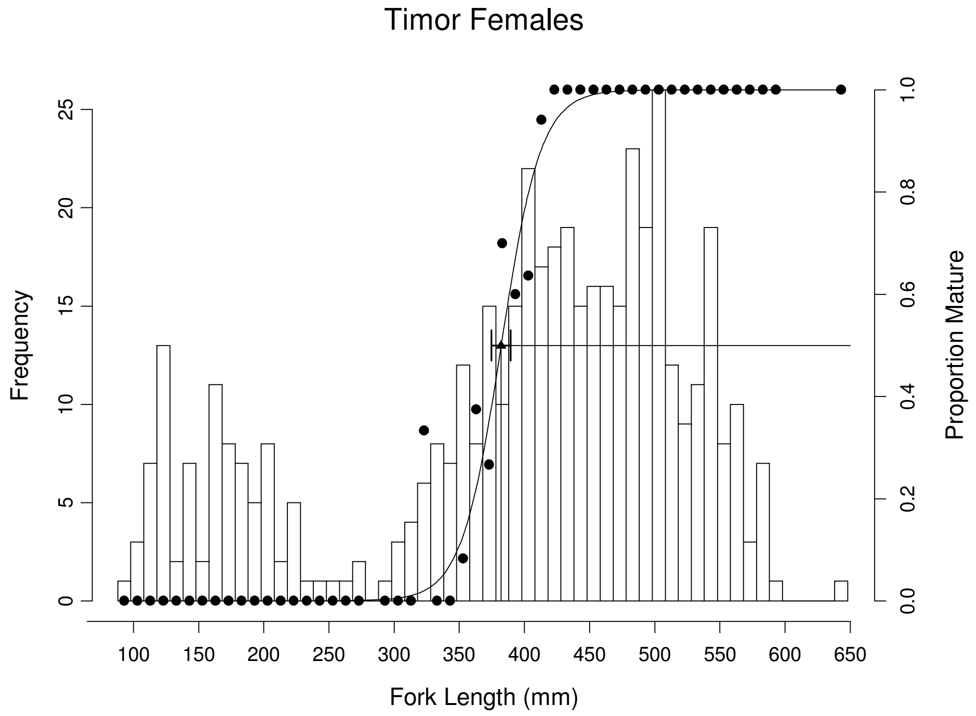


Figure 4.3.6. **Monthly mean Gonadosomatic Index (GSI) and % of ripe *Pristipomoides multidens* ± standard errors from a) Arafura Sea, b) Timor Sea and c) Indonesia**



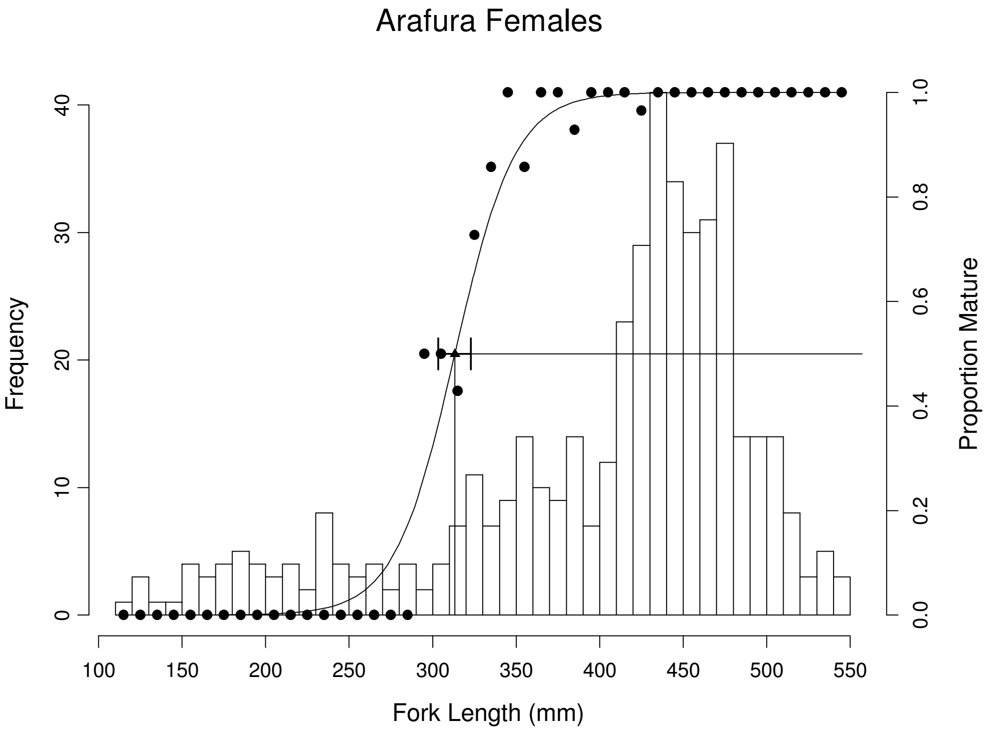


Figure 4.3.7. **Length at 50% maturity for *Pristipomoides multidens* samples from the Timor and Arafura Seas**

4.3.3. Sex ratio

The sex ratio of female: male fish from the Arafura Sea was 1:1 The Pearson's goodness of fit test indicates that there is not a significant difference between sex ratios for fish from the Arafura Sea (χ^2 =1.60, df =1, P=0.21). Sex ratio of female: male fish from the Timor Sea was 1:1 and the sex ratios are not significantly different as indicated by the Pearson's goodness of fit test (χ^2 =0.001, df =1, P=0.97).

4.3.4. Summary and discussion of Pristipomoides multidens results

Pristipomoides multidens in northern Australian waters have an extended spawning period throughout most of the year, with minimum activity occurring during the winter months. For both the Timor and Arafura Seas a peak in spawning activity was observed in December.

My results are consistent with studies on *Pristipomoides* species from published literature. Brouard and Granperrin (1984) observed that for *P. multidens* and *P. flavipinnis* in Vanuatu, GSI was lowest during the Southern Hemisphere winter, when water temperatures are lowest and daylight hours reduced. Peak spawning months determined from visual staging and GSI, were December-January for *P. multidens*, and December-February for *P. flavipinnis*. Kikkawa (1984) found a protracted spawning period for *P. filamentosus* from June to December in Hawaii with spawning peak in August.

It is difficult to determine with certainty what triggers spawning in the intermediate depth range where *Pristipomoides* species are found in greatest abundance. At these depths there is little temperature variation as observed from water temperature readings undertaken at 100 m in the study area from period February to October 1995, which showed a temperature range of 22-24°C (JL unpublished data). Hence other environmental signals, such as changes in oceanographic conditions are more likely to trigger spawning. While Brouard and Granperrin (1985) believe that even a slight drop in temperature can cause a decline in reproductive activity, they do not offer a hypothesis as to what might trigger the peak spawning activity they observed from December-February. In my study in northern Australia, the spawning period, is possibly triggered by a shift in oceanographic conditions that accompanies the change over from the South East Monsoon (SEM) to North West Monsoon (NWM). This occurs from September-December, which corresponds to the period when there is a rapid rise in GSI, an increase in the percentage of ripe fish and later histological stages. During this period conditions are generally very calm and fish are schooled up more so than at other times of the year.

The oceanography in this area is dominated by the Indonesian Throughflow (ITF), which is a complex system of surface currents flowing from the Pacific to the Indian Ocean through the Indonesian archipelago and is an integral part of the global climate system. The ITF is responsible for bringing warm, less saline Pacific Ocean water into the Indian Ocean, thereby providing an important means of heat exchange between major ocean basins. The ITF is at its strongest during the SEM (May-Sep), and during this period large scale upwelling events can occur (Wyrtki 1987, Meyers 1996). Moore et al. (2003) noted that "these upwelling events are one of the processes thought to control the productivity dynamics in the region". Therefore it is feasible that the stimulus for spawning in northern Australia maybe related to seasonal changes in strength of the ITF and the associated mixing events which accompany it. It is possible that this increase in productivity at the end of the SEM would provide an increase in prey species suitable for larvae and juvenile *Pristipomoides* species.

The mean GSI values for both the Timor Sea and Indonesian sites were lower than those observed in the Arafura Sea. This is possibly due to differences in environmental conditions, with less defined signals in the Timor Sea and Indonesian waters, and conditions suitable for spawning occurring throughout most of the year. Alternatively, it may relate to capture method. Samples taken from the Arafura Sea were obtained by trawling, whereas those from the Timor Sea were caught by trap or droplining methods, and Indonesian samples were taken predominantly using bottom-set long lines or droplines, although some samples came from trawlers. One possibility is that when fish are ready to spawn, they are not feeding, therefore are less susceptible to capture methods that require attraction to baited hooks and traps. Therefore we may not be getting a representative sample of ripe fish (with higher GSI) in those areas which were sampled with these methods.

Length at maturity for *P. multidens* in the Timor Sea was 382 mm FL and 313 mm FL for the Arafura Sea. This was similar to results obtained by Brouard and Granperrin (1985), who reported 320-370 mm FL depending upon which method used to calculated length at maturity. Min et al. (1977) found length at maturity for this species to be 350 mm SL, while Allen (1985) has reported the length at maturity to range from 40-50 cm TL.

4.4. Comparison between members of the lutjanid complex and general discussion

4.4.1. Spawning seasonality

Deeper water snappers show similar trends to *Pristipomoides* species in intermediate depths. Generally they exhibit a peak in activity during the summer months, although some species show two peaks in spawning. *Etelis carbunculus* shows a summer spawning peak in Vanuatu and Hawaii, but two peaks in PNG, one in August-September, the other February-March. While *E. coruscans* shows two spawning peaks in Vanuatu (December and March-May), but in Hawaii, peak spawning occurs in October. Everson et al. (1989) has postulated that this summer peak is linked to an increase in water temperature and day length. Brouard and Granperrin (1985) also believe water temperature affects spawning.

In the shallower waters, Russell et al. (2003) observed a summer spawning peak for *L. argentimaculatus*, with the majority of spawning occurring between October and February. They note that gametogenesis initially begins around the time that water temperature and photoperiod are increasing (September/October), and extends throughout the summer months. They cite work by Doi and Singhagraiwan (1993) who found a similar peak spawning period (November to January) for this species in Thailand, but identified high rainfall and falling water temperatures as the cue for spawning.

Davis and West (1993) found that *Lutjanus vittus* from the North West Shelf of Australia (NW Shelf) showed a summer peak in spawning activity from September-April. They also observed that *L. vittus* exhibited a semi-lunar spawning pattern with peaks in the proportion of spawning females, approximately 3 days after the new moon and 6 days after the full moon. The authors believe that the peak in spawning during summer relates to the period of increased nutrients on the NW Shelf, as a result of the subsiding of the South-East trade winds in late August/early September. This results in stratification of the water column and a concentration of plankton, which in turn enhances feeding conditions for larvae at the start of the peak spawning period. The authors also hypothesise that the lunar spawning activity is probably related to a lunar tidal cycle as the NW Shelf has strong semidiurnal tides, and spawning during spring tides would provide an advantage as the eggs would be distributed along-shelf rather than cross-shelf.

In general it appears that shallow water lutjanids appear to favour summer as the period of peak spawning activity, although smaller numbers of ripe females maybe found outside this period. In most tropical areas, summer is the time of highest rainfall. This results in a great deal of mixing and nutrient enrichment of the inshore waters due to flooding (Wolanski 1993). There is also considerable deal of turbidity in these shallow areas during this period, and it is possible that this increase in turbidity may provide favourable conditions for larval and juvenile growth in terms of food supply and protection. Blaber and Blaber (1980) found in studies undertaken in sub-tropical Queensland, turbidity was the most important factor for juveniles entering estuaries due to the protection it offered from predators and suitable food sources. Many shallow water lutjanids spent their juvenile phase in protected inshore waters and migrate offshore when they reach adult size. Examples of lutjanids which undergo inshore-offshore ontogenetic migration are *Lutjanus malabaricus, L. erythopterus*, *L. sebae*, *L. johnii*, *L. argentimaculatus*, *L. russelli* (Williams and Russ 1994).

For lutjanids distributed further offshore and those found in deeper water, it appears that oceanographic and tidal conditions play a more important role in determining the spawning season, as these are the important influences which affect productivity and enhance conditions suitable for larval survival.

4.4.2. Size at maturity

For many lutjanid species size at maturity can differ greatly between regions, which led Grimes (1987) to hypothesise that there is a correlation between the percentage of maximum length at which maturity occurs (Lmax) and habitat, with lutjanid populations associated with islands maturing at a larger size than those found on continental shelfs, and deep water populations maturing at a larger size than those in shallow waters. He speculated that these differences were probably due to variation in food resources between the habitats, with shallower waters and continental margins being more productive than deep water and island habitats.

Pauly (1994, 1998) has developed an alternative theory to explain what influences size at maturity and why this can differ for the same species in different habitats. Pauly's theory is based on the premise that sexual maturity occurs when growth slows as a result of gill surface area not being able to keep up with the growth in volume of the fish, hence there is a decrease in the availability of oxygen which leads to a decrease in growth rate, both in terms of length and weight. Maximum size occurs when oxygen consumption reaches the point where it is only sufficient to maintain metabolic functions. Pauly (1994) hypothesises that there is an observed constancy between size at maturity and asymptotic size, which he believes is the expression of the underlying constancy of relative oxygen consumption per unit weight of a fish at maturity (Q_m), divided by of relative oxygen consumption per unit weight of a fish at asymptotic size (Q_∞), i.e. $Q_m/Q_\infty \approx 1.4$. Pauly (1994) postulates that when a fish approaches $Q_m/Q_\infty \approx 1.4$, substances are produced which enable the brain to respond to the specific environmental stimuli which triggers reproduction. Therefore a fish cannot respond to environmental stimuli until it has reached the size at maturity.

Factors which can affect relative oxygen consumption (Q) are high temperature, low food density, low oxygen levels and stress factors such as crowding (Pauly 1994). This will in turn reduce L_∞, W_∞ and result in maturity occurring at a smaller size. Therefore the same species can have different sizes at maturity depending upon habitat conditions. This hypothesis can also explain the observations by Grimes (1987) regarding habitat and depth range and size at maturity. That is, deeper water populations would mature at a larger size because temperature is lower, therefore metabolic rate slower and the increase in the volume of fish with respect to gill surface area is slower, hence oxygen limitations occur at a larger size compared with warmer water species. Grimes (1987) observation that island populations mature at a larger size than those on a continental shelf, is also consistent with Pauly's theory as Q is affected by food density. Therefore if food is less abundant for island populations compared with continental shelf populations as hypothesised by Grimes (1987), then metabolic rate is slower and consequently growth is slower. With a slower growth rate, the increase in fish volume to gill area is slower and in turn oxygen limitations occur at a larger size, resulting in a larger size at maturity.

Although Grimes (1987) noted a constant ratio between length at maturity and asymptotic size within families of fish, he did not explore it further. However Pauly's work has provided a physiological explanation for these observations, and for the exceptions which have also been observed in the size at maturity for the same species in different areas, e.g. De Martini and Lau (1999) citing large differences among Pacific regions for *Etelis carbunculus*. Large differences in length at maturity have also been observed for *Lutjanus malabaricus*, e.g. McPherson et al. (1992), reported the length at maturity for *Lutjanus malabaricus* in Queensland (Australia) to be 54.8 cm. While Brouard and Grandperrin (1985) reported a value of 35 cm for this species in Vanuatu.

Further discussion on the factors that contribute to differences in metabolic rate and the implications for lutjanids with different depth ranges can be found in Section 3.1.1 in Chapter 3.

4.5. Conclusion

P. multidens has an extended spawning period from September in the Arafura Sea and October in the Timor Sea, reaching a peak in December, and remaining elevated (with some fluctuations), until March in the Timor Sea and April in the Arafura Sea. Minimum spawning activity was observed during the winter months for both locations.

There appears to be partitioning of the lutjanind complex with respect to spawning seasonality. Intermediate and deeper lutjanids show a protracted spawning season with a peak in activity during summer months, and in some regions two spawning peaks are observed, while shallow water lutjanids exhibit a restricted summer peak in spawning. This mixture of spawning patterns can occur for the same species in different locations. Therefore it appears that spawning is aligned to maximising the most favourable conditions locally, although there is some conjecture as to whether this relates to conditions most suitable for larvae or adults.

There are a number of different triggers that can induce spawning, and this also seems to vary locally, even amongst shallow water lutjanids that show the same spawning pattern of a restricted summer spawning period. For example Russell et al. (2003) found that an increase in water temperature and photoperiod appeared to be the trigger for *L. argentimaculatus* in north Queensland, while Doi and Singhagraiwan (1993) found that high rainfall and falling water temperature to be the cue for spawning for *L. argentimaculatus* at the same time of year in Thailand.

In the intermediate and deeper waters it unlikely the water temperature and photoperiod are spawning triggers, as these are fairly stable for most of the year (JLunpublished data). It is more likely that oceanographic currents play a more significant role at these depths. These triggers may be related to monsoonal patterns that can result in large scale upwellings and increased productivity. It has been observed in this study that *P. multidens* spawning peaks during the periods of transition between the monsoons. This is the period immediately after the upwelling events, which occur during the South East Monsoon as a result of a strong ITF. However as Davis and West (1993) noted with *L. vittus*, there is a need for stratification of the water column to ensure the concentration of plankton for larvae. This is most likely to occur during this period of calm between the monsoons. They also noted a semi-lunar pattern in spawning of *L. vittus* which they attributed to lunar tidal cycle. The strong semi-diurnal tides of the North West Shelf flow predominately alongshelf near the coast, and therefore spawning during spring tides would distribute eggs along the shelf.

Considerable differences in length at maturity have been observed between members of the lutjanid complex even within species in the same depth range. Grimes proposed a theory that length at maturity is linked to habitat, with shallow water and continental habitats having a smaller length at maturity than deeper water and island habitats. This is based on the premise that productivity is greater in the former than the latter. Pauly developed a theory which expanded this further by providing a physiological explanation for these observations, which also accounted for the exceptions to Grimes theory reported in the literature.

These studies illustrate how much length at maturity can vary within a species and the importance of not extrapolating length at maturity values from other regions even for the same species.

4.5.1. Implications for fisheries management

An understanding of the reproductive biology of a species is an integral part of developing management strategies to ensure a sustainable fishery. These management strategies focus on preserving spawning stock and preventing recruitment over-fishing.

For *Pristipomoides multidens*, the target species of a trap and line fishery in the Timor Sea, less than 10% of the commercial catch is below the length at maturity (382 mm FL), therefore it has not been necessary to introduce fish size or gear restrictions.

An understanding of the environmental drivers which may trigger spawning is important when predicting how stocks are likely to respond to increases in water temperature and changing environmental conditions as a result of climate change.

Extended seismic surveys in the Timor Sea have the potential to impact on *P. multidens* stocks, either directly through mortality to fish, larva and eggs or indirectly by disruption to breeding patterns (Popper 2003). Determination of the spawning period for *P. multidens* has provided guidance for the petroleum industry when planning surveys. By avoiding where possible, key *P. multidens* areas during the spawning period, companies can lower the impact that these surveys have on fish stocks.

Table 4.4.1. Spawning season of lutjanids. Adapted from Grimes (1987) and updated with subsequent literature. "P" denotes peak spawning period; "x" denotes ripe females found during these months.

Species	**Location**	**J**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**	**Source**
Small shallow-water species														
Lutjanus argentimaculatus	Nth Queensland, Aust	P	P								P	P	P	Russell et al. 2003
	Thailand	P										P	P	Doi and Singhagraiwan 1993
L. griseus	Florida Keys						P	P	P	P				Starck and Schroeder 1970
	Florida						x	P	P	x				Domeier et al. 1996
L. kasmira	Andaman Sea	x	x	x						x	x	P	P	Rangarajan 1971
	East Africa			x								x		Talbot 1960
L. lutjanus	Egypt	P	P	P	P	P	P							Allen 1985

Species	**Location**	**J**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**	**Source**
Small shallow-water species														
L. quinquelineatus	New Caledonia	P	P									P	P	Loubens 1980a,b
	Gulf of Aden			P	P	P	P	P	P	P	P	P		
L. russellii	Sth Africa	P	P								P	P	P	van der Elst 1981
L. vittus	North West Shelf, Aust	P	P	P	P					P	P	P	P	Davis and West 1993
	New Caledonia	P	P		x			x	x	x	P	P	P	Loubens 1980a,b
Large shallow water and intermediate species														
L. malabaricus	Queensland, Australia	x	x								P	P	P	McPherson et al. 1992
	Vanuatu	P	x	x		x	x	x			x	P	P	Brouard and Grandperrin 1984

Species	Location	J	F	M	A	M	J	J	A	S	O	N	D	Source
Large shallow water and intermediate species														
L. erythropterus	Queensland, Australia	P	P							P	P	P	P	McPherson et al. 1992
L. sebae	Queensland, Australia	x	x	x	x						P	P	P	McPherson et al. 1992
Intermediate depth species														
Pristipomoides filamentosus	Hawaiian Islands		x	x	x	P	P	P	P	P	x	x	x	Ralston 1981
	Sth China Sea			P										Min et al 1977
P. flavipinnis	Vanuatu	P	P	x	x	x	x	x	x	x	x	x	P	Brouard and Grandperrin 1984
P. multidens	Timor Sea, Australia	x	x	x	x	x				x	P	P	P	This study
	Arafura Sea, Australia				x					P	P	P	P	This study
	Vanuatu	P	x	x	x	x	x	x	x	x	x	x	P	Brouard and Grandperrin 1984

Species	Location	J	F	M	A	M	J	J	A	S	O	N	D	Source
Intermediate depth species														
P. multidens	Sth China Sea			P					P					Min et al. 1977
P. typus	Sth China Sea			P		P			P					Min et al. 1977
Deep water species														
E. carbunculus	Hawaii							P	P	P				Everson 1984
	Vanuatu			x	x	x		x	x		x	P	P	Brouard and Grandperrin 1984
E. coruscans	Hawaii						x	x	x	x	P	x		Everson et al. 1989
	Vanuatu	x		P	P	P		x	x	x	x	x	P	Brouard and Grandperrin 1984

Chapter 5. Implications of using proxy values

As previously discussed in Chapter 1, many fisheries in both developed and developing countries are data limited. The dilemma facing fisheries managers is how to ensure that these data-poor fisheries are managed in a sustainable manner? One option is to use proxy values from data-rich fisheries for stock assessment.

Key stock biomass inputs are the number of recruits to a population and the growth of existing individuals within the populations. This is balanced by natural mortality and fishing mortality. These variables form key stock assessment parameters, and biological reference points for fisheries management, but: in the absence of this information, is it acceptable to use proxy values from data-rich species? What would be the most suitable species to choose as proxies? Is it preferable to use a species from shallower depth range within the same area, or the same species from a different location?

In this chapter I will explore these questions further by examining the implications of using proxy values for *Pristipomoides multidens*, an important target species in developed and developing countries throughout the Indo-Pacific region. This will be undertaken by comparing growth, reproduction and mortality parameters for lutjanids which occur in the same area, but at different depth ranges. I will also compare the values for the parameters derived from my *P. multidens* study with values reported in the literature for this species from different areas.

5.1. Data

In this chapter I compare growth, reproduction and mortality parameters using data from my study for different species obtained from within the same area but occupying different depths: *Pristipomoides multidens* (intermediate depth), *Lutjanus malabaricus* and *L. erythropterus* (large shallow waters species) (Table 5.1.1). I also compare growth, reproduction and mortality parameters obtained in this study with values for *P. multidens* from other regions described in the literature (Table 5.1.2).

The specific parameters investigated were:

- asymptotic length (L_{inf}),
- the growth coefficient K,
- natural mortality (M),
- length at maturity (L_m),
- maximum age (t_{max}) and
- L_{opt} the length at which a fish will contribute the maximum yield to the population (Tables 5.1.1 and 5.1.2).

For biological parameters where the data was unavailable, parameters were derived utilising the invariant relationships discovered by Berverton and Holt (1959), Beverton (1992), Froese and Binohlan (2000).

L_{opt}, L_m and t_{max} were derived using the following equations described by Froese and Binohlan (2000):

$$\log L_{opt} = 1.0421 * \log L_{inf} - 0.2742$$

$$\log L_m = 0.8979 * \log L_{inf} - 0.0782$$

$$t_{max} = 3 / K$$

Natural mortality (M) was obtained from the empirical formula described by Beverton (1992) where M=1.5K.

Table 5.1.1. Comparison of growth and reproduction parameters between lutjanid species occupying intermediate and shallow depth ranges in the same area.

Parameter	***Pristipomoides multidens***	***Lutjanus malabaricus***	***L. erythropterus***
L_{inf}	71.4	58.5	50.3
K	0.15	0.19	0.25
M	0.18	0.29*	0.38*
L_{opt}	45.4*	37.3*	31.4*
L_m	38.2	32.5*	28.0*
t_{max}	18	31	27

*Figures derived from empirical relationships described by Froese and Binohlan (2000).

Table 5.1.2. Comparison of growth and reproduction parameters of *Pristipomoides multidens* within intermediate and shallow depth ranges from different areas.

Parameter	**Timor Sea**[a]	**Vanuatu**[b]	**Kimberley**[c]
L_{inf}	71.4	65.0	60.3
K	0.15	0.28	0.19
M	0.18	0.42	0.3
L_{opt}	45.4*	41.2*	37.3*
L_m	38.2	35.4*	32.5*
t_{max}	18	11*	16*

[a]This study. [b]Brouard and Granperrin (1984). [c]Newman and Dunk 2003. *Figures derived from empirical relationships described by Froese and Binohlan (2000).

5.2. Analysis

Auximetric plots (Figures 5.2.1 to 5.2.4) were used to compare the following relationships:

- asymptotic length and K (Figure 5.2.1)
- K and M (Figure 5.2.2)
- asymptotic length and natural mortality (Figure 5.2.3)
- asymptotic length and length at maturity (Figure 5.2.4)

5.3. Results and Discussion

The auximetric plots (Figures 5.2.1 to 5.2.4) demonstrate that the parameters reported for *P. multidens* from the Kimberly region are the most similar to *L. malabaricus* from my study in Northern Territory waters. This result is not consistent with either hypothesis for proxy choice, i.e. same species different area or same area different species. Therefore to choose proxy values based on the same species from other areas would be erroneous as would the choice of proxies from lutjanids within the same area, but different depth ranges.

While it may be tempting to assume that large lutjanids such as *L. malabaricus* may have similar growth patterns to *P. multidens* in the same area, factors which influence metabolic rate and growth in fish are complex. Although environmental temperature is an important regulating mechanism, other factors such as evolutionary trade-offs and food availability also contribute to observed differences (Clarke and Fraser 2004, Arnott et al. 2006).

The implications of choosing an inappropriate proxy may result in incorrect management strategies. If growth is slower and natural mortality lower than the proxy values, then limit reference points such as $F_{0.1}$ are likely to be higher than stocks can withstand and overfishing is likely to occur.

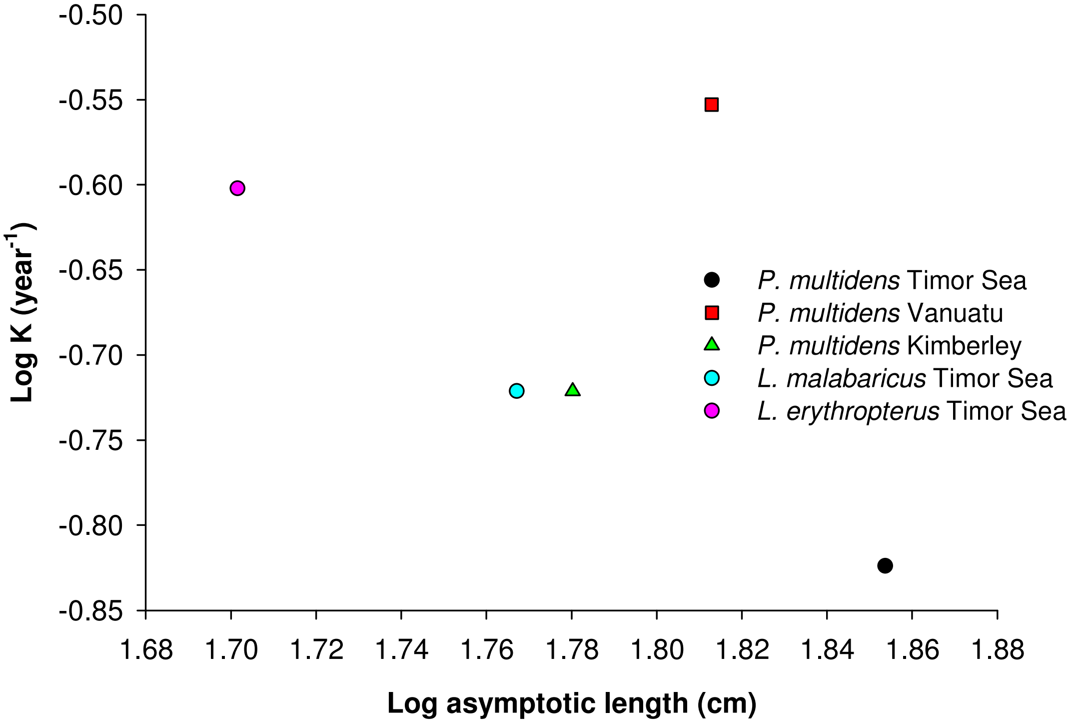


Figure 5.2.1. **Auximetric plots of the log of asymptotic length vs log of K for lutjanids from intermediate and shallow depth ranges**

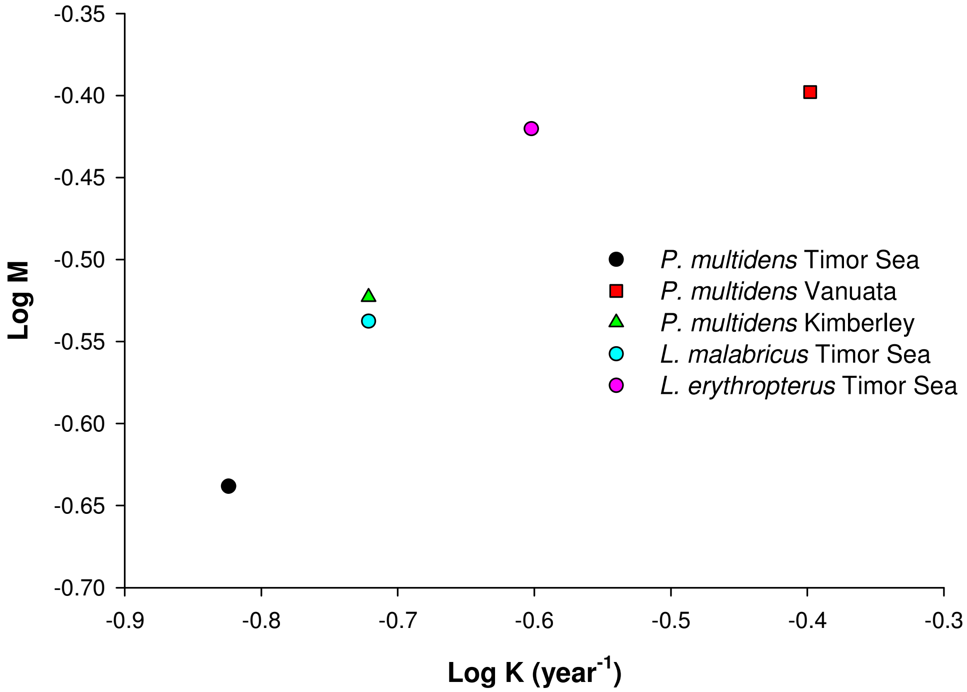


Figure 5.2.2. **Auximetric plots of the log of K vs log of natural mortality (M) for lutjanids from intermediate and shallow depth ranges**

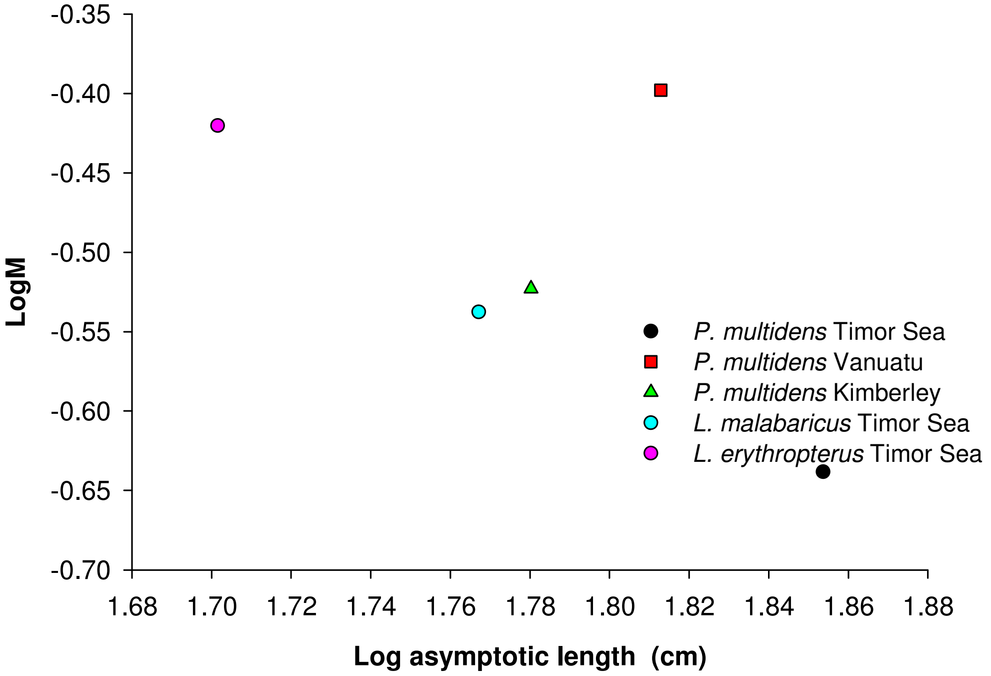


Figure 5.2.3. **Auximetric plots of the log of asymptotic length vs log of natural mortality (M) for lutjanids from intermediate and shallow depth ranges**

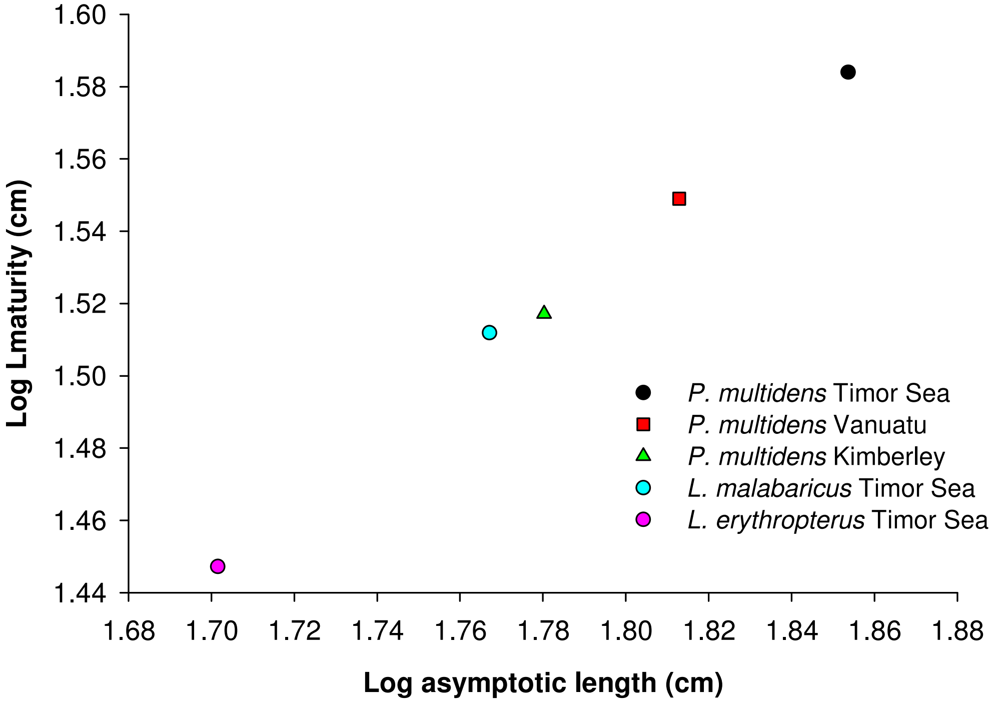


Figure 5.2.4. **Auximetric plots of the log of asymptotic length vs log of length at maturity for lutjanids from intermediate and shallow depth ranges**

In data-poor situations, M has been used as a proxy for the fishing mortality associated with maximum sustainable yield (F_{MSY}) (Gabriel and Mace 1999). In my study, catch-at-age for *P. multidens* indicated that M=0.18 (see Chapter 3), if a proxy M value was used for *P. multidens*, M could range from 0.29 *(L. malabaricus* in same area) to 0.42 (*P. multidens* in Vanuatu), therefore corresponding allowable fishing mortality could range from 0.18-0.42 depending upon the proxy used. Likewise, the length at which a fish will contribute the maximum yield to the population (L_{opt}) could range from 37.3 - 45.4 cm. Such large differences in proxy values can have a significant effect on the management strategies employed, resulting in a more lenient harvest strategy than is warranted.

Therefore the choice of appropriate proxy values is not a simple one. Never-the-less there is a need to maximise the information available from data-rich fisheries to assist in the management of date-poor fisheries.

Punt et al. (2005) have utilised the relationships which exist between biological parameters as described by Beverton and Holt (1959), Beverton (1992) and Jensen (1996) to investigate rapid assessment techniques using only life-history parameters. They explored the concept of 'similar species' to utilise the information from data-rich species for data-poor situations. Their results showed that although there were relationships between some biological parameters, the predictive ability of most parameters is weak. They concluded that as L_{inf} correlated well with most parameters, there was value in undertaking age studies for species where possible, even if only enough samples were taken to determine growth curve parameters.

5.4. Conclusion

While there is a recognised need to manage all fisheries in a sustainable manner, data-poor fisheries present a challenge to managers in both developing and developed countries. The obvious solution is to utilise information from data-rich fisheries as proxies for data-poor species. However caution must be exerted when using proxies. As illustrated in Figures 5.2.1 to 5.2.4, directly substituting biological parameters from a similar species within the same area or the same species from a different location may not provide appropriate proxy values.

The work of Punt et al. (2005) demonstrates that information from data-rich fisheries can be used to inform data-poor fisheries. These authors investigated the use of biological correlates to enable 'rapid assessments' to be undertaken for fisheries that lack suitable data to undertake formal stock assessment.

Cheung et al. (2005) took a different approach, using a fuzzy logic expert system to determine how vulnerable a species was to fishing pressure. Unlike conventional assessments of extinction vulnerability which require an in-depth understanding of the population dynamics of a stock, Cheung's method uses selected life history parameters, such as L_{max}, t_{max}, K, M and age at maturity which have been demonstrated in the literature to be related to intrinsic vulnerability, together with ecological parameters.

Chapter 6. General Discussion and Conclusion

Over-exploitation of inshore resources, together with advances in technology has led to increased exploration and development of deeper water fisheries (Pauly et al. 2003).

While there is good information for fisheries management on the shallow-water lutjanids, the increased expense of conducting research in deeper waters has been prohibitive for many developing countries and also for small-scale fisheries in developed countries. In the absence of research data, managers and scientists look to glean as much information as possible from data-rich fisheries which may provide proxy information for sustainable management strategies.

In this dissertation I have investigated whether lutjanid species throughout the different depth ranges have similar life history characteristics and therefore whether it is appropriate to use proxy values from data-rich species for data-poor fisheries.

Depth partitioning of genera within the lutjanid complex provides an opportunity to examine different life history strategies with respect to different environmental conditions. In this study I examined what this partitioning meant in relation to the demography of genera groupings within different depth ranges (shallow, intermediate and deep) and what were the possible mechanisms contributing to these differences.

I did this by conducting a detailed study of *Pristipomoides multidens* (intermediate depth range) and compared findings from this study with those reported in the literature for lutjanids from other depth ranges. This provided a framework for assessing whether it is acceptable to use proxies, and whether these proxies should be from lutjanids in same locality or from within the same depth range, even if the latter means using information from a different region.

In this chapter, I discuss the results of my detailed study of *P. multidens* and the implications of these results with respect to other lutjanid species.

6.1. Lutjanid demography with respect to depth

6.1.1. Trends in growth with depth

As discussed in Chapter 3, there appears to be demographic differences within the lutjanid complex in relation to depth. Small shallow water species show greater variability in growth across local scales compared with intermediate and deep water species, as indicated by the von Bertalanffy growth function (VBGF) parameters (Table 3.4.7). An examination of these parameters shows that for K in particular there can be considerable differences in values for shallow water species. For example, *Lutjanus vitta* can have K values ranging from 0.22-0.98, and *L. carponotatus,* can exhibit K values from 0.377-0.77 (Table 3.4.7). By comparison, species inhabiting intermediate and deep waters show a greater similarity for VBGF parameters despite regional and latitudinal differences (Table 3.4.7).

A possible explanation for this observation may relate to the tendency for small lutjanids to be more reef-associated and therefore their growth is more likely to be influenced by localised conditions compared with lutjanids in intermediate and deeper waters.

6.1.2. Trends in size and longevity with depth

Mean fork length was compared at ages 5, 7 and 9 years for *Pristipomoides multidens*, *Lutjanus malabaricus* and *L. erythropterus* from the Timor Sea and the Arafura Sea. For all three species, the results showed a general trend for a greater mean length at age for the Timor Sea when compared with the Arafura Sea. Likewise, longevity (defined by the upper 20% of ages for a species), was also greater for the Timor Sea when compared with the Arafura Sea. This is possibly due to the differences in depth as the Arafura Sea is considerably shallower than the Timor Sea. Samples taken from the Arafura Sea were caught at the 50-60 m depth range, while samples from the Timor Sea were taken in the 100-150 m depth range. However fishing gear selectivity may confound these observed differences as the samples from the Arafura Sea were taken by trawling and the Timor Sea samples were taken by trap and dropline methods. It is possible that larger, stronger fish may be able to swim faster than the trawled nets and therefore avoid capture. With trap and dropline, competition for bait may result in larger, more aggressive fish being caught in greater numbers than smaller fish.

6.1.3. Trends in spawning with depth

Lutjanids appear to exhibit different spawning patterns with respect to depth zonation. Shallow water lutjanids favour a restricted summer peak in spawning activity, compared with lutjanids inhabiting intermediate and deeper waters, which appear to show a more protracted spawning season with a peak in activity during summer months and in some regions two spawning peaks are observed (Table 4.4.1).

In my study *P. mutidens* displayed a protracted summer spawning period, which was consistent with findings for this species (Brouard and Grandperrin 1985), and for *P. filamentosus* (Kikkawa 1984).

There are numerous triggers for spawning, but those most commonly cited in the literature are water temperature, photoperiod, rainfall and lunar tidal cycles (Qasim 1956, Parrish et al. 1981, Bakun et al. 1982, Lambert and Ware 1984, Sherman et al. 1984). These conditions can vary locally in shallow water and it has been shown that even for the same species, different triggers can induce spawning in different areas. Russell et al. (2003) and Doi and Singhagraiwan (1993) found different spawning triggers for *L. agentimaculatus* in different countries. Russell et al. (2003) found spawning in Queensland was triggered by increasing water temperature, whereas Doi and Singhagraiwan (1993) found in Thailand, that spawning was triggered by decreasing water temperature and high rainfall. Therefore it appears that spawning is aligned to the most locally favourable conditions in shallow waters.

However in the intermediate and deeper waters, water temperature and photoperiod are relatively stable for most of the year, and rainfall and lunar cycles are unlikely to have any influence at these depths. It is more likely that oceanic currents play a significant role in these deeper waters, and spawning cues may be related to large-scale upwelling at certain times of the year, which may bring nutrient enriched water into these zones. As previously discussed in Chapter 4, the Indonesian Throughflow (ITF) current system is a significant presence in this region, and the strength of the ITF is affected by monsoonal patterns. I believe that *P. multidens* spawning in my study area may be triggered by these large-scale oceanic current systems and the resultant changes in productivity. However targeted studies would need to be undertaken to explore this theory.

6.1.4. Trends in length at maturity

Several different theories have been put forward to explain how length at maturity is affected by environmental conditions. Grimes (1987) has postulated that length at maturity is linked to habitat, with shallow water and continental habitats being more productive than deeper water and island habitats, and therefore species inhabiting shallow water and continental habitats would have a smaller size at maturity than species found in deeper water or island habitats.

The length at maturity for *P. multidens* in my study was 313 mm fork length (FL) for the Arafura Sea and 382 mm FL for the Timor Sea, this was similar to values obtained by Brouard and Grandperrin (1985) for this species in Vanuatu. Similar values were reported by Min (1977) for *P. multidens* from the South China Sea. In my study *P. multidens* is found on the continental shelf, whereas the studies undertaken by Brouard and Grandperrin (1985) in Vanuatu were from the island habitats. The similarity in these findings from the different habits does not support the Grimes hypothesis (1987) linking length at maturity to habitat.

6.2. Can proxy values be used?

Although there are trends in life history parameters between genera within the same depth range, as discussed in Section 6.1, are the life history parameters sufficiently similar to use proxy values for species where information is limited? This question was examined in Chapter 5, where growth, reproduction and mortality parameters for *P. multidens* were compared from different areas; two areas from northern Australia (NT sector of the Timor Sea and the Kimberley region of WA) and Vanuatu (South Pacific). The same comparisons were made between *P. multidens* and the large shallow water species *Lutjanus malabaricus* and *L. erythropterus* from the same area within the NT sector of the Timor Sea.

Auximetric plots of asymptotic length versus K, asymptotic length versus length at maturity, and natural mortality versus K, were used to compare relationships (Figures 5.2.1-5.2.4). Results showed that *P. multidens* from the Kimberley region of the Timor Sea had similar parameter values to *L. malabaricus* from my study in the NT sector of the Timor Sea. Therefore to use proxy values for a species based on values of the same species from a different area or a similar sized lutjanid from a different depth range within the same area is not valid.

Nevertheless there is a need to utilise information from data-rich fisheries to inform management decisions for data-poor fisheries. While direct substitution of life history parameters from other lutjanid species for stock assessment purposes is not applicable, there are other ways to maximise available information.

Beverton and Holt (1959), Beverton (1992) and Jenson (1996) found general patterns in population dynamics. They used these patterns to develop relationships which would provide information for missing parameters or parameters which are hard to determine (e.g. natural mortality). Beverton (1963) hypothesises that these patterns reflect natural selection.

Punt et al. (2005) have utilised these relationships between biological parameters and have investigated the use of biological correlates as an approach to utilising information from data-rich species for data-poor species.

Cheung et al. (2005) took a different approach, using a fuzzy logic expert system to determine how vulnerable a species was to fishing pressure. Unlike conventional assessments of extinction vulnerability which require an in-depth understanding of the population dynamics of a stock, this method uses selected life history parameters, such as L_{max}, t_{max}, K, M and age at maturity, which have been demonstrated in the literature to be related to intrinsic vulnerability, together with ecological parameters.

While these generalised relationships can provide valuable information, there is also a need to examine what drives the differences in patterns observed in species inhabiting different habitats. Pauly (1980) found a relationship between natural mortality, growth and mean water temperature. He proposed that differences in metabolic rate was the mechanism driving these observed differences, where fish inhabiting warmer waters have a higher metabolic rate, which in turn requires a more frequent need to feed and therefore greater exposure to predators. Other researchers (Clarke and Fraser 2004) believe that evolutionary trade-offs are responsible.

The methodologies developed by Punt et al. (2005), Cheung et al. (2005) and others, demonstrates innovative ways of using information from data-rich fisheries to assist in informing management strategies for data-poor fisheries.

There is a need for further development of techniques for utilising information from data-rich species to assist in fisheries assessment of data-poor species, and an understanding of the drivers behind these patterns of species groupings.

6.3 Conclusion

In conclusion, my study has shown that within the lutjanid complex there are different life-history strategies for lutjanids inhabiting different depth ranges, which are influenced by the environmental conditions within these depth ranges. However there are also confounding effects such as fishing and genetics which may also contribute to observed demographic patterns. Targeted studies would need to be undertaken to elucidate the effects these and other variables may have.

While direct substitution of the life history parameters of similar species into stock assessment models is generally unadvisable, nevertheless data-rich fisheries can be used to inform data poor fisheries by providing information on the inter-relationships between biological parameters. In the absence of comprehensive data required for formal stock assessment, rapid assessment which only uses basic life history parameters are becoming an increasingly important tool for assessment (Punt el al. 2005). Data-rich fisheries have the capacity to provide the necessary information about the underlying relationships between biological parameters, which can be utilised to estimate unknown parameters for data-poor fisheries, thereby providing valuable information for informed management.

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APPENDIX I- Histology Symbols

List of symbols corresponding to Figure 4.2.1.

Cn	Chromatin nuclear oocytes
Pn	Perinuclear oocytes
ePn	early perinuclear oocytes
YV	Yolk vesicle oocytes
YG	Yolk granular oocytes
Hy	Hydrated oocytes
pof	Post ovulatory follicles
epof	Early post ovulatory follicles
Nm	Nuclear migration
V	Yolk vesicles
ygr	Yolk granules
gr	Granulosa
nuc	Nucleoli
do	developing oocytes
A	atretic oocytes

Appendix II - Size at Maturity Tutorial

by John McKinlay (WA Department of Fisheries)

> args(sam)

Function (len, mature, size.mature = 0.5, binsize = 5, lab.left = "Frequency", lab.right = "Proportion Mature", lab.bottom = "Length", title = "Size at Maturity", boot.ci = F, conf.int = 0.95, boot.nbr = 500, model.logistic = F, model.glm = T, diagnose = F)

This function written in S-Plus, takes a vector of sizes (or ages) and a vector of maturity indicators (0's for immature and 1's for mature).

There are some advantages to using this routine over traditional approaches to calculating size-at-maturity:

It's very easy and quick to use - the four graphs below took less than 10 min (total) to produce, including importing the data into S-Plus. Graphs A-C took ~ 1 sec each, graph D with 1000 bootstrap samples took ~3min. Note that the original data are 238 fish.

A frequency histogram of the lengths (or ages) is displayed beneath the curve - this is important for showing multi-modality that may be present due to different cohorts or sexes.

Bin calculations are done automatically, so it is very easy to try a variety of bin sizes in order to choose the best size for presentation purposes.

The proportion mature (size.mature = 0.5) can be changed.

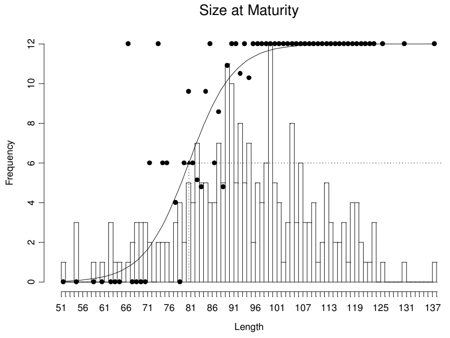
The logistic glm models all the (unbinned) data, not simply the mid-points of the size classes. The latter method is often carried out in fisheries contexts (eg. in Excel), but essentially "throws away" information. Additionally, fitting to the size-class mid-points means a different size-at-maturity for different choices of bin-size! Using a glm provides the “true” estimate of s-a-m according to the data (see Figure C to note the difference between the logistic glm and the logistic equation fit by least-squares to the class-midpoints).

Perhaps most importantly, bootstrap confidence intervals may be calculated for estimated size-at-maturity.

A variety of summary output is produced (parameter estimates, SE’s, bias estimation from the bootstrap – see below).

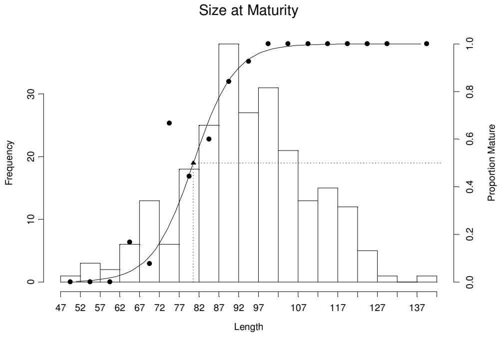
A.

```
sam(length,mature,binsize=1,size.mature=0.5,model.glm=T)
```



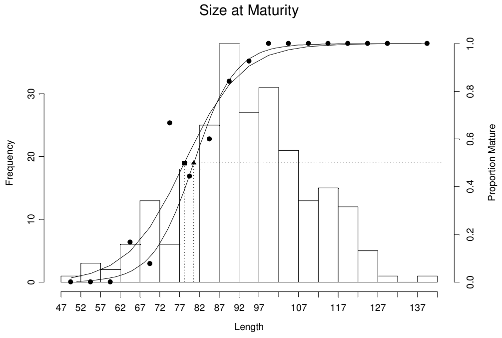
B.

```
sam(length,mature,binsize=5,size.mature=0.5,model.glm=T)
```



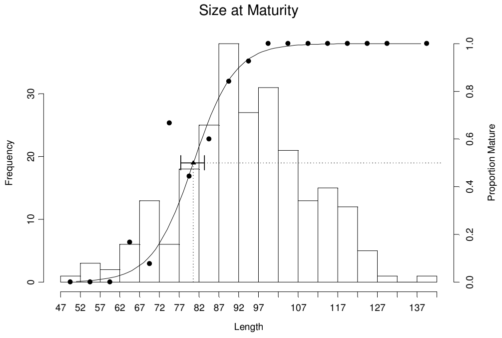
C.

```
sam(length,mature,binsize=5,size.mature=0.5,model.glm=T,model.logistic=T)
```



D.

```
sam(length,mature,boot.ci=T,binsize=5,model.glm=T,boot.nbr=1000)
```



Suggested usage:

The data should be presented as an excel sheet, one column of lengths (or ages), and one column of maturity indicators (0 for immature, 1 for mature). This will easily import into S-Plus.

Plot the data using a variety of bin sizes to choose the best bin-size for presentation purposes. For example, Fig A shows the raw data (bin.size=1), Fig B shows a preferable bin.size of 5.

Calculate the 100.(1-alpha)% CI for the estimated size at maturity. Generally choose 1000 bootstrap samples for calculating CI's (Fig D and output below).

Check that the bias to SE ratio of the bootstrap sample is not too large - generally < 0.25 is acceptable.

The text output appears below:

```
> sam(length,mature,boot.ci=T,binsize=5,boot.nbr=1000)

Range: 51 138

Break Points: 47 52 57 62 67 72 77 82 87 92 97 102 107 112 117 122 127 132 137 142

 0 1 pmature

 47+ thru 52 1 0 0.00000000

 52+ thru 57 3 0 0.00000000

 57+ thru 62 2 0 0.00000000

 62+ thru 67 5 1 0.16666667

 67+ thru 72 12 1 0.07692308

 72+ thru 77 2 4 0.66666667
```

```
 77+ thru 82 10 8 0.44444444
 82+ thru 87 10 15 0.60000000
 87+ thru 92 6 32 0.84210526
92+ thru 97 2 25 0.92592593
 97+ thru 102 0 31 1.00000000
102+ thru 107 0 21 1.00000000
107+ thru 112 0 13 1.00000000
112+ thru 117 0 15 1.00000000
117+ thru 122 0 12 1.00000000
122+ thru 127 0 5 1.00000000
127+ thru 132 0 1 1.00000000
132+ thru 137 0 0 NA
137+ thru 142 0 1 1.00000000
=======================================
SUMMARY OF GLM LOGISTIC LINK
Call: glm(formula = mature ~ len, family = binomial(link = "logit"))
Deviance Residuals:
 Min 1Q Median 3Q Max
-2.376894 0.02490801 0.1495473 0.4608529 2.311735
```

```
Coefficients:
            Value Std. Error t value
(Intercept) -15.4359831 2.41861218 -6.382165
len 0.1915752 0.02845735 6.732011
(Dispersion Parameter for Binomial family taken to be 1 )
Null Deviance: 252.4182 on 237 degrees of freedom
Residual Deviance: 128.3883 on 236 degrees of freedom
Number of Fisher Scoring Iterations: 6
Correlation of Coefficients:
(Intercept)
len -0.9956704
Predicted length at maturity: 80.574
95 % Confidence Interval based on 1000 bootstrap samples: 77.428 83.343
Bootstrap distribution mean 80.525
Bootstrap mean bias estimate 0.049
Bootstrap distribution SE: 1.485
Bias to SE ratio: 0.033
```