The biology and ecology of small tropical scorpaenoids inhabiting shallow coastal habitats in Singapore

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Abstract

Life history theory predicts a range of generic responses in life history traits with increasing organism size, among the most important of which are relationships between body size and growth, mortality and life span. Size-dependent bias in global extinction risk has recently been identified in fishes, with smaller fish thought to be at greater risk from habitat degradation. Potential relationships between body size, local extinction and ecological and life-history traits were investigated in common scorpaenoids inhabiting local coastal habitats. Sympatry in *Paracentropogon longispinis* and *Trachicephalus uranoscopus* is likely to be supported by partitioning of food resources, which may also have contributed to slightly disparate growth trajectories. Although some differences in growth and reproductive biology were detected between the two small species *P. longispinis*, *T. uranoscopus* and the larger *Synanceia horrida*, similarities in growth rates appeared to be associated with size-dependent life history strategies, while reproductive timing was associated with optimum conditions for larval survivorship during the northeast monsoonal season. Moreover, variations in life history tactics in both the small tropical scorpaenoids appeared to be associated with increased survivorship from either better physiological tolerances or defensive potentials, and occurred for both juveniles and adults inhabiting shallow estuarine habitats that are challenging habitats for many other fish species. The findings are discussed in terms of implications for risk of local extinction/vulnerability, and life history strategy adaptations along coastal habitats, given the rapid rate of coastal development in Singapore.

Chapter 1. General Introduction

Life history theory predicts a range of generic responses in life history traits with increasing organism size, among the most important of which are relationships between body size and growth, mortality and life span (Blueweiss et al., 1978; Stearns, 1992). Size-dependent bias in global extinction risk has also been identified in fishes, with small sized freshwater fish thought to be at greater risk from habitat degradation than small marine fish (Olden et al., 2007), although recent evidence has shown that small coral reef fishes (especially gobies), may just as susceptible to extinction (Munday, 2004). In addition, life history patterns have also been found to be a contributing factor to survivorships and mortality in small cryptic coral fish (Hernaman and Munday, 2005a; b). As such, if such small cryptic marine coral-dwelling fish are susceptible to anthropogenic effects along offshore habitats, would we then expect that other small cryptic but non-coral associated marine fish that are found closer inshore (and closer to sources of anthropogenic effects) be equally, perhaps even more susceptible to local extinctions? Or do they display certain life history characteristics that improve survivorship?

The scorpaenoids inhabiting the shallow habitats of Singapore are an ideal group of fish that can be used to try and answer these questions. The reasons for this include: 1) studies which have found that scorpaenoids are abundant among the benthic fish community along soft sediment coastal habitats of Singapore (Kwik et al., 2010); 2) while most fish inhabiting shallow coastal waters usually consist of juveniles to sub-adults (Blaber et al., 1995), scorpaenoids appear to utilise these habitats as adults; and 3) similar to the gobies inhabiting corals, scorpaenoids are also known to be closely associated with their habitats (Love et al., 1990a; Ordines et al., 2009) and are highly cryptic in behaviour (Ballantine et al., 2001;

Grobecker, 1983). To this effect, I propose to use small marine scorpaenoids to better understand potential relationships between body size, local extinction and ecological and life-history traits in local non-coral coastal habitats.

General life history patterns of small fish

The concepts of *r* and *K* selection (MacArthur and Wilson, 1967) and optimal life histories (Gadgil and Bossert, 1970) attempt to elucidate generalities in the relationships among habitat, ecological strategies and population parameters. These operate on the theory that natural selection operates on these characteristics to maximise the number of surviving offspring. Adams (1980) predicts from *r*-*K* selection theory that adult size, maximum age and age at maturity should all be positively correlated. Species that are exposed to a large component of non-selective or catastrophic mortality (i.e. *r* strategist) would be selected for characteristics that increase productivity through reproductive activity, implying: 1) early maturity, 2) rapid growth rates, 3) production of a large number of offspring at a given parental size, and 4) maximum production of offspring at an early age (Gadgil and Bossert, 1970). Other life-history traits associated with *r*-strategy resulting from the allocation of resources towards reproductive activity are 1) small body size; 2) high mortality; and 3) shorter life span (Gadgil and Solbrig, 1972; Pianka, 1974).

It is now widely accepted that there is a continuum of responses and strategies between *r* and *K*; to this end Winnemiller and Rose (1992) identified three life-history strategies in fish as the endpoints of a trilateral continuum based on trade-offs among survival, fecundity and age at maturation:

1. Opportunistic – maximises intrinsic rate of population growth through reducing mean generation time, i.e. small-sized individuals with early maturation that continuously

release small eggs to colonise rapidly created gaps (highly disturbed or constantly changing environments);

2. Periodic – highly fecund fish with some degree of delayed maturation that exploit predictable environmental patterns (e.g., seasonality);
3. Equilibrium – small to medium sized fish with delayed maturation that produce small clutches of large eggs and exhibit well developed parental care.

In a meta-analysis of early life-history data in relation to the three-endpoint model, Fonseca and Cabral (2007) associated life history patterns with habitat and latitude. Higher larval and juvenile growth rates and condition indices, together with earlier mean age at maturation were found in fish associated with complex or variable habitats in both tropical (coral reefs) and temperate (estuaries) latitudes, and also in tropical regions compared to temperate or polar regions (Fonseca and Cabral, 2007). Rapid growth rates in the tropics were attributed to opportunistic strategies, which at temperate latitudes attributed to periodic strategies that maximised resource allocation during periods of high availability (Fonseca and Cabral, 2007). Interestingly, their conclusions were somewhat at odds with the broad classification of coral reef fishes on the basis of life histories by Depczynski and Bellwood (2006). The first consists of relatively larger fish (100 mm TL) that have asymptotic growth, late maturation, low adult mortality, a pelagic seasonal broadcast spawning regime, and longevities of several years. The second group consists of small (<100 mm TL), often cryptic species that exhibit rapid, indeterminate growth, early maturation, short life spans and a reproductive mode that often includes parental care of eggs. Respectively, these roughly correspond to periodic and equilibrium strategies in the Winnemiller and Rose (1992) scheme.

Unfortunately, there were no tropical estuaries in Fonseca and Cabral's (2007) study and as such, no data were available for the meta-analyses. While estuaries are highly productive and dynamic environments (McLusky and Elliot, 2004), organisms inhabiting this environment receive benefits from a high food availability and relative refuge from predation but must be able to tolerate the fluctuating environmental conditions which can be extreme (Miller et al., 1985). The benefits include the potential for increased growth in these habitats for juvenile as well as adult fishes (Cabral, 2003; Islam and Tanaka, 2005; Yamashita et al., 2003). The resulting rapid growth appears to confer selective advantages, with better survival, at least in the reef fish species studied so far (Wilson and Meekan, 2002). Global climate change effects are expected to have particularly strong influences on species associated with vulnerable habitats (tropical reefs, estuaries and shallow coastal habitat) and with relatively small temperature ranges (Roessig et al., 2004). Within tropical clines, much more is known about the life-histories of fishes inhabiting coral reefs than any other ecosystem, but surprisingly little is known about other tropical fish that inhabit other ecosystems (e.g., seagrass, soft sediment or intertidal habitats).

Scorpaenoids in general

The suborder Scorpaenoidei (hereafter referred to as scorpaenoids) is a very diverse group of fish consisting of approximately 500 species from 40 subfamilies (Eschmeyer, 2010). Commonly called scorpionfishes, species from this suborder can be abundant and widely distributed in every ocean including tropical (Adrim et al., 2004; Randall and Lim, 2000; Winterbottom et al., 1989), subtropical (Motomura and Iwatsuki, 1997; Motomura et al., 2004; Randall et al., 1985), and temperate waters (Motomura et al., 2006; Motomura et al., 2005; Zajonz and Klausewitz, 2002), although most are known from the Indo-Pacific region (Grzimek, 2003; Poss, 1999). Scorpaenoids also inhabit many environments ranging from intertidal shores (Carpenter and Niem, 1999) and coastal areas (Kwik et al., 2010) to deep offshore waters (Malecha et al., 2007; Watters et al., 2006).

Correspondingly, it may be expected that scorpaenoids display as diverse a range of ecological traits relating to habitat utilisation, feeding ecology, offensive/defensive mechanisms, growth rates, and reproduction. However, despite being very well known for their venomous nature (Brenneke and Hatz, 2006; Isbister, 2001; Lee et al., 2004; Rual, 1999; Russell, 1973; Warrell, 1993; Wiener, 1963) as well as being highly recognisable and popular with aquarists (Cailliet et al., 2001; Echeverria, 1987; Key et al., 2005; Leaman, 1991; Love et al., 1990b; Sadovy, 1991), very little is known about the biology of these fishes. The few exceptions to this are several species of the families Sebastidae and Scorpaenidae which were harvested in the Mediterranean and USA in the early 1980s, and due to potential crashes in stock populations triggered a spate of reproductive biology and growth studies (Hightower and Grossman, 1985).

In the 1990s, there was another spike in interest in scorpaenoids, but this time it was focused on the ecological impacts of *Pterois volitans* (family Pteroidae)(Barbour et al., 2010; Hare and Whitfield, 2003; Meister et al., 2005; Morris et al., 2008), an invasive alien species in Florida. This introduction is believed to have originated from the accidental release of six aquarium specimens into the coastal waters that have formed an established population, which is reported to have an effect on the native fish community (Hare and Whitfield, 2003; Morris and Whitfield, 2009). More importantly, no ecological studies have been conducted on scorpaenoids in the equatorial tropics, resulting in a lack of basal knowledge on the ecological roles and importance of these fishes in the fish community. Additionally, the high diversity, variations in size and behaviour of this group of fishes makes them ideal for testing general paradigms in life-history patterns in tropical fishes.

Scorpaenoid diversity in Singapore

At present, the species records for scorpaenoids found in Southeast Asia are patchy and poor. The few records providing distributional information are either broad-ranged (e.g., South China Sea lists (Randall and Lim, 2000) or in specific countries like Indonesia (Adrim et al., 2004; Allen and Adrim, 2003). Published comprehensive fish species lists for Singapore are limited and taxonomically outdated (Fowler, 1938; Weber and De Beaufort, 1962) (but see Kwik et al. [2010] for a localised list for Changi Point). Although the historical catch abundances of scorpaenoids in Singapore appear low, species diversity is relatively high. A review of the most reliable historical records (Fowler, 1938; Herre and Myers, 1937; Weber and De Beaufort, 1962) indicate that there are 27 species, out of approximately 500 known species, recorded locally. However, it is possible that the number of species could be higher as a result of unrecorded species, which may not have been captured owing to sampling biases (i.e. sampling regime, use of different traps and nets).

As such, an initial aim of this thesis was to develop and update the scorpaenoid species found in Singapore. In addition to identifying the commonly found small scorpaenoids for ecological studies in this thesis, this aspect of the present study also helped to identify larger species for size-related life history comparisons. This taxonomic study would also identify other scorpaenoids (small or large) that may have become locally extinct through habitat degradation. This is reviewed in the general discussion.

Trophic ecology of scorpaenoids

To survive in any environment, adaptations to conditions occur when fish adopt certain life history strategies and tactics (Blueweiss et al., 1978; Ordines et al., 2009). These are usually associated with energy costs which is satisfied by food intake (Deng et al., 2003; Gerking, 1994; Johnston and Battram, 1993), and can play a crucial role with regards to life history patterns (Kamler, 1992). Food is also an important resource axis that has implications for intra- and inter-species co-existence, both numerical as well as distributional rarity of dietary items can also have an effect on the dietary patterns observed in predators (Gaston, 1996). Understanding the trophic ecology of species also provides insights into habitat utilisation (Angel and Ojeda, 2001; Grossman et al., 1980). Although information on the quality and quantity of food consumed by fish at any trophic level (which can be derived from feeding studies) is traditionally utilised for fisheries research through incorporation into appropriate fisheries models (Stergiou, 2002), diet composition data can also play a key role for the research on resource partitioning both within and between species (Harmelin-Vivien et al., 1989; Macpherson, 1981), prey selection by predators (Kohler and Ney, 1982; Stergiou and Fourtouni, 1991), relationships between predator and prey (Pauly et al., 2000; Scharf et al., 2000), ontogenetic diet shifts within a species (Labropoulou and Eleftheriou, 1997; Stergiou and Fourtouni, 1991), habitat selection (Labropoulou and Machias, 1998; Labropoulou et al., 1999) and testing predictions from foraging behaviour and optimal foraging theory (Burrows, 1994; Galis and de Jong, 1988 ; McArthur and Pianka, 1966).

Due to the wide variability in adult size of scorpaenoids as well as the habitats they are found, the diet found in this suborder can be very varied, though all appear to be carnivorous. While some are active foragers (e.g., pteroids and scorpaenids) (Harmelin-Vivien and Bouchon, 1976; Morris and Akins, 2009), others are ambush predators (e.g., synanceids) (Grobecker, 1983), and as such their position in the water column and activity levels varies between different species.

In spite of the several dietary studies conducted (Hallacher and Roberts, 1985; Love et al., 1990a; Mesa et al., 2007; Murie, 1995), the role of scorpaenoids in the benthic fish community has never been properly addressed. Preliminary studies have identified sympatry among in at least two species of scorpaenoids (*Trachicephalus uranoscopus* and *Paracentropogon longispinis*) along coastal areas of Singapore (Kwik et al., 2010), providing an opportunity to study the intra and inter-specific relationships that may occur between these two co-existing species, which adopt various strategies of resource sharing at a range of spatial and temporal scales, and may also occur in different age/size classes within a species (ontogeny) to decrease intra-specific competition (Rezsu and Specziár, 2006). Trophic studies investigating scorpaenoids indicate that larger scorpionfish feed primarily on fish (Harmelin-Vivien and Bouchon, 1976; Morris and Akins, 2009), while smaller sized scorpionfish have broader dietary ranges including polychaetes and decapods (Mesa et al., 2007). Given that the size ranges of *T. uranoscopus* (12–90 mm SL) and *P. longispinis* (10–70 mm SL) overlap (Kwik et al., 2010; Poss, 1999), it is conceivable that there may be overlaps in their diets as well and therefore a potential for resource competition. Trophic studies performed in these shallow habitats will help in the understanding of both the inter- and intra-specific relationships that can occur between scorpaenoids and other benthic fish species inhabiting these areas. This increased understanding of food webs and trophic groups would also be useful in elucidating the co-existence of sympatric species through partitioning of resources resulting from competition avoidance within the local fish community (Bulman et al., 2001; Gelwick and Matthews, 2007; Pasquaud et al., 2008). It is also likely that these dietary partitioning and prey selection will have effects on the life histories of sympatric species.

Growth patterns of scorpaenoids

In such a large and diverse suborder, many different and varied life history patterns have been observed in both the temperate and subtropical scorpaenoid species, but surprisingly there have been no growth studies performed on tropical scorpaenoids. Although it is assumed that growth rates, maximum size, and longevities of scorpaenoids are usually associated with depth (Cailliet et al., 2001) and latitude (Boehlert and Kappenman, 1980), studies on temperate scorpaenoids indicate that many species do not appear to follow normal patterns for age and growth rates. Some examples include the temperate and deep dwelling sebastids that are slow growing and longer-lived but not necessarily large-sized (Bakay and Mel'nikov, 2008; Echeverria, 1987; Sequeira et al., 2009; White et al., 1998), as well as some small-sized scorpaenids (*Scorpaenodes littoralis* and *S. maderensis*) which are also relatively long-lived but are instead found in shallow subtropical waters (La Mesa et al., 2005; La Mesa et al., 2010; Mesa et al., 2005).

Growth rates of temperate and subtropical scorpaenoids also differ with most sebastids having generally low Von Bertalanffy growth curve *K* values (between 0.1–0.3) (Haldorson and Love, 1991; Kelly et al., 1999; Love et al., 1990b) whereas scorpaenids have slightly higher K values (between 0.2–0.4) (Bilgin and Celik, 2009; La Mesa et al., 2005). However, these values are still relatively lower compared to most other non-scorpaenoid tropical fish species (e.g., snappers [Lutjanidae] and groupers [Serranidae]) which have generally higher K values (Ali et al., 2002; Pauly, 1983). With a lack of growth studies in tropical scorpaenoids and the high variations in life histories observed, it has yet to be determined if small tropical scorpaenoids conform to general size-related growth patterns which state that small species have short lifespans and faster growth rates (Blueweiss et al., 1978; Stearns, 1992).

Reproductive biology of scorpaenoids

Reproductive strategies and growth influence the success and competitive ability of any species. Moreover, both are important parameters in population biology and an understanding of them is critical for managing conservation risks of any species (Grandcourt et al., 2004; Williams et al., 2008). Documented reproductive strategies among scorpaenoids include viviparity (Sebastids, Wourms 1991; Fujita and Kohda, 1996; Fugita and Kohda, 1998), oviparity (Koya and Munoz, 2007) and broadcast spawning (Wourms, 1991). The different reproductive strategies that are found in broadcast spawners can also affect the dispersal methods (Hickford and Schiel, 2003) due to the different number and size of eggs produced (Hickford and Schiel, 2003; Wourms, 1991). The majority of scorpaenoids (approximately 60%) produce pelagic eggs (Washington et al., 1984) and a few species have demersal eggs (Suthers and Frank, 1991) surrounded by gel that is believed to be a deterrent for potential egg predators (Deblois and Leggett, 1991; Dulcic et al., 2007; Fewings and Squire, 1999).

Reproductive seasonality can also affect the abundances and dominant size classes of fish found in a given habitat. Spawning events (usually with broadcast spawners) are also usually associated with tidal and lunar cycles (Doherty, 1983; Lobel, 1978) as well as seasonal changes in subtropical to temperate countries (HjaltiÍJákupsstovu and Haug, 1988; Ward et al., 2003). During these spawning periods, aggregations of sexually mature adults form, which is usually reflected by greater numbers of larger sized sexually mature fish (Hunter and Macewicz, 1987; Richardson et al., 1997; Robertson, 1991; Samoilys and Squire, 1994; Skaret et al., 2003). Subsequent influxes into the system of smaller, post-settlement fish

(Richards and Lindeman, 1987) due to recruitment are reflected in periodic increases in the abundance of fish (Moser and Boehlert, 1991; Robertson et al., 1993; Svedang, 2003). While spawning events have never been observed in temperate scorpaenoids, a spawning aggregation was only recorded once in *Synanceia horrida* (see Fewings & Squire, 1999) in subtropical Australia. Moreover, recruitment events (where there were sudden spikes in abundances of juveniles) have been observed in both temperate sebastids (Moser and Boehlert, 1991) and subtropical scorpaenids (Ribas et al., 2006). However, it remains uncertain if similar spawning aggregations or recruitment events occur for the different species of tropical scorpaenoids.

Although all the subtropical to temperate scorpaenoids studied thus far display some form of seasonal breeding patterns (Bilgin and Celik, 2009; Echeverria, 1987; Fewings and Squire, 1999; Munoz et al., 2005), nothing is known of spawning cycles in tropical scorpaenoids, particularly in along the equator where seasonal cues (monsoonal periods twice a year) may be much less pronounced than in subtropics or temperate latitudes (Johannes, 1978). In addition, both diet and somatic growth have direct effects on reproductive effort in fish (Larson, 1991; Lester et al., 2004), which may be reflected by different reproductive strategies or tactics.

General Questions

The general question approached in this thesis looks at how small tropical marine fish (focusing on scorpaenoids) survive in impacted areas and whether this may be associated to certain traits in their life history patterns. This will addressed by looking at inter- and intra-specific relationships in trophic ecology and also by looking at the associations with life history patterns between the different species of sympatric scorpaenoids. Specific questions addressed within each chapter are:

1. To determine the current diversity of Singapore scorpaenoids and to identify the small and larger scorpaenoids which are ideal for life history studies. This also involves looking at historical information to determine which local species may have become numerically scarce or even potentially extinct due to anthropogenic impacts (Chapter 2);
2. Ascertain the ecological roles of small scorpaenoids in shallow tropical marine habitats by investigating their trophic ecology and functional morphology of common sympatric tropical scorpaenoids within the benthic fish community and potential reasons for the co-existence of sympatric scorpaenoids. This also involves looking at dietary requirements for scorpaenoids in relation to their life history patterns (Chapter 3);
3. Determine the similarities or differences in growth rates and longevities of various tropical scorpaenoids to see if small scorpaenoids display any particular growth patterns (Chapter 4)
4. Study if scorpaenoids display seasonal (monsoonal) breeding patterns independent of species size, which has implications on their survivorship and mortality (Chapter 5).

1.2 General Material and Methods

1.2.1 Description of local sites

During the initial study period, up to 24 sites along the coastal shores of Singapore were sampled in determining permanent sampling locations for each of the specific studies in this thesis (elaborated upon under individual chapters)(Figure 1.1). At each site, four different sampling methods (see 1.2.2) were used. Due to the extensive sampling methods employed during the study and the large number of sampling sites, application for permits from the National Park Board were done many months in advance with constant notification of location and feedback required prior and after sampling.

Selection of these sites were based on a few factors including: 1) accessibility and safety of sites - many sites were only accessible by boat, which was not always available due to tidal or mooring constraints; 2) site restrictions due to permit availability (as many areas along the coastal areas of Singapore are under the jurisdiction of the Singapore Armed Forces); and 3) representation of each of the various habitats (including soft sediment habitat, rocky habitats, seagrass/algae habitats and coral reef habitats)(Table 1-1). Other considerations were the constant thefts of the local fish traps or bubus which had to be left unattended over long periods of time at all of the sites except for sites at Sentosa due to the presence of the Sentosa Beach Patrol.

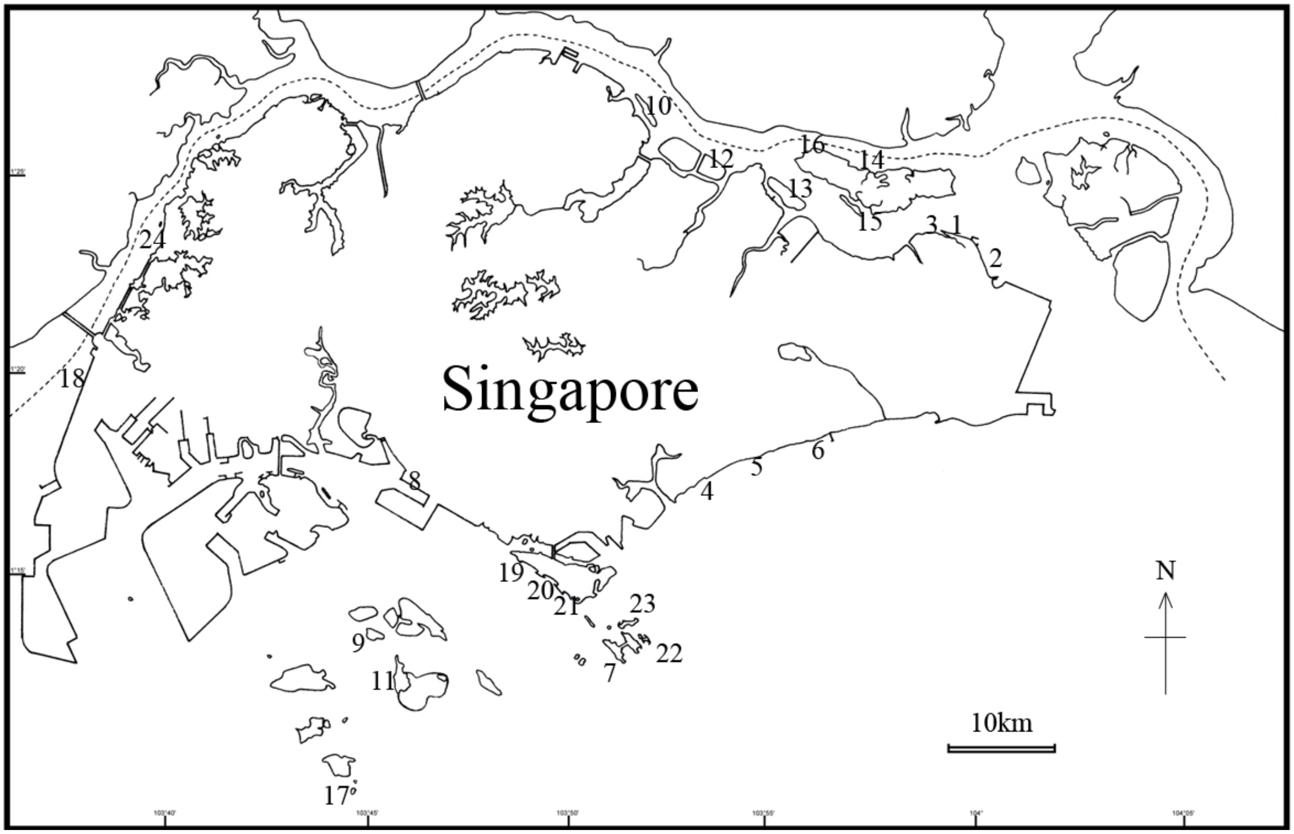

Figure 1.1 Map of Singapore indicating 24 initial sites sampled using beach seines, cast nets, angling and local traps between January and February 2006 (Refer to **Table 1-1**).

Table 1-1 Descriptions of 24 sampled sites during the initial two month survey using various techniques around coastal Singapore waters between January and February 2006.

Site no	Sampling Site	Geographical coordinates	Dominant benthos
1	Changi Beach (Car Park 1)	1^{o}23'35"N, 103^{o}59'16"E	Sand, Mud, Seagrass
2	Changi Beach (Car Park 6)	1^{o}22'30"N, 104^{o}0'21"E	Sand, Seagrass
3	Changi Beach (Changi Sailing Club)	1^{o}23'33"N, 103^{o}59'4"E	Sand, Mud, Seagrass

4	East Coast Parkway (Big Splash)	1°17'43"N, 103°53'57"E	Sand
5	East Coast Parkway (Marine Parade)	1°17'52"N, 103°54'24"E	Sand
6	East Coast Parkway (Sailing Centre)	1°18'23"N, 103°56'15"E	Sand
7	Kusu Island	1°13'25"N, 103°51'38"E	Sand, Coral
8	Pasir Panjang Beach	1°17'46"N, 103°45'35"E	Sand, Clay
9	Pulau Hantu	1°13'30"N, 103°45'4"E	Sand, Coral
10	Pulau Seletar	1°26'37"N, 103°51'46"E	Sand, Mud
11	Pulau Semakau	1°12'22"N, 103°45'41"E	Seagrass, Mud, Sand, Coral
12	Pulau Serangoon North	1°24'45"N, 103°55'17"E	Sand, Seagrass
13	Pulau Serangoon South	1°24'11"N, 103°55'39"E	Sand
14	Pulau Ubin, North	1°25'27"N, 103°56'36"E	Sand, Mud, Seagrass
15	Pulau Ubin, South	1°24'42"N, 103°56'33"E	Sand, Mud, Seagrass
16	Pulau Ubin, West	1°25'28"N,	Sand, Mud, Seagrass

		103^{o}55'43"E	
17	Raffles Lighthouse	1^{o}8'43"N, 103^{o}39’127"E	Coral, Rocky
18	Raffles Marina Beach	1^{o}20'19"N, 103^{o}38'1"E	Sand, Mud, Seagrass
19	Sentosa, Palawan Beach	1^{o}14'53"N, 103^{o}49'19"E	Sand, Rocky, Coral
20	Sentosa, Siloso Beach	1^{o}15'16"N, 103^{o}48'45"E	Sand, Rocky, Coral
21	Sentosa, Tanjong Beach	1^{o}14'31"N, 103^{o}49'44"E	Sand, Rocky, Coral
22	Sisters Island	1^{o}12'52"N, 103^{o}50'5"E	Sand
23	St John's Island	1^{o}13'18"N, 103^{o}50'57"E	Sand, Mud
24	Tuas Inlet (Fish Farms)	1^{o}26'9"N, 103^{o}41'45"E	Mud, Seagrass

1.2.2 Fish capture techniques

Several sampling methods were employed to capture scorpaenoids and other benthic fishes at the various sites sampled during the project. These included the following:

1) weekly beach seines (20 m x 2 m x 2 mm mesh and a 0.5 m cod end), consisting of three random seines performed at each site and conducted during low tides that were 0.5 m and below the standard datum to avoid tidal bias (seine area was estimated to be 800 m^2 per haul); 2) weekly collections of fish using locally made fish traps (referred to locally as bubus). Dimensions of these bubus are approximately 50 cm x 40 cm x 20 cm with a mesh size of 4 mm (Figure 1.2) and these traps are made from chicken wire.

Figure 1.2 Traditional fish trap (bubu) made from chicken wire.

Deployment of these traps includes tying three traps together at intervals of five meters, and due to the material used to make these traps, bubus are negatively buoyant and sink to the substratum quickly. Traps are deployed without baiting, as bubus act as miniature fish attracting devices (FADs) for smaller fish, which in turn attract larger piscivorous fish into the traps through the one-way opening of the bubu. These traps were checked every three days for captures. Due to the material of the bubus, replacement of traps due to corrosion of the chicken wire occurred occasionally;

3) full day (approximately 8 hours) cast netting (10 m diameter x 4 mm mesh) with two net casters performed weekly in waters less than 5 m depth; and

4) full day (approximately 8 hours) of conventional line angling (with two anglers using individual rods with single hooked lines tied) also performed weekly.

All scorpaenoids caught were immediately iced, preserved in 10% formalin and subsequently transferred to 70% alcohol for long-term storage. Specimens were identified, enumerated, and measured using a Bergman vernier caliper (± 0.1 mm) and a standard 30 cm ruler (± 1 mm) for specimens smaller and larger than 15cm, respectively. Voucher specimens were deposited in the Zoological Reference Collection (ZRC) of the Raffles Museum of Biodiversity Research, Department of Biological Sciences, National University of Singapore.

1.2.3 Periodic sampling of common scorpaenoids

***Monthly sampling for* Paracentropogon longispinis *and* Trachicephalus uranoscopus**

Between April 2006 and March 2008, monthly sample collections were performed at Changi Point Beach (1°23'18 N, 104°0'50 E) during spring low tides of each month. During each sampling period, three random seine pulls were performed. All scorpaenoids caught were identified, enumerated and measured using Bergman vernier calipers (SL ± 0.1 mm). Specimens collected were kept in ice, preserved initially in 10% formalin and stored in 70% alcohol. Back in the laboratory, both standard lengths and total weight of all specimens were remeasured for confirmation using a Bergman vernier calipers (± 0.1 mm) and an A&D FX-300 (± 0.001 g) respectively.

***Monthly sampling for* Synanceia horrida**

Between September 2006 and August 2008, monthly samples were collected from Tanjong Beach, Palawan Beach and Siloso Beach on Sentosa Island. At each of these sites, 10 bubus were deployed at depths ranging from 5 to 10 m and checked via snorkel every three days and were retrieved only when specimens of *Synanceia horrida* were observed in traps or when traps were damaged and required replacement. As per the agreement with the Sentosa Beach Patrol, all specimens were collected and kept in ice, preserved initially in 10% formalin and stored in 70% alcohol. Back in the laboratory, both standard lengths and total weight of all specimens was measured using a standard ruler (± 0.1 cm) and an Ohaus Scoutpro SPS-2001 weighing scale (± 0.1 g) respectively.

1.2.4 General morphometric measurements of scorpaenids

Different species of scorpaenoids were collected, external morphological measurements were taken including total length, standard length and total weight (Figure 1.3). With smaller specimens (< 100 mm SL), a pair of Bergman calipers (± 0.1 mm) and the A&D FX-300 weighing scale (± 0.001 g) were used. For larger specimens (≥ 100 mm SL), a standard ruler (± 1 mm) and an Ohaus Scoutpro SPS-2001 weighing scale (± 0.1 g) was used.

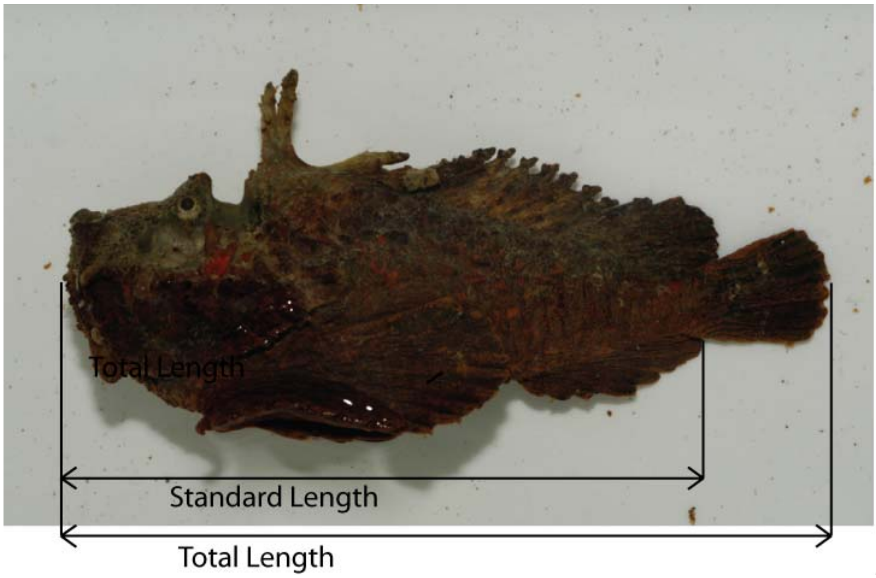

Figure 1.3 Lateral view of *Synanceia horrida* indicating length measurements recorded.

1.2.5 General dissection of scorpaenoids

A total of 76 *S. horrida*, 125 *Trachicephalus uranoscopus* and 305 *Paracentropogon longispinis* were collected during the monthly field trips. These specimens included a broad range of size for each species, and sex was determined by macroscopic examination of the gonads that were removed during dissections. In small specimens, gonads were observed by a light microscope to determine sex. During dissections of scorpaenoids, gross wet weights of gonads, liver, intestines, and stomach were measured using a Sartorius scale (± 0.0001 g). The stomach contents were removed and both the empty stomachs and gut contents were weighed.

Both sagittal otoliths were extracted from the vestibular apparatus during the dissections of the scorpaenoids. Sagittal otoliths were selected as these are the largest ones available in all three species, and were the easiest to extract without damaging otoliths. All otoliths extracted were cleaned, dried, labelled and stored for the growth measurement studies. All gonad samples extracted were placed into Bouin’s solution for preservation and initial staining for the reproduction assessment.

Chapter 2. Taxonomic diversity of the Scorpaenoidei in Singapore waters

2.1 Introduction

As has been discussed in the Chapter 1, scorpaenoids can be found in many different habitats and latitudinal gradients. Although the general distribution of some species are known on a regional basis (with a high degree of geographic variability in the maps) in the FAO fish guide (e.g., Poss, 1999), there have been few recent updates on the distribution of these fishes in Southeast Asia and particularly in Singapore. Records from the historical information (Fowler, 1938; Herre and Myers, 1937; Weber and De Beaufort, 1962) indicate 27 species from five subfamilies found in Singapore waters. This is approximately 5% of the global number and approximately 12.5% of global subfamilies. Other sources such as Chuang (1973) only mentioned three species - *Paracentropogon longispinis, Synanceia horrida*, *Cottapistus cottoides*, all of which were recognised in Herre and Myers (1937), Fowler (1938) and Weber and De Beaufort (1962). In a more recent study, Lim and Low (1998) reported only five species of scorpaenoids in Singapore. It would thus appear that scorpaenoid diversity in Singapore waters is relatively low compared with neighbouring countries. Comparatively, only 10 species were recorded from a recent survey in Indonesia (Adrim et al., 2004). At a broader regional scale, a total of 80 species of scorpaenoids were recorded from the South China Sea (Randall and Lim, 2000), but some of their data were also based on similar historical records (Fowler, 1938; Weber and De Beaufort, 1962).

Historically, Singapore is a small island which has undergone much coastal development over the last 40 years since it gained independence from Malaysia (Chia et al., 1988; Hilton and Manning, 1995). Reclamation of coastal areas has increased the size of Singapore by up to 10% in the early 1990s (Glaser et al., 1991) and is expected to rise beyond 20% in the future (Hilton and Manning, 1995) and the removal of coastal habitats and increased sedimentation due to such development has led to drastic changes to the marine habitat (Chou, 1996; Dikou and van Woesick, 2006). The impacts from coastal development (e.g., reclamation, decreased salinity through increased freshwater outflow, change in currents and tidal stream, intertidal and coral reef degradation) and other forms of pollution (noise from increased shipping, oil, marine litter)(Chia et al., 1988; Chou, 1996; Hilton and Manning, 1995), are known factors which can cause changes in fish communities and fish migrations out of coastal habitats (Chidester, 1922; Guidetti et al., 2002; Guidetti et al., 2003; Shahidul Islam and Tanaka, 2004).

With the drastic changes in original coastal habitats through development (Arul et al., 2008; Bo et al., 2005; Hilton and Manning, 1995; Koh and Lin, 2006; Wei et al., 1995) and the increase in trade and industry over the last 40 years especially in the areas of shipping or aquarium trade, both of these may have been unintentionally brought in unrecorded invasive species (e.g. *Pterois volitans* in USA (Hare and Whitfield, 2003)), resulting in changes to the diversity of fishes (including scorpaenoids) since the last survey performed in 1962. Changes in the diversity of a group of fishes might also indicate loss of a species through changes in habitats, and may also be affected through competition with invasive species. In maintaining updated records of scorpaenoids, such changes in diversity can be traced and will also provide an important source of information for future studies with regards to scorpaenoids locally.

Although several fish species may be present in a location, the effectiveness of methods employed would yield different species and sizes of fishes (Guest et al., 2003; Steele et al., 2006; Wells et al., 2008). These factors would affect interpretation of historical records as differences in sampling methods (e.g. trawling that occurred in the past but has declined over the last 20 years (Butcher, 2004), compared to primarily netting and trapping techniques used presently) between surveys over the different habitats and survey periods will result in different species of fish caught (Garcia et al., 2006). Another concern with historical records is whether revisions in taxonomy of fishes have been updated, with recognition and justification of synonymies that affect current taxonomic records (Motomura, 2004; Motomura et al., 2004; Prokofiev, 2008). The reliability of historical records is a major concern with regards to the accurate fish collections in Singapore and can be attributed to several factors including 1) complexities with regards to geographical boundaries leading to erroneous localities (i.e. Singapore gained independence from Malaysia in 1965 (Lee, 2000)), and 2) reliability of historical samples collected by biologists from local fish markets or contributors whose sources may occur outside of Singapore waters and were not verified. This may be exacerbated by the fact that Singapore is a focal point for many adjacent countries for both the import and export aquaria and food fish species both historically and presently (Cheong, 1996; Sinoda et al., 1977). While some taxonomist resolved such discrepancies with specimen sources, others may not have been as careful. As such, sources (whenever available) for specimens in historical records were taken into account in determining species localities as typographical and other errors have been found in previous historical fish records (see Alfred, 1966).

The main goal of this chapter is to produce an updated annotated species list of scorpaenoids found in Singapore. This was done by analysing the literature and historical specimens and revalidating these historical records, with additional supporting data from my present study. This list will help identify the common small species which will be used for the in depth biological and ecological studies in the following three chapters of this thesis. Additionally, this will also identify larger species of local scorpaenoids that could potentially be targeted as a food resource as well as species that may have been lost through coastal development. This will be discussed in the Chapter 6 with regards to potential harvesting and sustainability issues (which has occurred in some temperate scorpaenoid species), as well as issues with local extinctions or numerical scarcity of species.

2.2 Material and Methods

Present Study

Please refer to general material and methods (1.2.1) for details on sampling techniques involved.

Historical Records

Fish specimens from Raffles Museum Biodiversity Research (RMBR) in Singapore were checked, unidentified lots were sorted and all scorpaenoids re-identified for confirmation using available keys (Poss, 1999; Randall and Eschmeyer, 2001). All specimens were measured using either a Bergman vernier caliper (SL ± 0.1 mm) for specimens smaller than 15 cm, or a standard 30 cm ruler (SL ± 1 mm) for specimens larger than 15 cm. For broad based regional scorpaenoid records, the FAO guide (Carpenter and Niem, 1999; Poss, 1999), and the commonly used web-based fish reference guide Fishbase (Froese and Pauly, 2010) were used as a general reference for scorpaenoid locality. For historical fish records pertaining to Singapore, sources used included annotated fish lists (Fowler, 1938; Herre and Myers, 1937; Weber and De Beaufort, 1962), local pictorials and books (Chuang, 1961; 1973; Lim and Low, 1998; Tham, 1953; 1976). Classification of the scorpaenoids recorded was based on the recently updated Catalogue of Fishes (Eschmeyer, 2010). All sizes of the fishes are given as standard length, unless otherwise stated. Abbreviations used include: Sg. (Sungai = river), Pl. (Pulau = island), Sf. (subfamily), Ex. (examined), SL (standard length) and TL (total length). Records based on the literature and for which specimens have not been examined to confirm their identities are either indicated with a "**?**" for species that are doubtful, or a "**!**" for species that are highly unlikely to be found locally due to either misidentification, unreliable specimen collections and improbable geographical distributions based on literature and known localities. Photographs of all available confirmed species are provided. Synonomies used in this list were restricted to the original description and original locality, and relevant synonyms with regards to records from Singapore and adjacent regions (e.g., Malaysia and Indonesia).

2.3 Results

Of the 24 sampling sites that were surveyed, scorpaenoids were recorded at 18 sites (Figure 2.1). Sites where scorpaenoids were not found included East Coast Parkway, Pasir Panjang Beach, both sites of Pulau Serangoon, Pulau Ubin and Tuas Inlet (Table 1-1). Results from the four different sampling methods (seining, trapping, angling and net casting) performed at the 24 sampling sites (all with only soft sediment present but including six sites with mixed seagrass/algal habitats, two with rocky habitats, and four with coral habitats) indicated that beach seining caught the most species of scorpaenids, with six species captured using this technique. Results from the various surveys from historical and present day data on the diversity and species list of scorpaenoids found in Singapore is reported in the following annotated checklist.

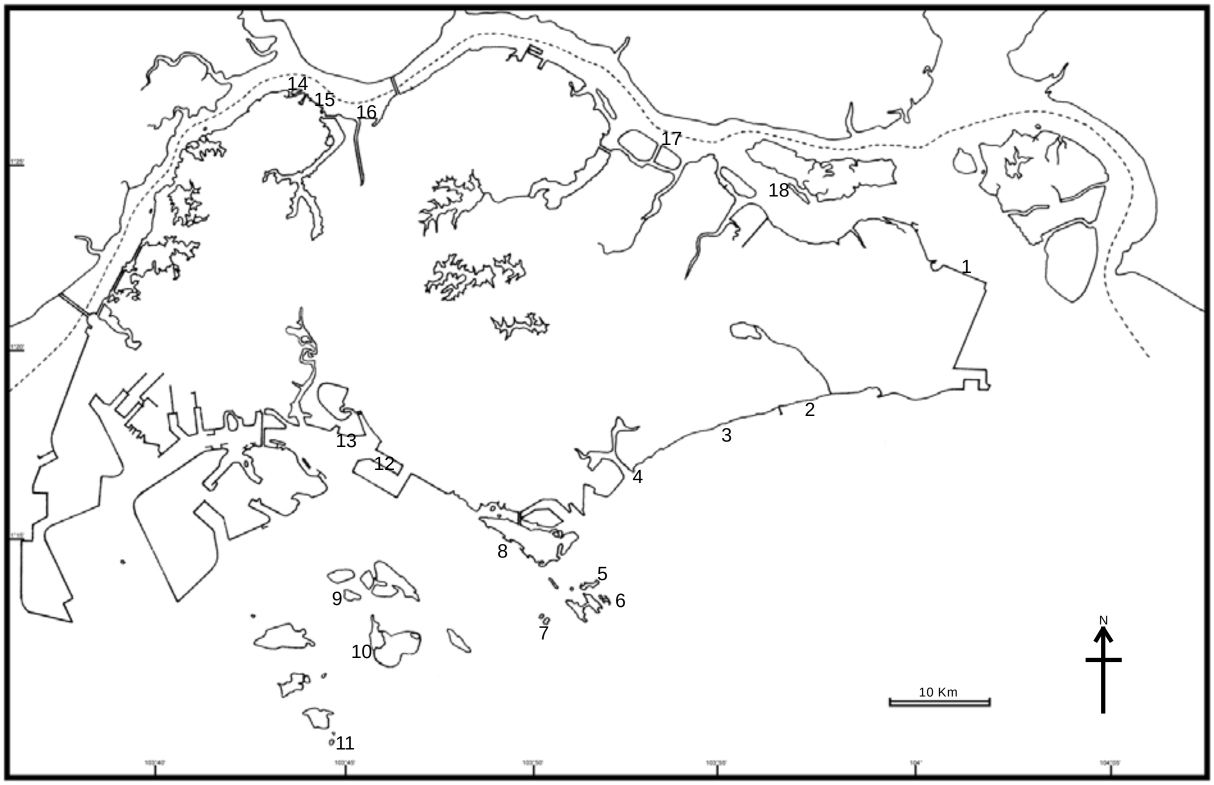

Figure 2.1 Map of Singapore indicating 18 sites where scorpaenoids were found using sampling methods such as beach seines, cast nets, angling and local traps. 1. Changi Beach, 2. Bedok Jetty Beach, 3. East Coast Parkway, 4. Marina East Beach, 5. St John's Island, 6. Kusu Island, 7. Sisters Island, 8. Sentosa Island, 9. Pulau Hantu, 10. Pulau Semakau, 11. Raffles Lighthouse (Pulau Satumu), 12. Pasir Panjang Beach, 13. Sungei Pandan, 14. Lim Chu Kang, 15. Sungei Buloh, 16. Sungei Mandai, 17. Pulau Seletar, 18. Pulau Ubin.

ANNOTATED CHECKLIST OF SCORPIONFISHES OF SINGAPORE

(SUBORDER SCORPAENOIDEI)

The first Singapore record for each species is listed, as well relevant synonyms from adjacent countries only. This checklist includes all doubtful records from the literature and provides correct identifications of misidentified Singapore species wherever possible. The catalogue number of verified material from the Raffles Museum of Biodiversity Research, the National University of Singapore (ZRC) and the original National Museum of Singapore (NMS) are provided for all available records. Localities where specimens have been collected are listed for each species and include records from South East Asia and wider regions when no additional records are available. On a finer scale, localities in Singapore where specimens have been collected are listed for each species. These are arranged in sequence following the shorelines of Singapore Island, beginning with Changi Point Beach (On the south-east), then southwards towards the southern island, then westwards, then ending with Pulau Ubin (off the east coast) (Figure 2.1).

In this checklist, a total of 25 (~5% of all species recorded worldwide) species from four families were recorded in Singapore. The families present are the Scorpaenidae, Synanceiidae, Tetarogidae and Aploactinidae.

FAMILY SCORPAENIDAE

Of the 210 globally recorded species from three subfamilies (Pteroinae, Scorpaeninae and Caracanthinae), a total of 10 (~5%) species from two subfamilies (Pteroinae and Scorpaeninae) were recorded in Singapore.

SUBFAMILY PTEROINAE (Cuvier, 1817)

!*Pterois antennata* (Bloch, 1787)

Scorpaena antennata Bloch, 1787: 21, Pl. 185 (Ambon Island, Moluccas Islands, Indonesia)

Pterois antennata - Weber and De Beaufort, 1962: 45 (Singapore); Allen and Adrim, 2003: 29 (Indonesia)

Material examined: none

Remarks: Cited from Weber and De Beaufort (1962). No material available for revalidation. Although recorded in Indonesia, this species has not been recorded in Malaysian waters so far, suggesting that this species might be found in cooler waters as is suggested by reliable records from Japan (Motomura et al., 2010), New Zealand (Paulin et al., 1989) and Australia (Allen and Swainston, 1988; Hutchins, 2001). Duncker (1903) also claims that this species was found in Singapore, but unfortunately no specimens were available for confirmation of this species locally. Source of specimens from Dunker (1903) and Weber and De Beaufort (1962) are dubious and records are treated with some scepticism.

!*Pterois lunulata* (Temminck and Schlegel, 1843)

Pterois lunulata Temminck and Schlegel, 1843: 45, Pl. 19 (figs. 1, 3) (Japan); Weber and De Beaufort, 1962: 44 (Singapore); Randall and Lim, 2000: 605 (South China Sea)

Material examined: none

Remarks: This record is from Weber and De Beaufort (1962). No recent material was examined. The issues with the identity of this species are similar to issues found in that discussed for *P. antennata*. This species is easily misidentified as *P. russelli* as the primary difference between these two species is based on only five vertical row scale counts (Poss, 1999). In addition, this species also appears to be found in more temperate waters such as Japan (Masuda et al., 1984; Motomura and Iwatsuki, 1997) and Australia (Hoese et al., 2006), a situation similar to *P. antennata*.

!*Pterois radiata* (Cuvier, 1829)

Pterois radiata Cuvier, 1829: 369 (Tahiti); Fowler, 1938: 202 (Singapore); Randall and Lim, 2000: 605 (South China Sea); Allen and Adrim, 2003: 29 (Indonesia)

Material examined: none

Remarks: This is from the list by Fowler (1938). No recent material was examined and this is also an unlikely record. This species could also be mistaken for *P. antennata*, with both having similar stripe patterns on body and can only be differentiated by slight differences in colouration of the supraocular cirrus (Poss, 1999). Similar to *P. antennata* and *P. lunulata*, this species has also been found in colder waters such as Australia (Hutchins, 2001) and Japan (Masuda et al., 1984). As was earlier discussed for *P. antennata* and *P. lunulata*, *P. radiata* has also never been recorded in Malaysia which makes historical records of this species highly suspect.

Pterois russelii (Bennett, 1831)

Pterois russelii Bennett, 1831:128 (India); Bleeker, 1849: 216 (Singapore); Weber and De Beaufort, 1962: 42 (Singapore); Mohsin and Ambak, 1996:573 (Malaysia); Randall and Lim, 2000: 605 (South China Sea); Allen and Adrim, 2003: 29 (Indonesia); Adrim et al., 2004: 119 (Indonesia)

Material examined: 2 ex.: 110 - 140 mm TL, ZRC 4298, 4299, Changi, coll. 1972; specimens collected during present study and preserved at Sentosa: 2 ex.: 110.5 - 120.3 mm TL, Sentosa Island, Sisters Island, coll. Kwik, J., 10 May 2011 (Figure 2.2).

Remarks: This is the only pteroine that was positively identified in Singapore waters, with >65 vertical scale counts and the absence of spots on the caudal fin and soft parts of dorsal and anal fins (Poss, 1999). Both the specimens caught locally were found inhabiting shallow coral reefs and were captured using traps and hand nets. The two preserved specimens remain at Sentosa Beach Patrol as part of their venomous animal collection programme.

Figure 2.2 Preserved *Pterois russelii* (present study but not catalogued - 120.3 mm TL) from Sentosa Island collection, 10 May 2011.

SUBFAMILY SCORPAENINAE (Bleeker, 1876)

!*Parascorpaena aurita* (Rüppell, 1838)

Scorpaena aurita Rüppell, 1838: 106, Pl. 27 (fig. 2) (Red Sea)

Sebastapistes tristis – Herre and Meyer, 1937: 33 (Singapore)

Sebastapistes bynoensis – Weber and De Beaufort, 1962: 30 (Singapore); Randall and Lim, 2000: 606 (South China Sea)

Parascorpaena aurita - Motomura et al., 2009: 45 (Andaman Sea, Thailand)

Material examined: none

Remarks: Although *S. bynoensis* was recorded by Herre and Meyer (1937) as well as Weber and De Beaufort (1962), it is possible that this may have been a misidentification of *P. picta* which is found locally in Singapore waters. This can occur as the key features separating these two species involve slight differences in the interorbital ridges and tympanic spines (Poss, 1999), which can be hard to differentiate in smaller specimens. Due to a lack of specimens, I am unsure if *P. aurita* is actually found in Singapore as the specimen captures for this species appear to occur in much cooler waters as compared to local waters in Singapore such as the Andaman Sea (Motomura et al., 2009) and Australia (Hoese et al., 2006), with no records of this species in either Indonesia or Malaysia.

Parascorpaena picta (Cuvier, 1829)

Scorpaena picta Cuvier, 1829: 321 (Indonesia); Bleeker, 1861: 31 (Singapore); Karoli, 1881: 157 (Singapore); Mohsin and Ambak, 1996:574 (Malaysia)

Parascorpaena picta - Bleeker, 1876: 25 (Singapore); Weber and De Beaufort, 1962: 7 (Singapore); Lim and Low, 1998: 81 (Singapore); Randall and Lim, 2000: 605 (South China Sea); Allen and Adrim, 2003: 29 (Indonesia); Adrim et al., 2004: 119 (South China Sea)

Material examined: 9 ex.: 50 – 154 mm TL, ZRC 17444, 30555, 35355, 35356, 41456, 40727, Sultan Shoal, Pl. Salu, Pl. Soringat, Pl. Semakau, Raffles Lighthouse, Labrador Beach, coll. Tay, S.W. (1977), Lim, K.P. and Low, S.L. (1991), Chia, D.G.B. (1993), Low, J.K.Y. (1993), Lim, K.P. (1997); specimens collected during present study 6 ex.: 67 – 123.3 mm TL, ZRC 50522, Changi Beach, East Coast Parkway, Marina East, Sentosa Island, coll. Kwik, J., 2006 (Figure 2.3).

Remarks: This species was differentiated from *P. aurita* using the characters mentioned earlier (Poss, 1999). Similar to *P. russelii*, this was another species that was found in Malaysian waters. This was also one of the larger species found amongst the scorpaenoids captured during this study.

Figure 2.3 Preserved *Parascorpaena picta* (ZRC 50522 – 123.3 mm SL) from Marina East, 21 March 2006.

!*Scorpaena aplodactylus* (Bleeker, 1852)

Scorpaena aplodactylus Bleeker, 1852: 698 (Indonesia); Duncker, 1903: 152 (Singapore); Ferraris et al., 2000: 295 (Indonesia)

Material examined: none

Remarks: Recorded by Fowler (1938) as a synonym of *Merinthe bandanensis* which is now *Parascorpaena bandanensis*, it has been recorded in Indonesia (Kuiter and Tonozuka, 2001), Papua New Guinea (Kailola, 1987) and Philippines (De la Paz et al., 1988). *Parascorpaena bandanensis* is a separate species from *S. aplodactylus* (Fricke, 2005) which was supposedly recorded in Singapore (Dunker, 1903). Fowler also recorded this species as *Scorpaena haplodactylus* (Günther, 1860: 117) which is a misspelling of *S. aplodactylus*. No recent material from Singapore observed. Although it is possible that this species could be found in Singapore, the lack of specimens from Duncker (1903) (they will need to be re-examined) and no records of this species being found in Malaysian waters make this a dubious record at present.

?*Scorpaenodes guamensis* (Quoy and Gaimard, 1824)

Scorpaena guamensis Quoy and Gaimard, 1824: 326 (Guam)

Scorpaenodes guamensis – Herre and Myer, 1937: 33 (Singapore); Weber and De Beaufort, 1962: 33 (Singapore); Randall and Lim 2000: 605 (South China Sea); Allen and Adrim, 2003: 29 (Indonesia); Allen and Erdman, 2009: 596 (Indonesia)

Material examined: none

Remarks: I cannot ascertain if Herre and Meyer's (1937) or Weber and De Beaufort's (1962) record of *S. guamensis* from Singapore is valid. Besides western Indonesia (Allen and Erdman, 2009), this species has been found in cooler waters such as New Zealand (Paulin, 1982), Mauritius (Fricke, 1999), South east Australia (Johnson, 1999) and Japan (Senou et al., 2006). Moreover, this species has also never been recorded in Malaysia which has been a good indicator of similar species present so far.

Scorpaenopsis cirrosa (Thunberg, 1793)

Perca cirrosa Thunberg, 1793: 199, Pl. 7 (Japan)

Scorpaenopsis cirrhosus - Bleeker, 1861: 31 (Singapore)

Scorpaenopsis oxycephala - Allen and Adrim, 2003: 29 (Indonesia)

Scorpaenopsis cirrosa – Weber and De Beaufort; 1962: 15 (Singapore); Randall and Lim, 2000: 606 (South China Sea)

Material examined: 1 ex.: 109.1 mm SL, ZRC 45743, Raffles Lighthouse, coll. Tan, H.H., 23 Apr 1999; specimens collected during present study and presently being catalogued , 1 ex.: 94.5 mm SL, Raffles Lighthouse, coll: Kwik, J., 2006. (Figure 2.4)

Remarks: The single specimen was positively identified based on the multiple characteristics that differentiated this species from other species within this genus (Poss, 1999; Randall and Eschmeyer, 2001). This is another reef associated species that appears to be found only offshore along the southern islands of Singapore.

Figure 2.4 Preserved *Scorpaenopsis cirrosa* (ZRC 45743 – 109.1 mm SL) from Raffles Lighthouse, 23 April 1999.

?*Scorpaenopsis diabolus* (Cuvier, 1829)

Scorpaena diabolus Cuvier, 1829: 166 (Indo-west Pacific); Martens, 1876: 389 (Singapore); Duncker, 1903: 152 (Singapore)

Scorpaenopsis diabolus - Randall and Lim, 2000: 606 (South China Sea); Randall and Eschmeyer, 2001: 79 (Malaysia); Allen and Adrim, 2003: 29 (Indonesia)

Material examined: none

Remarks: Fowler (1938) had erroneously included *S. diabolus* as a synonym of *S. gibbosa*, and current revisions have also identified *S. diabolus* as a separate species (Randall and Eschmeyer, 2001). This species has been recorded in Malaysia suggesting that this species could still be found locally as habitat conditions between Singapore and Malaysia were similar historically, but could presently be in much lower abundances, perhaps due to habitat loss.

FAMILY SYNANCEIIDAE

Remarks. – Of the 35 species recorded globally, nine species (~26%) were recorded in Singapore waters including members from all three sub-families (sf Choridactylinae, Synanceiinae and Minoinae).

SUBFAMILY CHORIDACTYLINAE (Jordan and Starks, 1904)

?*Inimicus brachyrhynchus* (Bleeker, 1874)

Pelor brachyrhynchus Bleeker, 1874: 5, Pls. 2 (fig. 4), 3 (fig. 2) (Singapore)

Inimicus brachyrhynchus – Weber and De Beaufort, 1962: 106 (Singapore)

Material examined: none

Remarks: This is the only scorpaenoid holotype identified from Singapore (RMNH 5907), but has not been found since 1874. Very little is known about this species besides it being a demersal species that buries itself in soft sediment habitats (Eschmeyer et al., 1979). With the constant coastal changes, I suspect that this species might still be present but in much lower abundances. Surprisingly, this species has not been recorded in Malaysia though this may be due to different sampling methods involved (e.g., trawling).

?*Inimicus cuvieri* (Gray, 1835)

Pelor cuvieri Gray, 1835: Pl. 90 (fig. 2) (India); Bleeker, 1859: 216 (Singapore)

Inimicus cuvieri – Weber and De Beaufort, 1962: 108 (Singapore); Randall and Lim, 2000: 605 (South China Sea); Allen and Adrim, 2003: 30 (Indonesia)

Material examined: none

Remarks: This record is based on Bleeker (1859). Although no material was available for examination, both the specimen source (Bleeker, 1859) and identification of the specimen (Eschmeyer et al., 1979) are deemed reliable. As such, this is another species which may still be present locally but as with *I. brachyrhynchus*, this species is probably present in lower numbers or requires a different technique for capture.

Inimicus didactylus (Pallas, 1769)

Scorpaena didactyla Pallas, 1769:26, Pl. 4 (figs. 1-3) (Indonesia)

Pelor didactylus - Bleeker, 1874:7 (Singapore)

Inimicus didactylus – Weber and De Beaufort, 1962: 104 (Singapore); Mohsin and Ambak, 1996: 571 (Malaysia); Randall and Lim 2000:605 (South China Sea); Allen and Adrim 2003:30 (Indonesia); Kimura and Matsuura 2003:38 (Indonesia); Adrim et al. 2004:119 (South China Sea)

Material examined: 1 ex.: 123 mm SL, ZRC 208, Sultan Shoal, coll. Monteiro, A., Oct 1931; specimens collected during present study, 2 ex.: 45 – 55.3 mm SL, ZRC 53085, Changi Beach, coll: Kwik, J., 20 April 2006 (Figure 2.5).

Remarks: This species was differentiated from *Inimicus brachyrhynchus* by the presence of broad dark transverse bar along the medial surface of pectoral fins (Eschmeyer et al., 1979; Poss, 1999). As described by Eschmeyer et al. (1979), this species was collected over soft sediment habitats locally. As expected, this species was also recorded from Malaysia (Mohsin and Ambak, 1996).

Figure 2.5 Preserved *Inimicus didactylus* (ZRC53085 – 55.3 mm SL) from Changi Point Beach, 20 April 2006.

SUBFAMILY SYNANCEIINAE (Bloch Schneider, 1801)

!*Erosa erosa* (Cuvier, 1829)

Synanceia erosa Cuvier, 1829:459, Pl. 96 (Japan); Karoli, 1881: 158 (Singapore)

Erosa erosa - Randall and Lim 2000:605 (South China Sea)

Material examined: none

Remark: I agree with Fowler (1938) who suspected that Karoli (1881) may have misidentified this species or made an error with the locality, as no specimen of this species has ever been recorded since 1881. This species has also not been recorded in any of the adjacent countries surrounding Singapore.

Leptosynanceia asteroblepa (Richardson, 1844)

Synanceia asteroblepa Richardson, 1844:69, Pl. 39 (figs. 1-3) (New Guinea)

Leptosynanceia asteroblepa - Kottelat et al. 1993:102 (Indonesia); Kottelat and Lim 1995:245 (Indonesia); Randall and Lim 2000:605 (South China Sea).

Material examined: 2 ex.: 44-50 mm TL, uncatalogued ZRC specimens, Sg. Mandai, coll. unknown, 19 Dec 1996; Specimens examined during present study, 1 ex.: 76.7 mm SL, ZRC 52524, Lim Chu Kang, coll: Ng. H.H., 16 April 2011.

Remarks: There are no historical records of this species and has only recently been identified along our shores. Although this species has been recorded in Indonesia (Kottelat and Lim, 1995), this species is a new record for Singapore (Figure 2.6). This species inhabits soft sediment shores and buries itself and may be misidentified as *T. uranoscopus*. However, *L. asteroblepa* can be differentiated by the more prominent and abundant preopercular spines (>4), and a larger size in adults (> 90 mm SL).

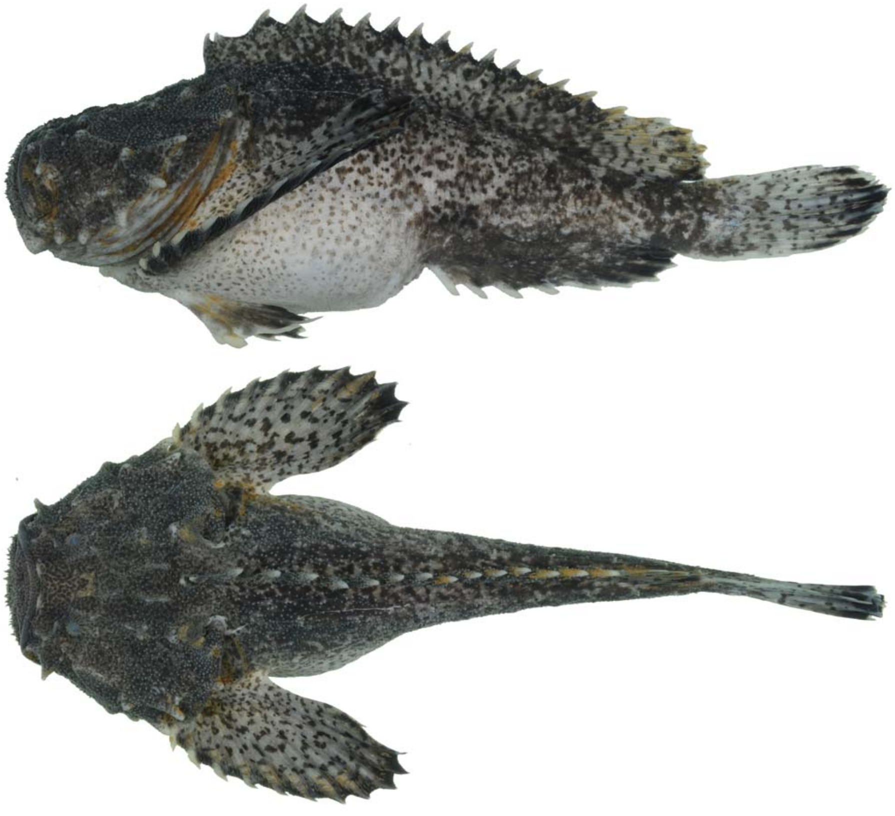

Figure 2.6 Fresh *Leptosynanceia asteroblepa* (ZRC52524 – 76.7 mm SL) from Lim Chu Kang, 16 April 2011.

Synanceia horrida (Linnaeus, 1766)

Scorpaena horrida Linnaeus, 1766:453 (Indonesia)

Synanceia horrida - Bleeker, 1859: 253 (Singapore); Weber and De Beaufort, 1962: 95 (Singapore); Lim and Low, 1998: 82 (Singapore); Randall and Lim 2000:606 (South China Sea); Allen and Adrim 2003:30 (Indonesia)

Material examined: 18 ex.: 103 - 247 mm TL, ZRC 3583, 35368, Pl. Semakau, Raffles Lighthouse, coll. Low, J.K.Y. (1993); Specimens collected during present study but not catalogued, 8 ex.: 48.3 – 195 mm SL, St John's Island, Pl. Kusu, Pl. Sentosa, Pl. Hantu, Pl. Seletar, coll: Kwik, J. Jun. 2008 (Figure 2.7).

Remarks: *Synanceia horrida* has been one of the more common species caught over the last few decades and appears to still be abundant during recent surveys using local traps. This is also the largest scorpaenoid caught locally so far, and has been found inhabiting both rocky shores and soft sediment habitats. Surprisingly, this common species has not been formally recorded in Malaysia so far.

Figure 2.7 Fresh *Synanceia horrida* (present study and not preserved – 240 mm SL) from Marina Barrage, 21 June 2005. Photograph by Tan H.H.

!*Synanceia verrucosa* Bloch and Schneider, 1801

Synanceia verrucosa Bloch and Schneider, 1801:195, Pl. 45 (India); Herre and Meyer, 1937: 34 (Singapore); Weber and De Beaufort, 1962: 98 (Singapore); Randall and Lim 2000:606 (South China Sea); Allen and Adrim 2003:30 (Indonesia)

Material examined: none

Remarks: Although both Herre and Meyer (1937) as well as Weber and De Beaufort (1962) have indicated that this species was found locally, there have been no specimens available or any records for *S. verrucosa* being caught locally over the last 40 years. It is unlikely that *S. verrucosa* would be misidentified as *S. horrida* as both have clear distinguishing facial structures that easily differentiate them (Poss, 1999). It seems unlikely a species as prominent as this could have been missed, especially since the related *S. horrida* is common. It may be that this species is not found locally.

Trachicephalus uranoscopus (Bloch and Schneider, 1801)

Synanceia uranoscopa Bloch and Schneider 1801:195 (India)

Synanceia elongata - Cuvier, 1829:456 (India, Indonesia); Bleeker, 1859:216 (Singapore)

Polycaulis uranoscopus – Herre and Meyer, 1937: 34 (Singapore); Weber and De Beaufort, 1962: 100 (Singapore)

Trachicephalus uranoscopus - Lim and Low, 1998: 82 (Singapore); Randall and Lim, 2000: 606 (South China Sea)

Material examined: 14 ex.: 33 – 94 mm TL, ZRC 17460, 4528, 4529, 40585, 40571, 40677, Angler's buoy, Punggol Beach, coll. Rahman, A. (1967), SEADEC (1975), Ng, P.K.L. (1986, 1994), Ng, P.K.L and Yeo, K.L. (1990);

specimens collected during present study, 15 ex.: 33.3 – 79.5 mm SL, ZRC 53081, Changi Beach, East Coast Park, coll. Kwik, J., 20 April 2006 (Figure 2.8).

Remarks: *Trachicephalus uranoscopus* was another small species that was commonly found inhabiting the soft sediment shores of coastal Singapore waters, and was consistently caught using seine nets. Both *T. uranoscopus* and *P. longispinis* appeared to be sympatric species inhabiting similar areas.

Figure 2.8 Preserved *Trachicephalus uranoscopus* (ZRC 53081 – 70.5 mm SL) from Changi Point Beach, 20 April 2006.

SUBFAMILY MINOINAE (Cuvier and Valenciennes, 1829)

Minous monodactylus (Bloch and Schneider, 1801)

Scorpaena monodactyla Bloch and Schneider, 1801: 194 (locality not stated);

Minous mondactylus - Bleeker, 1861: 31 (Singapore); Herre and Meyer, 1937: 34 (Singapore); Weber and De Beaufort, 1962: 111 (Singapore); Mohsin and Ambak 1996:571 (Malaysia); Randall and Lim 2000:605 (South China Sea); Allen and Adrim 2003:30 (Indonesia)

Material examined: Four previously catalogued ZRC specimens are presently on loan to Motomura, H. (Kagoshima University Museum); Specimen collected during present, 1 ex.: 51.8 mm SL, ZRC 53084, Changi Beach, coll. Kwik, J., 10 Jan 2006 (Figure 2.9).

Remarks: This species was also found in similar habitats where *T. uranoscopus* and *P. longispinis* were recorded. However, this was not a common species caught. A recent review by Eschmeyer and Hallacher (1979) was used to differentiate this species from other species in this genus. This was another species that was also found in Malaysia (Mohsin and Ambak, 1996).

Figure 2.9 Preserved *Minous monodactylus* (ZRC 53084 – 51.8 mm SL) from Changi Point Beach, 10 January 2006.

FAMILY TETAROGIDAE

Remarks. – Only four (10%) of the 40 known species in this family (with one subfamily) were recorded locally.

SUBFAMILY TETAROGINAE (Bleeker, 1876)

Cottapistus cottoides (Linnaeus, 1758)

Perca cottoides Linnaeus, 1758:291 (East Indies)

Sibogapistus cynocephalus - Weber, 1913:501, Fig. 103 (Singapore)

Paracentropogon cynocephalus - Herre and Myers, 1937: 33 (Singapore)

Cottapistus cottoides - Weber and De Beaufort, 1962: 84 (Singapore); Randall and Lim 2000:605 (South China Sea)

Material examined: 3 ex., 69.4-73 mm S.L., NHS 3528, ZRC 50567, Bedok, Pasir Panjang, coll. unknown, undated, Wang, H.P., 3 Aug 1975 (Figure 2.10).

Remarks: Since the last specimen capture in 1975, there have been records of this species locally. However, this may be due to the sampling method involved as this species has been known to be part of the by-catch in trawling activities around the region (Sinoda et al., 1977). As trawling has been banned locally over the last few decades, this might explain the absence of records for this species to date.

Figure 2.10 Preserved *Cottapistes cottoides* (ZRC 50567 – 69.4 mm SL) from Pasir Panjang Beach, 3 August 1975.

Paracentropogon longispinis (Cuvier, 1829)

Apistus fuscovirens Cuvier, 1829: 409 (Ambon Island, Indonesia); Bleeker, 1861: 31 (Singapore)

Centropogon fuscovirens - Karoli, 1881: 158 (Singapore)

Paracentropogon leucoprosopon - Herre and Meyer, 1937: 33 (Singapore)

Paracentropogon longispinis - Weber and De Beaufort, 1962: 80 (Singapore); Lim and Low, 1998: 81 (Singapore); Randall and Lim, 2000: 605 (South China Sea); Allen and Adrim, 2003: 30 (Indonesia)

Material examined: 77 ex.: 17 – 67 mm TL, ZRC 4533, 7570 – 7585, 11046-11049, 11499-11500, 46657, 48672 , NMS 3530, NMS 3529, Coney Island, Bedok ,Sg. Seletar, Pl. Ubin, Sg. Punggol, Changi beach, Pl. Seringat, Siglap, Pl. Sentosa, coll. Lim, C.F. (1973), SEADEC (1975), Yang, C.M. (1985), Jaafar, Z. (2001); specimens collected during present study, 23 ex.: 31.4 – 68.3 mm SL, ZRC 53082, Changi Beach, St John's Island, Pl Semakau, Pl. Ubin, coll. Kwik, J., 20 April 2006 (Figure 2.11).

Remarks: The most commonly found scorpaenoid species from both historical and present surveys in Singapore waters. This is also the smallest species of scorpaenoid found locally so far. *P. longispinis* also inhabits shallow habitats together with other species such as *T. uranoscopus*, *M. monodactylus* and *I. didactylus*. The abundance of specimens for this species in the ZRC records suggests that this species has been present in relatively high numbers over the last few decades, and that this species can be found along many coastal areas locally.

Figure 2.11 Preserved *Paracentropogon longispinis* (ZRC 53082 – 55.6 mm SL) from Changi Point Beach, 20 April 2006.

!*Richardsonichthys leucogaster* (Richardson, 1848)

Apistes leucogaster Richardson, 1848:5, Pl. 5 (figs. 1-2) (South China Sea)

Tetraroge leucogaster – Weber and De Beaufort, 1962: 69 (Singapore)

Richardsonichthys leucogaster - Randall and Lim 2000:605 (South China Sea); Allen and Adrim 2003:30 (Indonesia); Adrim et al. 2004:119 (South China Sea)

Material examined: none

Remarks: This species is based on Weber and De Beaufort (1962). No materials were available for examination. Although recorded in Indonesia (Allen and Adrim, 2003) and Vietnam (Prokofiev, 2008), this species was never recorded in Malaysia. In addition, this species has been recorded in cooler waters such as Australia (Hoese et al., 2006) and New Caledonia (Wantiez, 1993), suggesting that this might be an erroneous record.

Vespicula trachinoides (Cuvier, 1829)

Apistus trachinoides Cuvier, 1829: 401, pl. 92, fig.1 (Java)

Vespicula trachinoides – Herre and Meyer, 1937: 33 (Singapore); Weber and De Beaufort, 1962:74 (Singapore); Lim and Low, 1998: 81 (Singapore); Randall and Lim 2000:606 (South China Sea)

Material examined: 7 ex., 20-51 mm TL, ZRC 766, 4056, Sg. Seletar, Sg. Buloh, coll. Dali, M. & Paul, H., 28 Jun 1966; specimens collected during present study but not catalogued, 1 ex.: 13.7 mm SL, Sg. Pandan, coll. Tan, K.S., April 2011 (Fig. 12).

Remarks: This is another small species that was found in soft sediment mudflats where *L. asteroblepa* was captured. Several specimens of *V. depressifrons* were also found in the ZRC records but these were recognised as misidentifications of *V. trachinoides* based on identification keys (difference in dorsal fin and ray counts) (Poss, 1999).

Figure 2.12 Preserved *Vespicula trachinoides* (ZRC 4056 – 47.3 mm SL) from Sungei Buloh, 21 May 1992.

FAMILY APLOACTINIDAE (Richardson, 1848)

Remarks. – Of the 44 globally known species in this family (with one subfamily), only two species (~5%) were recorded locally.

Sthenopus mollis (Richardson, 1848)

Sthenopus mollis Richardson, 1848:10, Pl. 2 (figs. 6-7) (South China Sea); Weber and De Beaufort, 1962: 90 (Singapore); Randall and Lim, 2000: 606 (South China Sea)

Material examined: 5 ex.: 26 – 54 mm TL, ZRC 36711, NMS 2006, Pl. Semakau, coll. Ommaney, F.D. (1955), Sim, T.M. and Teo, R. (1994); Specimens collected during present study, 2 ex.: 46.8 – 50.1 mm SL, ZRC 53083, 51991, Changi Beach, coll. Kwik, J., 20 April 2006, 1 March 2008 (Figure 2.13).

Remarks: Uncommon species that was found in soft sediment habitats together with *P. longispinis* and *T. uranoscopus*. There are few records of localities of this species outside of the localities mentioned earlier, including Thailand (Monkolprasit et al., 1997) and China (CAFS, 2007).

Figure 2.13 Preserved *Sthenopus mollis* (ZRC 53083 – 46.8 mm SL) from Changi Point Beach, 20 April 2006.

?*Cocotropus echinatus* (Cantor, 1849)

Corythobatus echinatus - Cantor, 1849: 1027, pl. 13 (Penang, Malaysia; Singapore)

Cocotropus echinatus – Fowler, 1938: 199 (Singapore)

Material examined: none

Remarks: This species was based on Fowler (1938). No material was examined. But as reliable sources for this species was found in Malaysia and recently validated (Johnson, 2004), it is possible that this species was present locally but is now present in lower numbers.

2.4 Discussion

Of the 25 species recorded, only 12 were positively identified to be found in Singapore presently on the basis of collected specimens. Of the remaining 13 dubious species, five might potentially be present as the historical evidence was reliable but may have been in lower abundances due to habitat change over the last four decades resulting in fewer captures, while the remaining eight were either misidentifications of other species or erroneous records of locality (Table 2-1).

Table 2-1 Scorpaenoid species recorded from both historical (n=201) and present (n=285) study collections with indications of occurrence reliability in Singapore waters.

Found locally (certain)	Possible but dubious (?)	Highly unlikely (!)
Pterois russelii	*Scorpaenodes guamensis*	*Pterois antennata*
Parascorpaena picta	*Scorpaenopsis diabolus*	*Pterois lunulata*
Scorpaenopsis cirrosa	*Inimicus brachyrhynchus*	*Pterois radiata*
Inimicus didactylus	*Inimicus cuvieri*	*Parascorpaena aurita*
Leptosynanceia asteroblepa	*Cocotropus echinatus*	*Scorpaena aplodactylus*
Synanceia horrida		*Erosa erosa*
Trachicephalus uranoscopus		*Synanceia verrucosa*
Minous monodactylus		*Richardsonichthys leucogaster*
Cottapistus cottoides		
Paracentropogon longispinis		
Vespicula trachinoides		
Sthenopus mollis		

Additionally, as a result of Singapore being considered part of Malaysia prior to gaining its independence in 1965 (Lee, 2000), discrepancies in localities appeared to occur in at least one species which was previously considered a Singapore catch (i.e. *Pterois radiata*). Although appearing comprehensive to date, it is uncertain if more species might still be found due to the relatively high coastal development occurring in Singapore presently (Hilton and Manning, 1995). Moreover, methods used during this study may have been very different in relation to both effort and techniques involved as trawling along the coast of Singapore was provided a good source of specimens for taxonomists (Sinoda et al., 1977). Trawling methods not only cover more area but it also enabled sampling over much deeper waters which are not attainable presently due to restrictions and regulations. Although sampling during the present study was intense, it was also limited to shallow coastal waters and rarely exceeded 3 m depth (with the exception of SCUBA diving along the Southern Islands). As such, due to limitations in sampling methods, there exists the possibility that some of the species attainable only by trawling (e.g., *Cocotropus echinatus*) were not captured during the present study. It is also possible that with improved sampling techniques and designs (e.g., pop traps, FADs), more or different species of scorpaenoids might be captured and added to this annotated species list. Especially as many scorpaenoids are highly cryptic and usually closely associated with the benthos (Ballantine et al., 2001; Grobecker, 1983; Starrett, 1993), effective captures can be limited by the capture techniques and methods used, and the habitats sampled. An example being *S. horrida* which although was the most widely distributed scorpaenoid, was only caught using the local traps (also known as bubus) at nine locations around Singapore.

In comparison, five species of scorpaenoids (including the two most abundant species, *P. longispinis* and *T. uranoscopus*) were only caught using the seine nets. It is apparent that the seining was the most effective when used over the soft sediment and vegetated habitats, as the nets would not get entangled and torn as compared to netting over hard substrates such as coral and rocky areas. Seining also covered the greatest area sampled with the added effect of the net weights stirring up fish buried in the sediment. Although netting techniques have been recognised as effective methods for collection of different fish species (Gray and Kennelly, 2003; Guest et al., 2003), the use of angling as a sampling technique has been overlooked especially if we consider that not all habitats are easily seined due to depth or habitat complexity. In addition, the use of baiting has also been shown to be an effective method for sampling cryptic species over complex habitats (Stewart and Beukers, 2000), further emphasizing the importance of using various techniques when performing diversity surveys. This also appeared to be the case for the larger scorpaenoids (*Synanceia horrida* and *Scorpaenopsis cirrosa*) which were only caught using the local traps and angling.

The relatively high discrepancies with historical records show the importance of maintaining up-to-date specimen records or validating specimen sources, as unreliable specimens (e.g., donations or collections from unvalidated sources) could lead to erroneous records. For example, when making the comprehensive freshwater fish catalogue of Singapore, Alfred (1966) found many errors in identification as well as several species which were inaccurately ascribed to Singapore. To make matters worse, some authors incorporated these misidentified species in their respective lists even when these errors were highlighted. Though time constraints and ability for researchers to collect specimens personally may not always be possible, great care should be taken to validate specimens that are provided by external sources which may not be reliable.

Additionally, the loss of habitats (Pihl et al., 2006) through environmental changes or pollution (Waldichuk, 1974) might also result in changes to the biodiversity of fishes. Studies over complex habitats such as coral reefs have shown that there are close associations between species diversity and the health and viability of coral reefs (Chabanet et al., 1997; Feary et al., 2007; Jones et al., 2004). This loss of diversity is even apparent in less complex habitats such as seagrass beds (Pihl et al., 2006). Considering that both these habitats are present in Singapore (Chou, 1996; Hajisamae et al., 2003) but have been reduced over time due to reclamation (Hajisamae and Chou, 2003; Hilton and Manning, 1995; Jaafar et al., 2004). With the production of the present checklist, it will be interesting to see if scorpaenoid diversity changes as coastal development continue along Singapore shores. Perhaps with repeated surveys, scorpaenoids might be used as a bioindicator of coastal impacts as many of these scorpaenoid species are sedentary in behaviour (Endean, 1962; Zimmermann and Kunzmann, 2001) and are likely to be affected by changes to shallow coastal habitats which they inhabit (Poss, 1999).

Many of the unconfirmed species during survey were recorded in the 1930s to 1960s (Fowler, 1938; Herre and Myers, 1937; Weber and De Beaufort, 1962), it is possible that the scorpaenoid diversity found locally has changed immensely from historical records, and that the absence of these unconfirmed species could be linked to habitat change and more realistically changes in sampling methods and the accuracy of historical records. As advancements in techniques develop, misidentification of species (Beerkircher et al., 2009; Vecchione et al., 2000) from past records is also a major issue that can only be addressed by maintaining good records, and updating specimen collections with present taxonomic literature and databases available (Eschmeyer, 2010). At present, historical records are still important as they provide a basis of comparison for taxonomic studies. Although these may not always be totally accurate or reliable, historical data can at least provide a measure of information if educated assumptions on certain species are required. In spite of these issues, it would appear that the scorpaenoid diversity in Singapore is still relatively rich (12 confirmed and 13 unconfirmed species) when cursory comparisons were made to records found at the Phuket Marine Biological Centre, Thailand (18 species - unpubl. data), with some overlaps in similar species. In addition, the new record of scorpaenoid (*L. asteroblepa*) suggests that even with the short-term depth-limited sampling during the present study, more species can still be discovered with increased sampling effort, different techniques, and perhaps targeting new habitats.

Results during this study indicate that there are three species of scorpaenids commonly found locally both historically and presently (this will expanded in the Chapter 3). This includes the large estuarine stonefish, *S. horrida*, the small sized stargazer waspfish, *T. uranoscopus* and long spinned scorpionfish, *P. longsispinis*. These fish were found in similar habitats but different locations locally. As such, different techniques were found to be effective for capturing *T. uranoscopus* and *P. longispinis* with seine nets, while local traps (i.e. bubus) were effective for *S. horrida*. Although *S. horrida* was caught along many of the inshore islands, these animals were only caught consistently using the local traps (i.e. bubus) and this it is suspected that the effectiveness of these traps is related to the traps working inadvertently as prey attracting devices for *S. horrida*. Both *T. uranoscopus* and *P. longispinis* were caught along soft sediment shore along the coast of Singapore and were consistently caught using seine nets due to their smaller size. The following chapters will delve into the biology and ecology of the three common species in greater detail.

Chapter 3. Trophic ecology of common scorpaenoids at Changi Point Beach

3.1 Introduction

Patterns of resource utilisation affect community structure at a number of organisational levels. Diversity in resource utilisation (i.e. resource partitioning) supports inter-specific, and to a lesser extent, intra-specific sympatry, in the absence of which communities are numerically dominated by competitive superiors (Macpherson, 1981; Platell and Potter, 2001; Schafer et al., 2002). Specialists tend to have a narrower distribution range and occur in smaller numbers than do generalists (Munday, 2000; Munday et al., 1997), unless the resource to which they are specialised is prevalent (Megina et al., 2002). Among resource axes, food is a primary resource that is partitioned. Specialisation and niche diversification in trophic ecology has been linked to speciation and habitat overlap (Huh and Kitting, 1985; Macpherson, 1981; Sverker, 1983), and has impacts on community structure. Trophic ecology also has implications on the abundance of organisms that can be found in the community; typically herbivores and secondary producers occur in much greater abundance than do predators (Odum, 1959). As such, trophic ecology studies are useful and one of the fundamental principles in determining the community or ecosystem roles of sympatric fish species that can be found in similar habitats (Blaber et al., 1995; Hajisamae et al., 2003). In the absence of a diversity of other major resources such as habitat complexity, trophic organisation therefore becomes of primary importance in structuring assemblages and communities.

Among shallow-water marine habitats, coastal sandy habitats are relatively depauperate of habitat complexity and, by association, fish species richness (Gratwicke et al., 2006). Coastal habitats are perhaps at greatest risk from expanding human populations, as coastal developments either directly change habitats through reclamation (Glaser et al., 1991; Hilton and Manning, 1995) or have indirect effects by altering water conditions which are deleterious to coastal fish communities (Al-Mandany et al., 1991).

In this Chapter, the study examines the trophic ecology of the fish assemblage at Changi Point Beach (CPB), Singapore. The fish community at CPB is unusual for a number of reasons. Firstly, a relatively high degree of sympatry (five species from four families of scorpaenoids)(see Chapter 2), which was not observed at any of the other sampling sites. This contrasts strongly with other studies in this tropical region where scorpaenoids are rarely caught in abundance (Hajisamae and Chou, 2003; Hajisamae et al., 2003) and have never been considered to play a major role in the benthic fish community. Secondly, two of these species, a zoobenthivore (*Paracentropogon longispinis*) and a piscivore (*Trachicephalus uranoscopus*), were numerically dominant in the fish community, although species richness was relatively high, consisting of 70 taxa from 41 families (Kwik et al., 2010). This is atypical as abundances are usually inversely correlated with trophic level, i.e. piscivores are usually least abundant in a community (Helfman et al., 1997). Finally, the scorpaenoids potentially live their entire life cycles at CPB, with mature adults persistently found in samples throughout the year (Chapter 5). Ontogenetic change in habitat is common in scorpaenoids, with several species of sebastids moving from shallow waters as juveniles to deeper waters as adults (Love et al., 1990a). The persistence of scorpaenoids through all life stages at CPB creates intra-specific competition for resources, which may be self defeating. However, this can be ameliorated by ontogenetic changes in diets. Ontogenetic shifts in diets and habitats have been observed in several species of scorpaenoids. This includes *Sebastes mystinus* whose diets range from plankton as juveniles to fish when adult (Hallacher and Roberts, 1985). Another species in the Mediterranean (*Scorpaena maderensis*) preyed on larger more vagile decapods as adults but small amphipods and isopods during juvenile stages (Mesa et al., 2007). In another species (*Sebastapistes nuchalis*), the diet shifted from smaller brachyurans and small crustaceans for juveniles to larger brachyurans and fish as dominant prey items as individuals grew larger (Harmelin-Vivien and Bouchon, 1976).

It is important to differentiate true ontogenetic changes in diet from perceived changes in diet due to ontogenetic habitat shifts and the associated differences in prey availability. Under such circumstances, it is easy to misinterpret true ontogenetic shifts in diets based on gut contents alone. Ecomorphology, specifically concerned with form relative to ecological roles (de Medeiros and Costa Ramos, 2007), determines patterns between structure and behaviour on patterns of prey use (Foster and Baker, 1995; Wainwright and Richard, 1995). As such, ontogenetic changes in prey type should correspond to changes in feeding morphologies and behaviour of the predators (Hallacher and Roberts, 1985; Schafer et al., 2002; Wainwright, 1988) that occur throughout their development (Grossman et al., 1980; Locket and Suthers, 1998; Olson, 1996). Ecomorphology is also valuable for elucidating trophic types and identifying potential competition where sample sizes are limited. Although important morphological characteristics are usually identified through dietary studies, we observe that dietary ecomorphology based on qualitative descriptions of dentition (de Medeiros and Costa Ramos, 2007), jaw structure (de Medeiros and Costa Ramos, 2007; Motta, 1982) or body shape (Wainwright and Richard, 1995) can be an useful alternative tool, at least for identifying potential competitors for resource (Gosline, 1996), though it should not completely replace traditional methods such as gut content analyses (Hajisamae et al., 2003; Huh and Kitting, 1985).

As such, in trying to better understand the trophic ecology of tropical scorpaenoids in the fish community, a goal of this study is to determine if scorpaenoids are major predators in the shallow habitats of CPB. The specific aims of this study are to:

1. utilise ecomorphological characteristics of the fish taxa found at CPB to develop a hypothetical model of potential competition and resource overlap;
2. test model developed in (1) against data based on stomach contents, with a focus on scorpaenoids and their primary competitors.
3. elucidate key aspects of trophic ecology that support:
    a) coexistence of scorpaenoid taxa
    b) numerical dominance of the two scorpaenoid species
    c) intra-specific sympatry through ontogenetic shifts in diet

3.2 Material and Methods

Changi Point Beach, Singapore

The shallow coastal habitat of Changi Point Beach (CPB) is located along the eastern coast of Singapore (1^{o}23'35"N, 103^{o}59'16"E), and is situated at the entrance of Sungei Changi facing the Straits of Singapore (Figure 3.1). CPB stretches a long a distance of approximately 1500 m, consisting of a mixed sandy and muddy substratum with a patchy distribution of dugong seagrass, *Halophila ovalis* (Hydrocharitacea), and sea lettuce, *Ulva lactuca* (Ulvaceae), found along the subtidal zone.

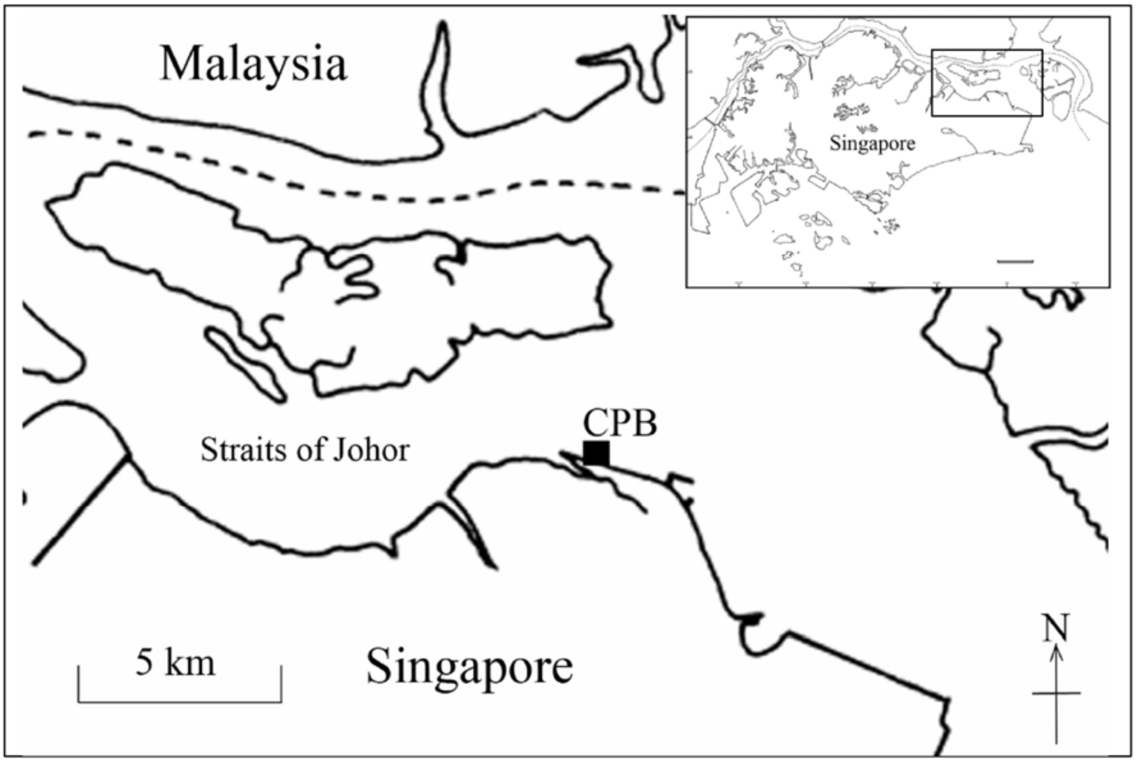

Figure 3.1 Map of Changi Point Beach along the eastern coast of Singapore

Ecomorphological studies

To investigate ecomorphological differences between behaviourally and/or morphologically similar benthic fishes (in relation to scorpaenoids), a hierarchical cluster dendogram comparing within groups was performed on eight characters (defined through literature and supported by short term tank observations (48 hours per species) of all benthic species identified) including eye position, body shape, position in water column, associated environment, activity level, feeding behaviour type, mouth size and mouth position (Table 3-1) which were equally weighted using the statistical package SPSS 18.0 (PASW, 2009). Based on these clusters, comparisons of jaw morphology were performed using relative proportions of mouth width and gape in relation to standard length as well as tail length (anal pore to tail tip) in relation to total length, 1-way ANOVAs were used to compare averages of these measurements using SPSS 18.0 (PASW, 2009). Dentition types (cardiform – small set conical teeth in a close set patch or band, villiform – small, slender teeth forming velvety bands, caniniform - shaped like a canine tooth, conical in form, molariform - blunt and rounded grinding teeth) and position of teeth along jaw structures in the smallest and largest specimens of each species were also performed for descriptive ecomorphological comparisons.

Table 3-1. Eight characters with descriptions used for determining morphological groups in benthic fish of Changi Point Beach.

Characters	Descriptions
Eye position	1. lateral, 2. dorsal
Body shape	1. laterally compressed, 2. dorso-ventrally compressed, 3. tubular
Position in relation to benthos	1. lying on benthos, 2. above benthos, 3. buried
Associated environment	1. none, 2. sediment, 3. vegetation
Activity	1. low, 2. medium, 3. high
Feeding behaviour	1. forager, 2. winnower, 3. browser, 4. lie-in-wait predator
Mouth size	1. small, 2. medium, 3. large
Mouth position	1. terminal, 2. superior, 3. inferior

Gut analysis of common scorpaenoids and other benthic fish

Between January and December 2008, all specimens of scorpaenoids from the sites of CPB were collected using beach seines (as described in Chapter 1.2.2). In addition, other benthic fish species at only CPB were also collected during these sampling periods for dietary comparisons of the benthic species at CPB. All specimens were iced, put in 10% formalin within 30 minutes, and stored in 70% alcohol after three days for longer storage. In the laboratory, the stomach was removed, all gut contents were extracted and identified to the lowest taxonomic level possible, diet type was enumerated and weighed using a A&D FX-300 (± 0.001 g) when large enough or a Sedgewick rafter counting cell (50 mm x 20 mm x 1 mm, volume = 1 ml) when samples were too light to be weighed. Both the weights of the full and emptied stomach were also weighed. In guts where dietary items were sufficiently large enough for measurement using the weighing scale, proportions of each dietary item were calculated based on the formula:

$$\text{Proportion of Diet type}_i = \text{weight}_i \,/\, \text{Total wet weight of all stomach contents} \times 100$$

However, when dietary items were approximated in the counting cell, relative proportions of each identified diet type was measured using the formula:

$$\text{Proportion of Diet type}_i = (\text{no. of squares of item}_i \,/\, \text{total no. of squares of all dietary types}) \times (\text{Total wet weight of full stomach} - \text{total wet weight of empty stomach})$$

Dietary comparisons of benthic fish at Changi Point Beach

In trying to determine the trophic relationships with the fish community, calculation of dietary breadth was used for comparisons of benthic species at only Changi Beach where the benthic fish diversity was previously investigated and known (Kwik et al., 2010). Trophic indices have been used to describe the importance of different food types in diets of different fish species (Hyslop, 1980). To evaluate the rate of feeding activity, the *vacuity index* (VI) was calculated and refers to the proportion of empty guts in relation to total number of stomachs sampled in each species. *Total number of food items* refers to the total number of food types found in all stomachs of each species. *Major diet* refers to the relative volume of a prey item in excess of 50%. In order to show the relative level of dietary specialisation of the species, the dietary breath (DB) of a given species was calculated using Levin's measure

(Krebs, 1999), based on volume value data. Hurlbert's formula (1978) was applied to standardise the trophic niche measure (with a range from 0 to 1), according to the formula:

$$Bi = \frac{1}{(n-1)}\left(\frac{1}{(\sum_j\ P_{ij}^2)} - 1\right)$$

where: B_i = Levin's standardised index for predator i; pij= proportion of diet of predator i that is made up of prey j; n= total number of food items

In addition, based on the percentage of individual prey volume over total volume of stomach contents for each fish from each species, dietary proportions of the all benthic fish species (including the two common scorpaenoids: *P. longispinis* and *T. uranoscopus*) were square root transformed before a similarity matrix was constructed. This was desirable because analyses of untransformed data tend to be affected by patterns from the most abundant category(s). The Bray-Curtis similarities in species composition among samples were used to construct a two-dimensional multi-dimensional scaling (MDS in PRIMER 6.0) plot. The stress values associated with MDS plots indicate the magnitude of distortion between original ordination and the 2-dimensional graphs (Clarke, 1993). The values presented within the graphs indicate that they are adequate for interpretation (where Stress <0.1 indicates “no real prospect of misleading interpretation,” stress <0.2 gives a “useful” two dimensional picture, and stress >0.2 “should be treated with a great deal of scepticism” (Clarke and Warwick, 2001). SIMPER analysis (in PRIMER 6.0) was used to determine the contribution of each species to the average Bray-Curtis dissimilarity between dietary types. This method of analysis determines the similarities within each group and the breakdown for specific fish individuals.

Based on the ecomorphological comparisons, chi-square tests were performed comparing prey selectivity by the two dominant fish predators found at CPB (*T. uranoscopus* and *C. nematophthalmus*). This involved comparisons within each species between expected habitat population proportions (π_i) against the standardised dietary population (B_i), where expected population proportions were calculated based on fish abundances (at the family level) observed during fish surveys at Changi Point Beach (Kwik et. al, 2010).

Chi square tests were done based on the formula described by Manly et al. (1993):

$$x^2 = \sum_{i=I}^{I} (u_i - u_+\pi_i)^2 \,/ (u_+\pi_i)$$

Where *I* is the number of resource categories, u_i is the observed number of used resource units of type i, $u_+\pi_i$ is the expected counts of type i.

Ontogenetic shifts in diets

Due to the limited information with regards to these species, results on maximum and minimum sizes of samples obtained during surveys and museum specimens in Chapter 2, were compared to the maximum sizes found in Chapter 4 (growth of common scorpaenoids) to determine appropriate size classes for the three common species. As such, fish samples of *P. longispinis* and *T. uranoscopus* were arbitrarily divided into six size classes (< 21 mm to > 61 mm, with 10 mm increments for *P. longispinis* and < 31 mm to > 71 mm, with 10 mm increments for *T. uranoscopus*). Ontogenetic changes in feeding habits of these scorpaenoids were assessed using a multivariate analysis of data. Cluster analysis was applied to the data set constituting dietary proportions of prey type calculated for each size class of the three common scorpaenoid species. Food items were pooled in several categories dependant on the dominant and identifiable food found in each size category for each scorpaenoid species. Adequate sample size within each size range was also a consideration when determining the size classes for each species. Within each species, Bray-Curtis similarities in size ranges among samples were used to construct a two-dimensional multi-dimensional scaling (MDS in PRIMER 6.0) plots to determine the length at which dietary changes occurred. A SIMPER analysis (in PRIMER 6.0) was also used to determine the contribution of size classes within each species to the average Bray-Curtis dissimilarity between dietary types. In addition, ecomorphological comparisons described earlier were also used to compare changes in dentition and jaw structure with regard to size.

Index of Relative Importance of diets

The measurements of numbers, volume, and frequency of occurrence used traditionally in evaluating stomach contents of fish usually fall short of depicting true relative value, with numerous small organisms sometimes overshadowing the importance of a few large ones (Pinkas et al., 1971). The "importance" of a food category for this study is taken to mean the amount (number) and bulk (volume or weight) in the diet. By considering both bulk and the amount in association a more accurate picture of dietary importance can be gained (Hyslop, 1980: 417). As such, an additional assessment for observing changes in the diet with size within each scorpaenoid species, and the contribution of each prey to the diets of both species based on the previously mentioned size classes, was determined by frequency of occurrence (FO), numerical composition (%N) and weight composition (%W) (Hyslop, 1980). The Index of Relative Importance (IRI) (Pinkas et al., 1971) was calculated for consumed prey items:

$$\text{IRI} = (\%\text{N} + \%\text{W})\ (\text{FO})$$

3.3 Results

Cluster dendograms based on behavioural and morphological traits of the 19 benthic fish types found at CPB indicated that there were seven main groups (at a rescaled distance of 10) that could be identified (Figure 3.2). Amongst these seven groups, the groups with the greatest similarity and distinction from others included the pair consisting of fringe-eye flathead, *Cymbacephalus nematophthalmus* and the stargazer waspfish, *Trachicephalus uranoscopus* (Group A), at a rescaled distance of 1 (in relation to the start of the dendogram) (Figure 3.2). A high level of ecomorphological similarity was also noted between *Paracentropogon longispinis* and the false scorpionfish, *Centrogenys vaigiensis* (Group B1), though these also shared characteristics with Group B2, consisting of Schaap's dragonet, *Callionymus schaapi*, the slender seamoth, *Pegasus volitans*, and the speckled tongue-sole, *Cynoglossus puncticeps* (Figure 3.2).

While somewhat similar, ecomorphological characters of the blue-speckled pipefish, *Hippichthys cyanospilus* (Group B3) were distinct from these groupings (Figure 3.2). There was also a high level of similarity between the fan-bellied leatherjacket, *Monacanthus chinensis*, and the white-spotted spinefoot, *Siganus canaliculatus* (Group C1), while *Upenaeus tragula* and the *Sillago* sp. also showed high similarities (Group C2). Although somewhat similar to Group C2, Group C3 was also distinct and consisted of the wrasse, *Haliochoeres* sp., pink-ear emperor, *Lethrinus lentjan*, white-patch tuskfish, *Choerodon oligocanthus*, trumpeter perch, *Pelates quadrilineatus*, striped eeltail catfish, *Plotosus lineatus*, three-spine toadfish, *Batrochomoeus trispinosus* and two similar gobies (*Acentrogobius caninus* and *Yongeichthis nebulosus*) (Figure 3.2). As such, it was expected that a certain degree of competition would occur within these defined groups, with even higher competition occurring between species in the more defined groups (e.g., *T. uranoscopus* and *C. nematophthalmus*; *P. longispinis* and *C. vaigiensis*).

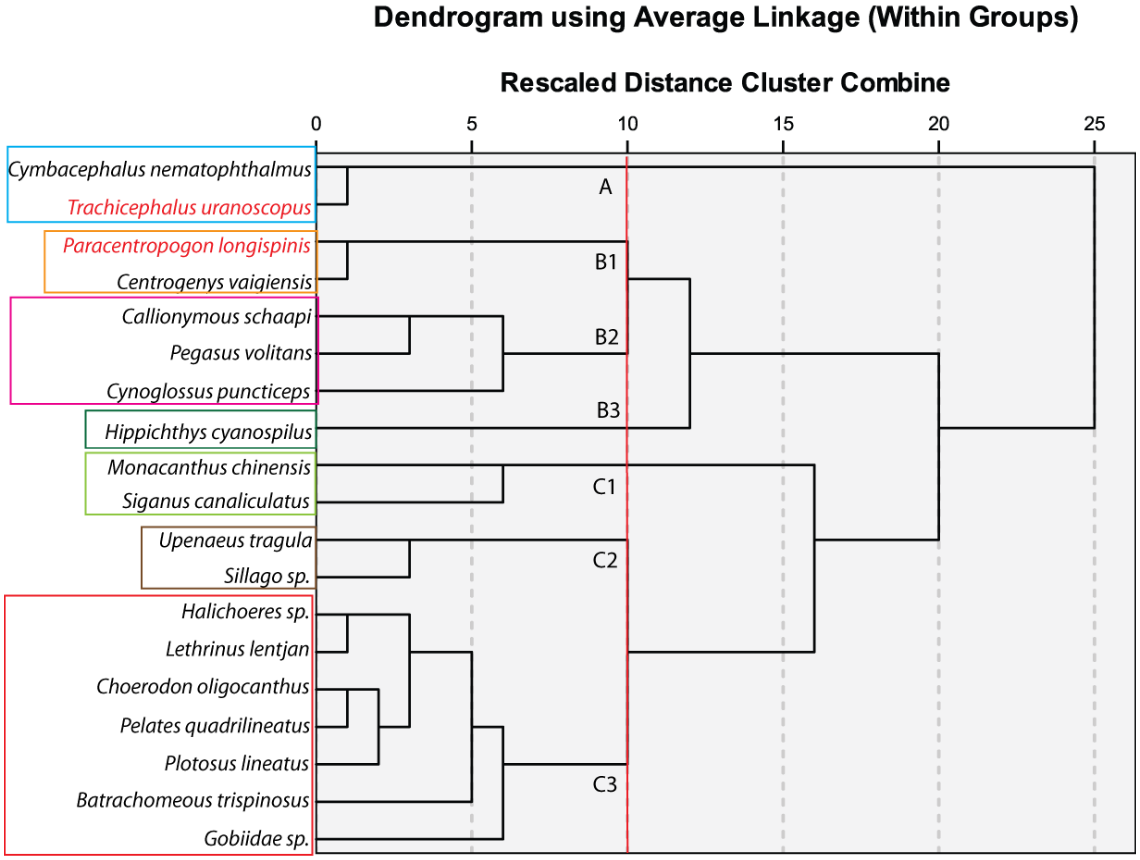

Figure 3.2 Hierarchical dendogram of eight gross ecomorphological character described in Table 4-1 of the 19 benthic fishes at Changi Point Beach. Seven groupings (A = blue, B1 = orange, B2 = pink, B3 = olive green, C1 = light green, C2 = brown and C3 = red) are defined based on rescaled distance of 10. Common scorpaenoids are also highlighted in red.

Based on these finer resolutions of fish, crustaceans, polychaetes and vegetation diet types (11 diet types), the MDS and SIMPER analyses confirmed that competition for resources would likely occur between *T. uranoscopus* and *C. nematophthalmus* (Figure 3.3) with both clustered based on similar diets (SIMPER showed 52% similarity of diets between the two species with fish contributing around 95% in Group A). As expected, another pair which was clustered included the herbivores of *M. chinensis* and *S. canaliculatus* (SIMPER showed 84% similarity in diets with vegetative matter contributing around 97% in Group C1), as well as *U. tragula* and the *Sillago sp.* which fed on polychaetes (45% similarity with polychaetes contributing 56% in Group C2) (Figure 3.3).

As expected, *C. vaigiensis* clustered closely with *P. longispinis*, but the MDS revealed that while *P. longispinis* preyed primarily on smaller crustaceans such as amphipods together with several other species such as *C. schaapi*, *C. puncticeps* and *P. volitans*, all of which were closely related on the cluster dendogram (Figure 3.2), *C. vaigiensis* preyed primarily on other larger crustaceans such as prawns and shrimp in addition to amphipods (SIMPER analysis showed 41% similarity with amphipods contributing 85% in Group B1) (Figure 3.3). Other clusters included *B. trispinosus* which fed on crabs, and another group consisting of *P. quadrilineatus*, *H. cyanospilus* and *P. lineatus* (which were also clustered together in the dendogram) that fed primarily on copepods while *Haliochores* sp., *L. lentjan* and *C. oligocanthus*, which were grouped in the similar cluster (Group C3), fed primarily on polychaetes (Figure 3.3).

Similar to the cluster dendogram presented earlier (Figure 3.2), groups of benthic fish could also be defined based on specific diets, this included the two species of piscivores (10% of all benthic fish) which were also the most defined pair based on the dendogram consisting of *T. uranoscopus* and *C. nematophthalmus*; two species of herbivores (10%) which were another pre-defined pair consisting of *M. chinensis* and *S. canaliculatus*; while the majority of other benthic fish being zoobenthivores (16 species, 80%) which also included the other defined pairings of *C. vaigiensis* and *P. longispinis*, and also *U. tragula* and *Sillago* sp. amongst the remaining zoobenthivores (Table 3-2).

Dietary studies on the 20 benthic fish species showed that out of 790 specimens, 648 had prey items in their stomachs (~82%) (Table 3-3), consisting of three main dietary groups. Dietary breadth was found to differ between many of the species with most benthic fish being opportunistic feeders (50% of fish with B_i between 0.33-0.66), while seven species (35% with $B_i < 0.33$) had narrow dietary breaths and only three species (15% with $B_i > 0.66$) had wide dietary breadths (Table 3-3). Although *P. longispinis* appeared to be a generalist feeding on many prey types (Table 3-2), a closer inspection of the diet in this scorpaenoid species indicated that though many prey types had been found in the stomachs of samples (9 types), amphipods contributed the highest proportion amongst prey items and increasing the relative contribution of this prey type to the rest of the dietary items found in *P. longispinis* (Table 3-3).

Table 3-2. Dietary composition (11 broad based diet types) of the 20 benthic fish species found at Changi Point Beach (n = 790). Major trophic groups (Piscivory, zoobenthivory and herbivory) displayed as coloured diet percentages, and based on dominant taxa within each species (where pink = amphipods, red = crabs, blue = fish, brown = polychaetes, orange = prawn/shrimp, olive green = copepods and green = vegetative matter). Species groupings are based on morphological characters defined in cluster dendogram (**Figure 3.2**).

Family	**Species**	**Amphipods**	**Bivalves**	**Copepods**	**Crabs**	**Fish**	**Isopod**	**Nematodes**	**Polychaetes**	**Prawn/shrimp**	**Vegetative matter**	**Unidentified**
Group A (Piscivory)												
Platycephalidae	*Cymbacephalus nematophthalmus*	3.2%			24.8%	33.7%			7.3%	31.0%		
Trachicephalidae	*Trachicephalus uranoscopus*	10.1%				86.7%				1.7%		1.4%
Group B1 (Zoobenthivory)												
Scorpaenidae	*Paracentropogon longispinis*	58.8%			11.6%	1.0%	3.2%		11.7%	12.3%		1.3%
Serranidae	*Centrogenys vaigiensis*	7.5%		1.8%	15.7%	7.1%			8.4%	59.6%		
Group B2 (Zoobenthivory)												
Callionymidae	*Callionymus schaapi*	84.4%	12.8%					2.8%				
Cynoglossidae	*Cynoglossus puncticeps*	38.1%	12.5%	8.3%					36.9%	4.2%		
Pegasidae	*Pegasus volitans*	75.0%						25.0%				
Group B3 (Zoobenthivory)												
Syngnathidae	*Hippichthys cyanospilus*	11.3%		83.2%						5.5%		
Group C1 (Herbivory)												
Monacanthidae	*Monacanthus chinensis*	11.6%			0.8%				3.5%	0.5%	83.5%	
Siganidae	*Siganus canaliculatus*										100.0%	
Group C2 (Zoobenthivory)												
Mullidae	*Upenaeus tragula*	42.3%	3.5%						40.0%	14.2%		

Sillaginidae	*Sillago* sp.	36.6%		7.9%				52.6%	3.0%		
<u>Group C3 (Zoobenthivory)</u>											
Batrachoididae	*Batrachomoeus trispinosus*				77.8%				22.2%		
Gobiidae	*Acentrogobius caninus*	52.5%	0.3%			33.5%		12.0%			1.8%
	Yongeichthys nebulosus	44.7%		6.9%			2.1%	30.0%	16.3%		
Labridae	*Choerodon oligacanthus*	4.8%	1.5%		11.7%			60.0%	22.1%		
	Halichoeres sp.	44.0%						56.0%			
Lethrinidae	*Lethrinus lentjan*	11.4%						61.6%	26.9%		
Plotosidae	*Plotosus lineatus*	19.2%	4.9%	36.8%	3.1%	2.3%		2.6%	31.2%		
Terapontidae	*Pelates quadrilineatus*	18.0%		30.1%	11.9%		1.2%	19.8%	4.8%	14.4%	

Table 3-3. Dietary attributes of benthic fish communities based on major trophic types found at Changi Point Beach where N = sample size, S>0 = number of specimens with non-empty stomachs, VI = vacuity index, B_i = dietary breadth. Species groupings are based on morphological characters defined in cluster dendogram (**Figure 3.2**).

Family	Species	N	S>0	VI	DB	Food items
Group A						
Platycephalidae	*Cymbacephalus nematophthalmus*	41	31	75.61	0.65	5
Trachicephalidae	*Trachicephalus uranoscopus*	125	69	55.2	0.1	4
Group B1						
Scorpaenidae	*Paracentropogon longispinus*	277	248	89.53	0.2	9
Serranidae	*Centrogenys vaigiensis*	27	17	62.96	0.3	6
Group B2						
Callionymidae	*Callionymus schaapi*	12	12	100	0.18	3
Cynoglossidae	*Cynoglossus puncticeps*	17	12	70.59	0.57	5
Pegasidae	*Pegasus volitans*	3	2	66.67	0.6	2
Group B3						
Syngnathidae	*Hippichthys cyanospilus*	52	47	90.38	0.21	3
Group C1						
Monacanthidae	*Monacanthus chinensis*	38	31	81.58	0.1	5
Siganidae	*Siganus canaliculatus*	31	29	93.55	0	1
Group C2						
Mullidae	*Upenaeus tragula*	13	13	100	0.59	4
Sillaginidae	*Sillago* sp.	17	12	70.59	0.46	4
Group C3						
Batrachoididae	*Batrachomoeus trispinosus*	8	6	75	0.53	2
Gobiidae	*Acentrogobius caninus*	21	20	95.24	0.37	5
	Yongeichthys nebulosus	27	24	88.89	0.92	5
Labridae	*Choerodon oligacanthus*	30	24	80	0.34	5
	Halichoeres sp.	12	12	100	0.97	2
Lethrinidae	*Lethrinus lentjan*	14	14	100	0.57	3
Plotosidae	*Plotosus lineatus*	13	13	100	0.44	7
Terapontidae	*Pelates quadrilineatus*	12	12	100	0.67	7

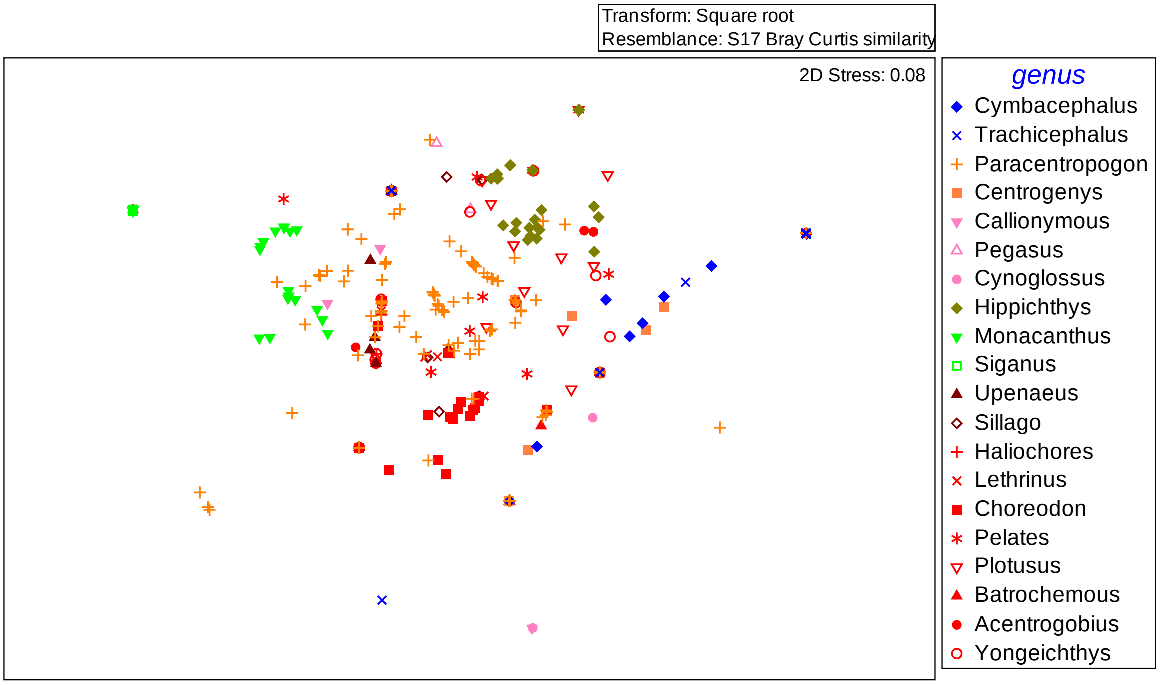

Figure 3.3 Multi-dimensional scaling ordination of diets for 20 benthic fish genera caught from Changi Point Beach between January 2006 and December 2007. Dietary data was allocated into 11 food groups and was square root transformed (N = 790). Species were grouped based on morphological characteristics (where blue = group A (displaying mainly piscivory); orange = group B1, pink = group B2, olive green = group B3, brown = group C2 and orange = group C3 (consisting of mainly zoobenthivory); and light green = group C1 (displaying mainly herbivory).

In determining how morphologically similar yet potentially competitive pairs (in which both scorpaenoids are present) can co-exist, a more detailed comparison based on resources between the piscivorous pair of *T. uranoscopus* and *C. nematophthalmus* indicated that while both fed on fish, *T. uranoscopus* fed primarily on gobies while *C. nematophthalmus* fed mainly on sillaginids (Figure 3.4). Comparisons based on expected proportions of prey items in the habitat versus observed proportions of prey in diet indicate that the shadow goby, *Y. nebulosus,* were consumed by *T. uranoscopus* at about three times the probability of these gobies observed in the habitat, while sillaginids were consumed by *C. nematophthalmus* at almost six times the probability observed in the habitat (Table 3-4). A chi-square test comparing the occurrence of gobies and sillaginids within the stomach contents and the relative abundance of these prey items found at this site indicated that prey items were consumed in significantly greater proportions then abundances observed in the environment in both the piscivorous *T. uranoscopus* (χ^2 = 65.3, df = 2, $P < 0.05$) and *C. neopthalmus* (χ^2 = 48.6, df = 2, $P < 0.05$) respectively. The differences in the diets of these two piscivores were also reflected in similarities in body and jaw morphology as well as dentition in both these species. While there were no significant differences in mouth width ($F_{1,44}$=0.05, P>0.05) and gape ($F_{1,34}$=4.11, P>0.05) between *C. nematophthalmus* and *T. uranoscopus*, *T. uranoscopus* had a significantly longer tail (anal pore to end of caudal fin) ($F_{1,15}$=143.1, P<0.05) (Figure 3.5) as well as an extremely broad rounded glossohyal (Figure 3.6- Figure 3.7), which in the case of *T. uranoscopus* could be used for faster burying and more powerful suction feeding. There were also teeth found over more jaw structures in *C. nematophthalmus* (i.e. premaxillary, dentary, vomer and palatine) compared to *T. uranoscopus* (only premaxillary and dentary) (Figure 3.6 and Figure 3.7).

Besides primarily eating fish, *C. nematophthalmus* was also found to have a diet including the larger crustaceans such as prawns, shrimps and crabs, and polychaetes to a lesser extent (Figure 3.4). In addition, all the gobies that were consumed by *T. uranoscopus* were identified as the shadow goby, *Yongeichthys nebulosus*.

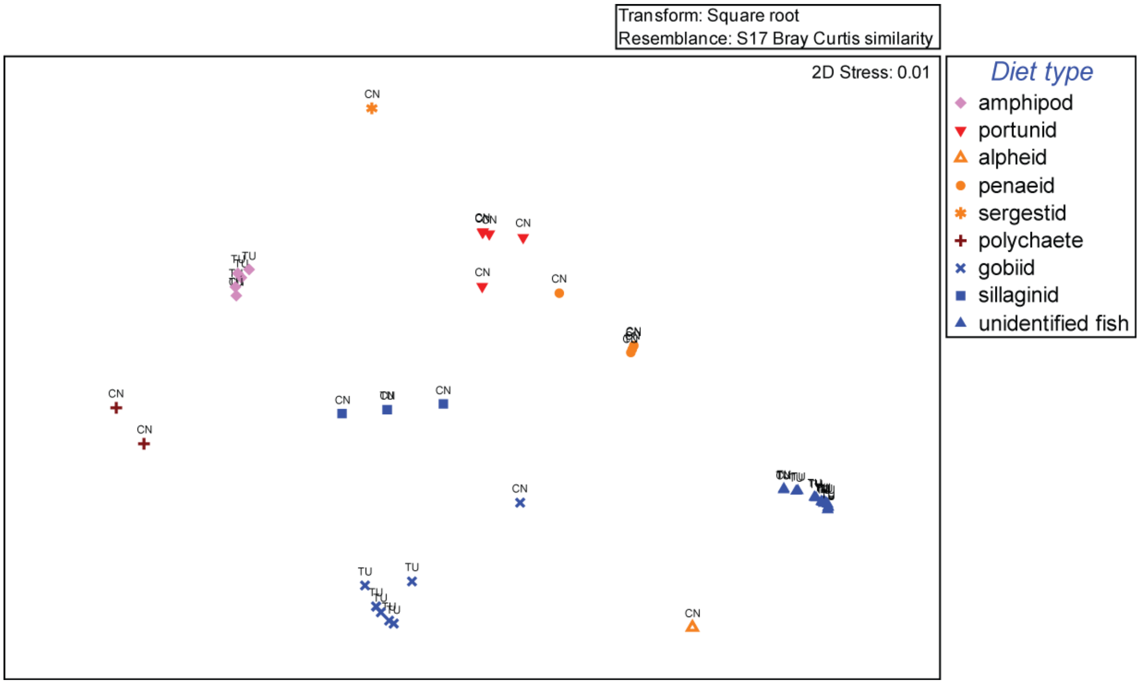

Figure 3.4 Multi-dimensional scaling ordination of diets for the morphologically and behaviourally similar pair of *Trachicephalus uranoscopus* (TU) and *Cymbacephalus nematophthalmus* (CN) caught from Changi Point Beach. Finer scale dietary data was allocated into 12 food groups and was square root transformed (N = 100). (Colours represented are based on major categories where pink = amphipods, red = crabs, orange = prawns/shrimp, brown = polychaetes and blue = fish).

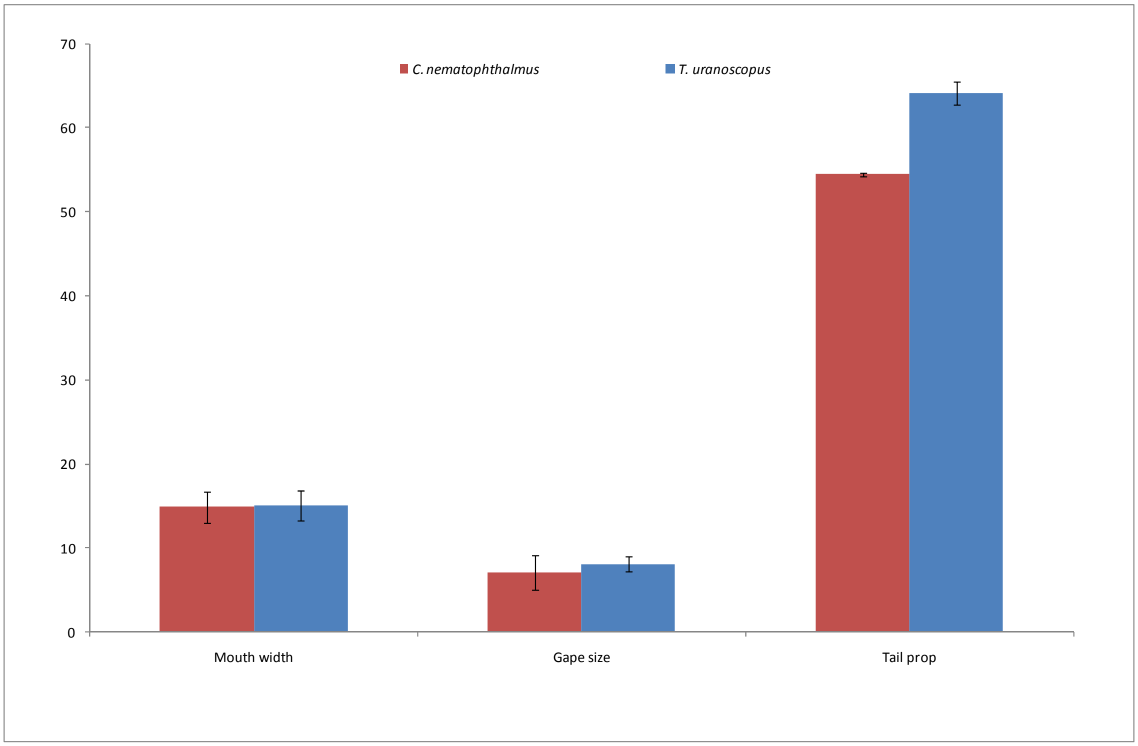

Figure 3.5 Average relative proportions of mouth widths, gapes (in relation to standard length) and tail lengths (anal pore to tail tip in relation to total length) in *Trachicephalus uranoscopus* and *Cymbacephalus nematophthalmus* at Changi Point Beach. (n = 20 and error bars are means ± s.d.).

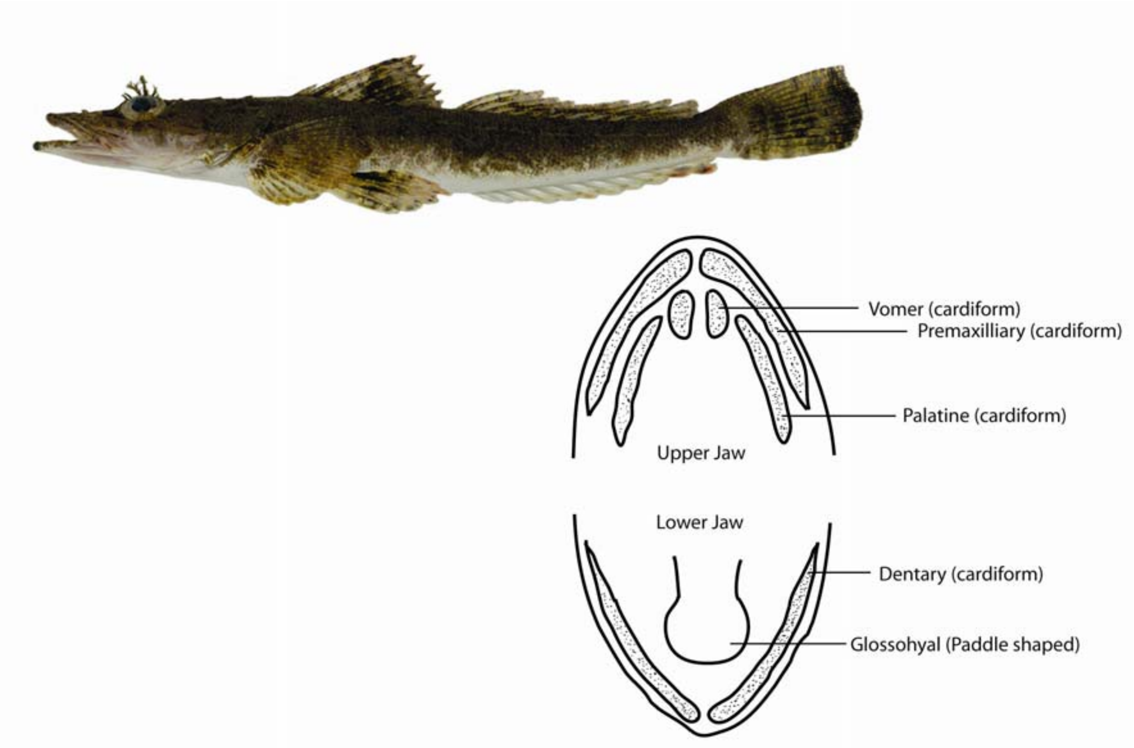

Figure 3.6 Dentition, tooth placement and jaw structure of the fringe-eyed flathead, *Cymbacephalus nematophthalmus* (S.L – 125 mm SL, photo by Tan H.H.).

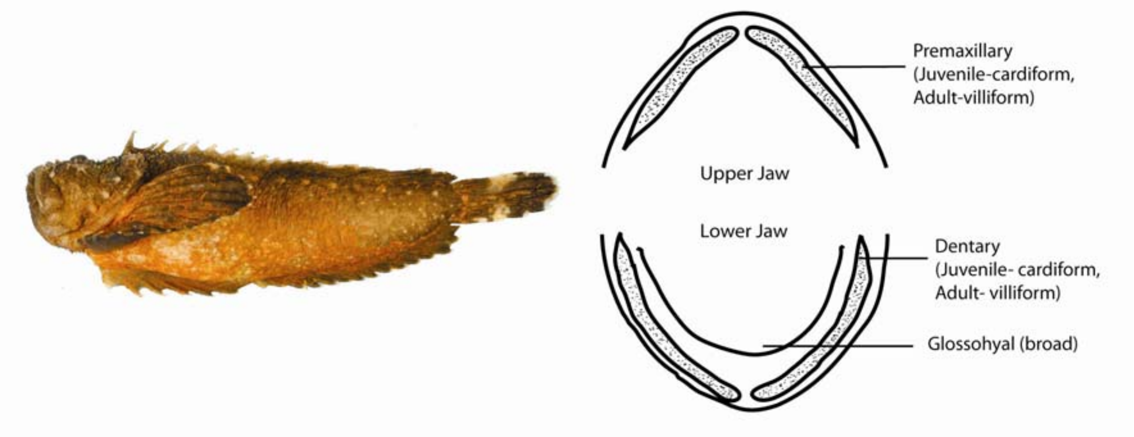

Figure 3.7 Dentition, tooth placement and jaw structure of the stargazer waspfish, *Trachicephalus uranoscopus* (Juvenile – 16.5 mm SL; Adult – 72.2 mm SL).

Table 3-4 Relative probabilities of selection of prey items by *Cymbacephalus nematophthalmus* and *Trachicephalus uranoscopus* at Changi Point Beach.

	Habitat population proportion (U_i)	Standardised dietary proportion (B_i)	
Prey item		*C. nematophthalmus*	*T. uranoscopus*
Gobiids	0.32	0.05	0.94
Labriids	0.53	-	0.01
Sillaginids	0.15	0.95	0.04

In comparison, diets of the zoobenthivorous *C. vaigiensis* and *P. longispinis* differed in the composition of crustaceans preyed upon. Although both consumed amphipods (Table 3-2 and Figure 3.8), *C. vaigiensis* primarily ate larger prey such as prawns and shrimp (Figure 3.8). The capability for *C. vaigiensis* to consume larger crustaceans (as compared to *P. longispinis*) was supported by the significantly larger mouth widths and gapes recorded in *C. vaigiensis* (Figure 3.9), as well as differences in dentition where cardiform teeth (which is important for holding on to prey) were found over more jaw (vomer and palatine) structures than *P. longispinis* (Figure 3.10 and Figure 3.11).

It would appear that though both these pairs were morphologically and behaviourally similar, and that both fed on similar broadly defined prey items, coexistence between these sympatric species occurs as both the piscivorous pair (*T. uranoscopus* and *C. nematophthalmus*) fed on different families of fish prey, while the zoobenthivorous pair (*C. vaigiensis* and *P. longispinis*) fed on different sized crustaceans.

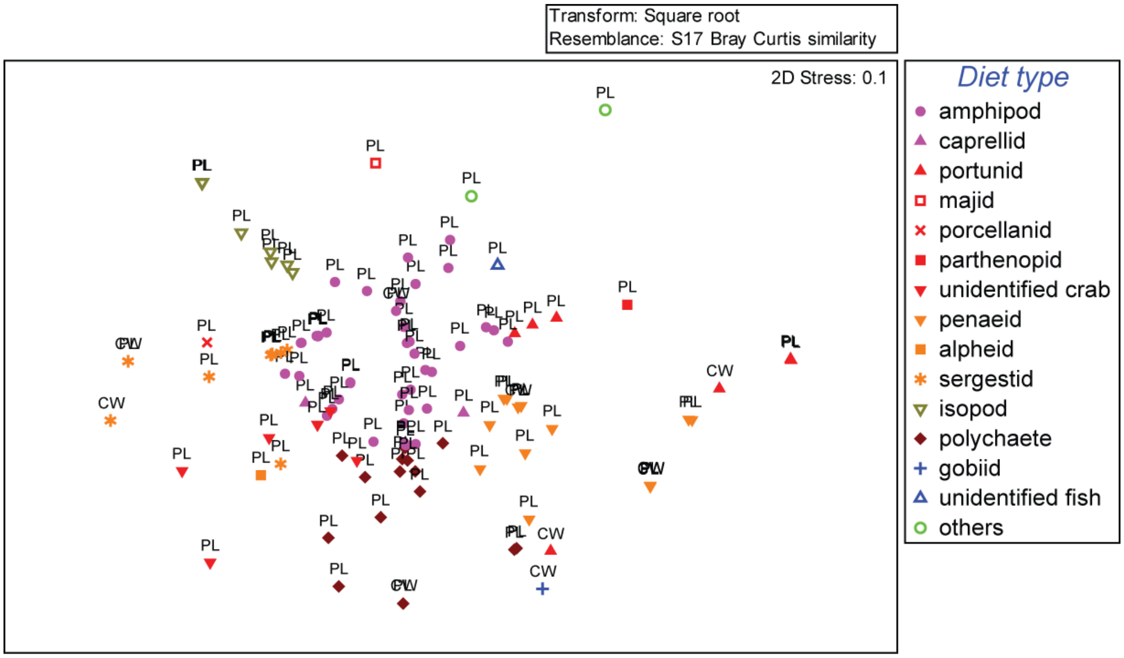

Figure 3.8 Multi-dimensional scaling ordination of diets for the morphologically and behaviourally similar pair of *Paracentropogon longispinis* (PL) and *Centrogenys vaigiensis* (CW) caught from Changi Point Beach. Finer scale dietary data was allocated into 20 food groups and was square root transformed (n = 264). (Colours represented are based on major categories where pink = amphipods, red = crabs, orange = prawns/shrimp, olive = isopods, brown = polychaetes, blue = fish and light green = others).

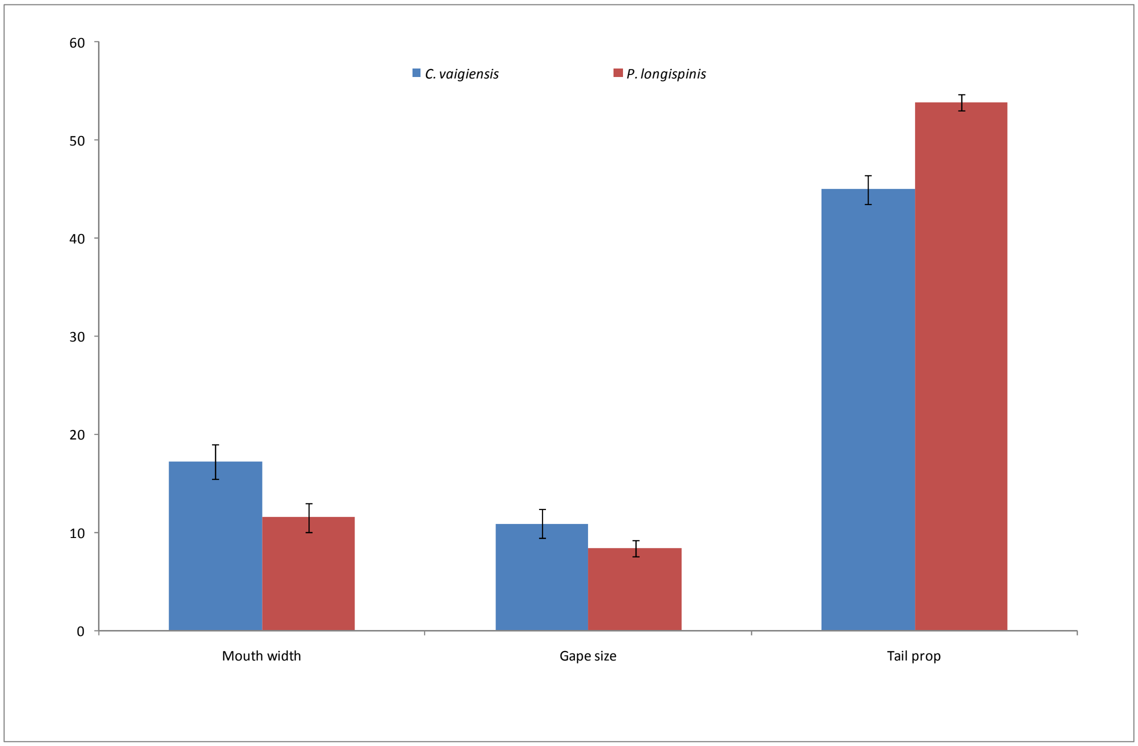

Figure 3.9 Average relative proportions of mouth widths, gapes (in relation to standard length) and tail lengths (anal pore to tail tip in relation to total length) in *Paracentropogon longispinis* and *Centrogenys vaigiensis* at Changi Point Beach. (n = 20 and error bars are means ± s.d.).

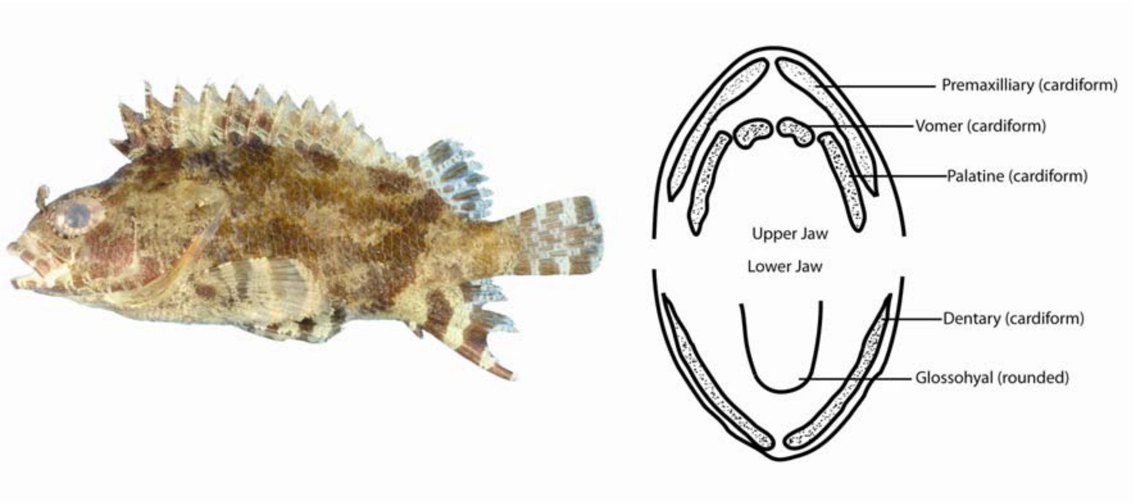

Figure 3.10 Dentition, tooth placement and jaw structure of the juvenile and adult false scorpionfish, *Centrogenys vaigiensis* (90.9 mm SL).

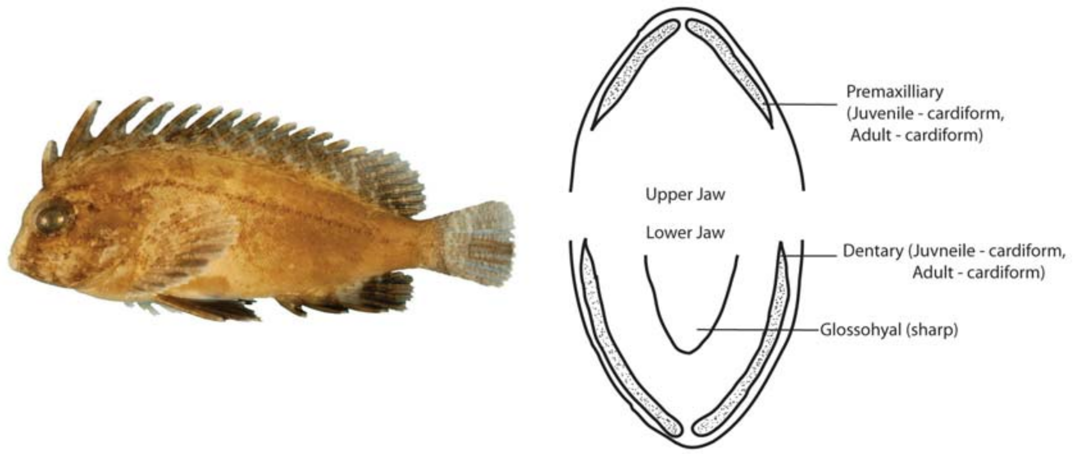

Figure 3.11 Dentition, tooth placement and jaw structure of the long spinned scorpionfish, *Paracentropogon longispinis* (Juvenile – 13.8 mm SL; Adult – 52 mm SL).

Observations on the jaw morphology and dentition between the juvenile and adult of both common scorpaenoids (Figure 3.7, Figure 3.11) also suggest that while *P. longispinis* is unlikely to display any clear ontogenetic shifts (no obvious changes in teeth type of structures) (Figure 3.11), some shifts might be observed in *T. uranoscopus* (change from cardiform to villiform teeth between juvenile and adult specimens) (Figure 3.7). MDS of diets with size classes as a factor supported these observations with no obvious clusters observed in *P. longispinis* regardless of size (Figure 3.12). Conversely, there were clear changes in the diets of *T. uranoscopus*, with juveniles smaller than 31 mm SL feeding only on amphipods but larger individuals fed only on fish (Figure 3.13). In addition to the MDS plots, the dietary indices based on IRIs of diets in both these scorpaenoids, confirmed that amphipods were consistently important in diets of all the size classes of *P. longispinis* (above 8900 IRI values for all size classes) (Table 3-5) supporting the lack of dietary changes in the size classes of *P. longispinis* sampled. However, other larger invertebrates (e.g., crabs, polychaetes and prawns/shrimp) were also important to a lesser degree as size increased in *P. longispinis* (Table 3-5). In comparison, amphipods were only found in the diets of *T.*

uranoscopus at size classes less than 31 mm SL, with all size classes above 31 mm SL dominated by fish diets (above 11250 IRI values) (Table 3-6). This observation supports changes in tooth dentition (cardiform to villiform teeth) observed between juveniles and adult *T. uranoscopus* (Figure 3.7).

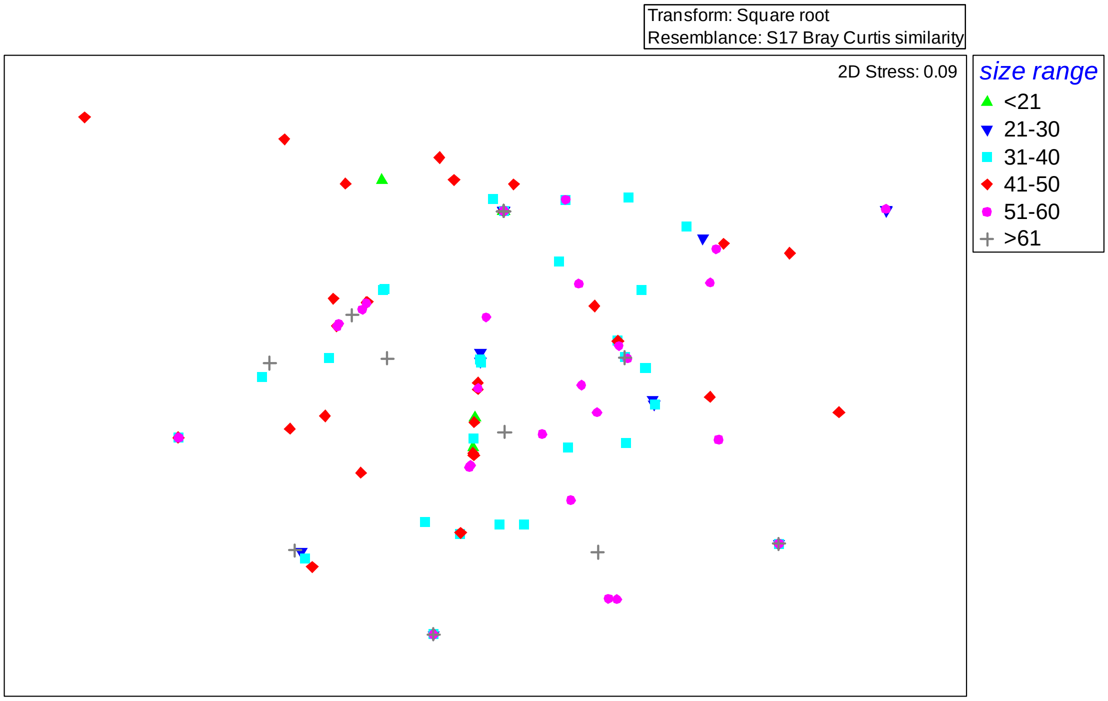

Figure 3.12 Multi-dimensional scaling ordination of diets for six size classes of *Paracentropogon longispinis* caught from Changi Point Beach between January 2006 and December 2008. Fine scale dietary data was allocated into nine food groups and was square root transformed.

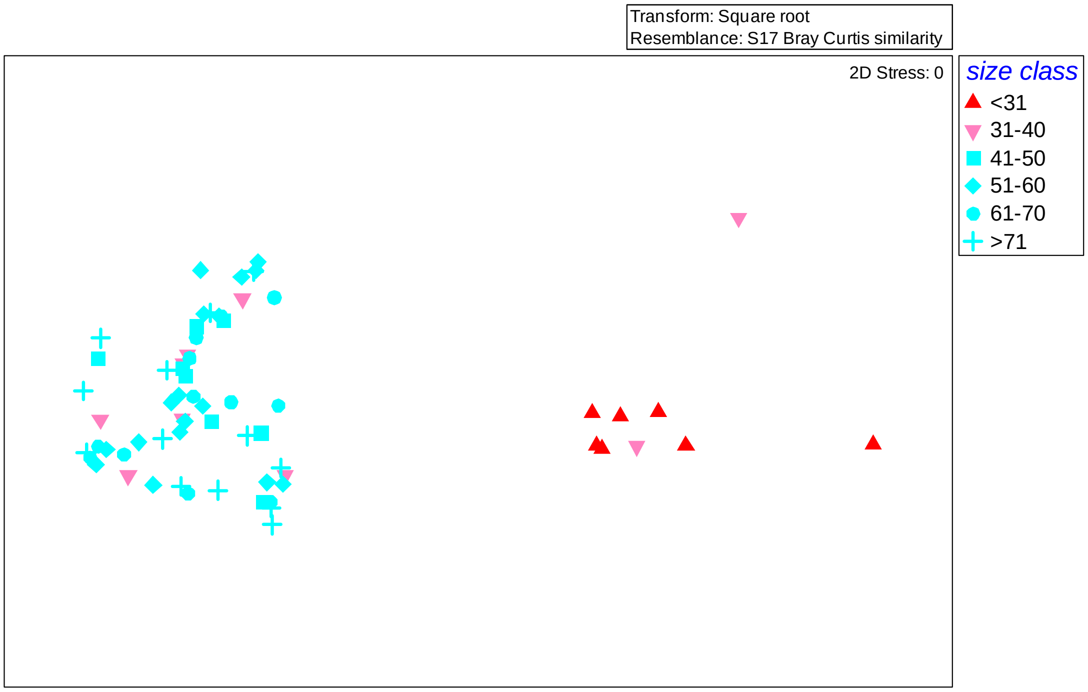

Figure 3.13 Multi-dimensional scaling ordination of diets for six size classes of *Trachicephalus uranoscopus* caught from Changi Point Beach between January 2006 and December 2008. Fine scale dietary data was allocated into four food groups and was square root transformed.

Table 3-5 Relative importance of food types found in different size classes present in *Paracentropogon longispinis* caught along Changi Point Beach between April 2006 and March 2008. N = sample size, FO = frequency of occurrence, %N = numerical composition, %W = weight composition, IRI = Index of relative importance.

		Amphipods				**Bivalves**				**Crabs**				**Fish**				**Isopod**				**Polychaetes**			
size range	n	FO	%N	%W	IRI	FO	%N	%W	IRI	FO	%N	%W	IRI	FO	%N	%W	IRI	FO	%N	%W	IRI	FO	%N	%W	IRI
<21	21	100.00	95.34	93.08	18842.88	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
21-30	31	83.87	77.69	75.16	12819.63	-	-	-	-	3.23	1.61	1.61	10.41	-	-	-	-	9.68	8.06	8.60	161.29	9.68	6.45	7.90	138.92
31-40	59	84.75	70.26	62.39	11241.80	-	-	-	-	13.56	6.74	8.09	201.03	3.39	0.34	1.03	4.65	5.08	1.84	1.45	16.70	25.42	11.17	14.08	641.88
41-50	65	72.31	58.08	49.91	7808.94	1.54	0.19	0.08	0.41	20.00	11.66	14.49	523.04	1.54	0.10	0.38	0.75	6.15	3.33	3.65	42.97	18.46	11.86	14.06	478.55
51-60	55	69.09	58.60	48.49	7398.68	-	-	-	-	27.27	16.31	18.81	957.77	1.82	0.30	1.36	3.02	9.09	3.03	3.77	61.83	23.64	9.38	13.26	535.10
>61	15	73.33	67.86	53.51	8900.41	-	-	-	-	33.33	10.65	17.36	933.68	-	-	-	-	6.67	0.23	0.26	3.29	26.67	10.70	15.02	685.93

		Prawn/shrimp				**Pycnogonid**				**Unidentified**			
size range	n	FO	%N	%W	IRI	FO	%N	%W	IRI	FO	%N	%W	IRI
<21	21	9.52	4.13	5.77	94.28	-	-	-	-	4.76	0.53	1.14	7.96
21-30	31	12.90	6.18	6.72	166.49	-	-	-	-	-	-	-	-
31-40	59	20.34	8.88	12.48	434.36	-	-	-	-	5.08	0.77	0.49	6.42
41-50	65	21.54	11.42	13.20	530.19	1.54	0.31	0.15	0.71	9.23	3.04	4.07	65.67
51-60	55	20.00	11.41	13.33	494.80	-	-	-	-	1.82	0.61	0.99	2.89
>61	15	26.67	10.56	13.84	650.77	-	-	-	-	-	-	-	-

Table 3-6 Relative importance of food types found in different size classes present in *Trachicephalus uranoscopus* caught along Changi Point Beach between April 2006 and March 2008. N = sample size, FO = frequency of occurrence, %N = numerical occurrence, %W = weight occurrence, IRI = Index of relative importance.

		Amphipods				**Prawns/Shrimp**				**Fish**				**Unidentified**			
size class	n	FO	%N	%W	IRI	FO	%N	%W	IRI	FO	%N	%W	IRI	FO	%N	%W	IRI
<31	8	87.50	87.50	87.50	15312.50	-	-	-	-	-	-	-	-	12.50	12.50	12.50	312.50
31-40	8	25.00	25.00	25.00	1250.00	-	-	-	-	75.00	75.00	75.00	11250.00	-	-	-	-
41-50	9	-	-	-	-	-	-	-	-	100.00	100.00	100.00	20000.00	-	-	-	-
51-60	17	-	-	-	-	-	-	-	-	100.00	100.00	100.00	20000.00	-	-	-	-
61-70	13	-	-	-	-	-	-	-	-	100.00	100.00	100.00	20000.00	-	-	-	-
>71	15	-	-	-	-	13.33	10.00	8.02	240.33	93.33	90.00	91.98	16984.36	-	-	-	-

3.4 Discussion

During this study, several perspectives in trophic ecology were addressed using the scorpaenoids at CPB as a study case. Based on the aims of this chapter, we first addressed the used of ecomorphology and utilised this method in this study. Although ecomorphological comparisons have been used in other studies (de Medeiros and Costa Ramos, 2007; Motta, 1982; Wainwright, 1988), its usefulness as a comparative tool for numerically limited samples has frequently been overlooked. However, during this study, comparisons based on ecomorphological descriptions could be effectively used to predict both competition for food resources (even between two similar morphs of piscivores) as well as ontogenetic diet change. It reiterates the relative importance of this non-statistical method for ecological studies.

Next, I looked at both intra- and inter-specific competition for dietary resources in the scorpaenoids as well as against the other benthic fish species that can be found at CPB. These comparisons were either based on species that were taxonomically or morphologically similar; such similarities can result in competition for similar resources (Gatz, 1979; Wainwright and Richard, 1995). With such morphological similarities and the exploitation of similar dietary resources amongst the benthic fish of CPB, implications arise that there are likely to be some competition between some species. This appeared to be the case for *P. longispinis* which shared similar diet types with many of the other benthic fish at CPB. However, an important consideration that was not quantified presently was the amount of dietary resource (e.g., meiobenthic fauna) that is available at CPB, which is the deciding competitive factor for predatory fish that exploit this abundant resource (Coull, 1999). Additionally, piscivores are usually thought to be few in number in certain habitats because they are feeding on fish and occupy the top of the trophic hierarchy (Gerking, 1994). This certainly appears not the case for the benthic fish at CPB which though has only few piscivorous fish species (e.g., *Trachicephalus uranoscopus* and *Cymbacephalus nematophtlamus*) identified in these shallow habitats so far, are present in relatively high abundances. Especially interesting is *T. uranoscopus* that feeds primarily on shadow gobies (*Yongeichthys nebulosus*), suggesting either a more specialist diet or dietary adaptability to this abundant prey resource.

As such, though dietary overlap appeared to occur between several species of benthic fish at CPB, there appeared that the sympatry between the different scorpaenoids species could be attributed to the lack of competition for similar dietary resources. This lack of competition between taxonomically similar species but the presence of competition between morphologically similar species (which are phylogenetically less related), supports the idea that some aspect of guild competition is more likely to occur with the benthic community at CPB (Root, 1967). In addition, it was also demonstrated that some intra-specific competition (at least between the two scorpaenoids) could be negated by a shift in diet of at least one scorpaenoid species.

Dietary niches of scorpaenoids at CPB

In general, diets of the Singapore scorpaenoids are similar to those found in both sub-tropical to temperate waters (Connell, 1998; Fishelson, 1997). This includes scorpaenoids that fed on invertebrates such as polychaetes (Harmelin-Vivien and Bouchon, 1976; Platell and Potter, 2001), shrimp (Brewer et al., 1995; Bulman et al., 2001), small cephalopods (Taylor and Chen, 1969), as well as other large and small crustaceans including decapods, amphipods and isopods (Mesa et al., 2007). Although larger species of scorpaenoids such as *Synanceia horrida* (see Endean, 1962), *Synanceia verrucosa* (see Grobecker, 1983), *Scorpaenopsis gibbosa* (see Harmelin-Vivien and Bouchon, 1976) and *Pterois volitans* (see Morris and Atkins, 2009) tend to be piscivores, there have been instances where smaller species such as *Iracundus signifer* (see Shallenberger and Madden, 1972) and *Dendrochirus brachypterus* (see Fishelson, 1997) also appeared to feed primarily on fish. The majority of smaller species such as *Scorpaena maderensis* (see Mesa et al., 2007), *Scorpaenodes guamensis* (see Harmelin-Vivien and Bouchon, 1976) and *Maxilicosta scarbriceps* (see Platell and Potter, 2001) are zoobenthivores (Love et al., 1990a; Love et al., 1990b). Although both zoobenthivorous and piscivorous scorpaenoids were found at CPB, the small size of *T. uranoscopus* compared to the other species of piscivorous scorpaenoids makes it unique as the smallest scorpaenoid piscivore recorded so far.

While *T. uranoscopus* was not the only major piscivore inhabiting CPB, it appeared to feed primarily on the shadow goby, *Y. nebulosus* (even with other abundant goby species such as *Acentrogobius caninus* available). This goby has been found to be poisonous to humans containing high concentrations of tetradotoxin (TTX) (Lin et al., 2000). While fishes of this genus tend to be abundant in this soft sediment habitat (Kwik et al., 2010), their diminutive size would suggest that they are susceptible to piscivory. However, predation pressure on these species might also be presumed to be low, as found in other fish that also contain TTX (e.g. pufferfish) (Allen and Randall, 1977). As such, it would appear that *T. uranoscopus* has developed a specialised dietary niche for this abundant prey resource that is not utilised by other piscivores (i.e. *C. nematophthalmus* was found to feed primarily on non-poisonous sillaginids) in this habitat.

Similarly, though diets of *Paracentropogon longispinis* were varied (consisting of up to nine diet types); amphipods were the major diet in this zoobenthivorous scorpaenoid regardless of size of *P. longispinis.* Although amphipods have always played an important role in the initial juvenile diets of some scorpaenoids (Love et al., 1990a; Mesa et al., 2007) as well as other fish species (Brickle et al., 2003; Labropoulou et al., 1997; Schlacher and Wooldridge, 1996), amphipod specialisation in diets of adult sized fish is not common and has only been observed in the similarly small-sized Magellan plunderfish, *Harpagifer bispinis* (Duarte and Moreno, 1981). The high selectivity for amphipods (even when other prey species are available) by *P. longispinis* is likely due to their high foraging activity (pers. obs.) and the abundance of amphipods in these habitats (Virnstein et al., 1983). Even though competition for amphipods with other similar sympatric species is likely to occur for *P. longispinis*, it is likely that the high density and abundance of epibenthic prey available at CPB will reduce both inter and intra specific competition.

Furthermore, while it is possible that other less morphologically and behaviourally similar benthic fish species might also compete for similar resources, the abundance of benthic invertebrates (especially amphipods) is unlikely to cause major resource overlaps for *P. longispinis*. In comparison, the scenario is different for *T. uranoscopus* which appears to be adapted to feeding on a poisonous fish that is unlikely to be eaten by other piscivores that may be present at CPB. It was also interesting to note that the shape of the glosshyals were similar within both the piscivores (rounded) and zoobenthivore (sharp) pairs.

Scorpaenoids as predators in shallow habitats at CPB

A common assumption is that shallow water habitats act as nurseries for juvenile fishes of many species and that these areas limit access to prey due to size constraints of larger predators (with exception of avian predators) (Blaber et al., 1995; Hajisamae and Chou, 2003). However, some studies have recently refuted this idea and claim that shallow water habitats may not necessarily be safer but it is the high abundance of juveniles in these areas that dampen the predator effects on juvenile fish populations (Baker and Sheaves, 2005; Sheaves, 2001). In addition, most predators are limited in their access to this area but some piscivores (e.g., flatheads) can access these areas based on their dorso-ventrally compressed bodies and burrowing behaviour, and in some studies have been found to be major predators in such shallow habitats (Baker and Sheaves, 2006). Similarly, *T. uranoscopus* also displays similar morphological and behavioural traits when compared to *C. nematophthalmus*, and is found to be as abundant as *C.*

nematophthalmus in the shallow waters of CPB but has never been considered a major predator in shallow water habitats.

Results from this study indicate that while *P. longispinis* is primarily an amphipod eater, *T. uranoscopus* appears to be the primary piscivore found in the shallow habitats of CPB. Although several other species of zoobenthivores and one other species of piscivore can be found at CPB, studies in this area indicate that both *T. uranoscopus* and *P. longispinis* are found ranging from juvenile to adult sizes (Chapter 2) and are likely to be permanent residents of this habitat (supported by size of sexual maturity and reproduction in Chapter 5), compared to almost all the other benthic fish species which are only transient species that inhabit these areas from juvenile to sub-adult sizes. Such permanent residency (and longer time spent in these habitats) would likely mean that these small scorpaenoids might have a greater predatory effect on the prey populations in these shallow areas (or at least at CPB) as compared to the transient species. It is also possible that the roles of scorpaenoids has been neglected due to their cryptic behaviour and are more likely to be overlooked when compared against other more active and obvious predators in the marine system.

Ontogenetic shifts of scorpaenoids at CPB

All fish species undergo ontogenetic dietary shifts, and many teleost fishes experience several of them (Galis and de Jong, 1988; Wainwright and Richard, 1995). These shifts are usually explained by developmental changes in morphological traits that limit the size of potential prey (Mummert and Drenner, 1986). This type of shift is especially common in carnivores, which may shift to larger- or harder-bodied prey as they grow. As these morphological changes are linked developmentally through time, then both growth rates and longevity must play a factor to when and how many ontogenetic shifts can occur for individual species (Arendt and Wilson, 1997).

Dietary changes in *P. longispinis* were similar to findings on the temperate Mediterranean scorpaenoid *S. maderensis*, where dietary types increased from primarily smaller prey such as amphipods in smaller individuals to include larger benthic fauna (e.g., polychaetes) in larger individuals (Mesa et al., 2007). In comparison, *T. uranoscopus* preyed on fish throughout all the size classes above 31 mm, while specimens less than 31 mm only fed on amphipods showing a distinct dietary shift. However, size of prey fish consumed increased in the guts of larger individuals of *T. uranoscopus* which can be attributed to larger gape size found in larger specimens. Zooplankton (e.g. copepods) are assumed to be the initial diet for many juvenile fish during their planktonic and pre-settlement stages (Moreno and Castro, 1995). The absence of a clear dietary shift in *P. longispinis* suggests that this species follows a strategy for maximum growth and reproduction (i.e. isometric growth) during its shorter lifespan (Chapter 4), whereas the longer lived and allometric growth found in *T. uranoscopus* follows a different strategy where dietary shifts occur from a lower (amphipods) to a higher (fish) energy source. Prey capture techniques and behaviour also support these two strategies with *P. longispinis* being a constantly moving, active forager requiring a constant low energy source, whereas *T. uranoscopus* is a sedentary ambush predator (supported by the high tail ratio observed) frequently capturing high energy prey. Assuming that both these common scorpaenoids display zooplanktivory at a smaller size range, then the absence of zooplankton in the diets of either *P. longispinis* or *T. uranoscopus* indicates that the size class that might exhibit zooplanktivory are either still in the plankton or found in other habitats before settling over the soft sediment areas of CPB. Diet types between the common scorpaenoid species appeared similar only at the juvenile stages (i.e. but only for very small *T. uranoscopus* and for a very short period), supporting the notion that the dietary overlap between *P. longispinis* and *T. uranoscopus* gets progressively lower as juveniles develop into adults at CPB.

There is a general paucity of ecological studies on tropical scorpaenoids. This includes studies on the trophic ecology of scorpaenoids and their roles in the shallow marine habitats. If we consider that these fishes are an abundant and specious group that can be found not only in shallow tropical waters in Singapore (Chapter 2) as well as in many other countries, then these fish may have a greater impact on the trophic community (to both zoobenthic and fish prey) in shallow waters than ever suspected (especially with both the broad range and specialised diets observed in scorpaenoids so far). Additionally, the relatively high amount of dietary types consumed by these small scorpaenoids suggests that nutrient resource may not be as limited (i.e. abundance and/or specialised prey items) in estuaries that are known to be highly productive habitats. This would likely have an impact on resource allocation towards life history strategies in both of these fish that inhabit shallow estuarine habitats throughout their lifetime, and could affect successful survivorship or adaptations in this environmentally variable habitat.

Chapter 4. Life histories of common coastal scorpaenoids in Singapore - relationships with size

4.1 Introduction

Body size in animals has been linked to a host of community and population traits such as species richness, geographic distribution, population size and density (Blackburn and Gaston, 1994; Blackburn et al., 1999; Hildrew et al., 2007; Palumbi et al., 2009; Pauly, 1998; Schaffer and Elson, 1975; Solan et al., 2004), trophic interactions (Hildrew et al., 2007), vulnerability and extinction risk (Olden et al., 2007; Reynolds et al., 2005). The size of an organism is also believed to exert a considerable influence on other life history characteristics (Roff, 1992; Stearns, 1992). Body size can exert major constraints on energy assimilation and metabolic rates, resulting in limited growth, reproduction and survival (Calder, 1985; Reiss, 1989; Rochet, 2000). This may be further exacerbated by higher temperatures (Cailliet et al., 2001), which can be extreme in tropical shallow water environments. Small (< 120 mm TL) fish typically exhibit 1) steep continuous growth throughout their lives, 2) attain sexual maturity earlier, and 3) have shorter life-spans (Depczynski and Bellwood, 2006). Such short life-expectancies in small fish are thought to result from high predation rates (Munday and Jones, 1998), contributing to high instantaneous mortality rates and short generation times. These predictions arise primarily from two major theories, that of *r* and *K* selection (MacArthur and Wilson, 1967), and optimal life histories (Gadgil and Bossert, 1970). In both, the underlying theory is that natural selection operates on life history characteristics to maximise the number of surviving offspring. In terms of population parameters, these should translate to the following: 1) low age at first maturity; 2) high value of *K* from the Von Bertalanffy growth function (VBGF); 3) small L_∞ from the VBGF; 4) high rates of instantaneous mortality (*M*) and 5) low maximum age (Adams, 1980).

There is now a large body of conflicting evidence regarding the generality of these predictions. Research has found negative links between adult size, lifespan and age at maturity in four orders of commercially exploited temperate fish (Rochet, 2000), which is also supported by similar results during a large comparative study of life-history traits in North American fishes (Winnemiller and Rose, 1992). More recently, size and age were also decoupled within and between reef taxa (Choat and Robertson, 2002; Munday and Jones, 1998), though demographic data for small cryptic fish (Depczynski and Bellwood, 2006) demonstrated better accordance with general life history theories. Depczynski and Bellwood (2006) further posit that growth trajectories appeared to be related with species life span, with longer-lived (years) species most appropriately modelled by the VBGF, medium longevities (months) by the broken stick model (see Toms and Lesperance, 2003), while the shortest-lived species (days) may have linear patterns of growth.

Unfortunately, the majority of these studies have focused on either commercially exploited taxa (Rochet, 2000), or reef fish (Choat and Robertson, 2002; Depczynski and Bellwood, 2006; Hernaman and Munday, 2005a; b; Munday and Jones, 1998), with hardly any work on tropical fish inhabiting shallow estuaries. Considering Bergmann's rule, which suggests positive relationships between latitude and body size (Blackburn et al., 1999), and the utilisation of coastal and estuarine habitats by early fish stages (Miller et al., 1985), size distributions of fish in tropical coastal and estuarine habitats should be significantly left-skewed, i.e. dominated by small sized fish. Since extinction risk in small fish have been linked primarily to habitat degradation (Olden et al., 2007), and shallow coastal habitats are thought to be greatest risk for habitat destruction (Harley et al., 2006), it becomes doubly critical to understand the life histories of small-bodied fish in these habitats.

In Singapore, at least two small (*Trachicephalus uranoscopus* and *Paracentropogon longispinis*) and one large (*Synanceia horrida*) species of scorpaenoids are commonly found along coastal habitats (Chapter 2). While all three species are found inhabiting shallow waters (<5 m), only the two smaller species (*T. uranoscopus* and *P. longispinis*) appear to be sympatric (Chapter 3). While both *P. longispinis* and *T. uranoscopus* reach a maximum length of around 70 mm and 80 mm standard length (SL) respectively (Chapter 2), which will potentially make them the smallest scorpaenoids studied. *Synanceia horrida* attains lengths (~25 cm SL) comparable to some temperate scorpaenoids, e.g., *Sebastes dalli*, *Sebastes semicintus* and *Sebastes umbrosus* (Love et al., 1990b). These scorpaenoids (*P. longispinis* and *T. uranoscopus*) are an ideal group to test the relationships between size and other life history characteristics of small tropical fish inhabiting areas other than coral reefs. The addition and comparison of a large tropical scorpaenoid (*S. horrida*) can provide more evidence for any variations in life-history patterns observed in small tropical fish. Specifically this chapter aims to quantify the growth, maturation, longevity and mortality rates of these three species based on field collection data.

Growth trajectories are usually best described using growth/mathematical models, and in light of Depczynski and Bellwood's (2006) suggestion that species life span may in themselves affect growth trajectories, care must be taken in the selection of the appropriate model. Although not without flaws, the Von Bertalanffy growth function (VBGF) is perhaps the most widely used growth model in the literature (Chen et al., 1992). Further advantages to using the VBGF are that the model parameters offer additional information useful for life histories. For example, Charnov (2008) demonstrated that the Bertalanffy K is proportional to reproductive effort, and therefore the Beverton-Holt K/M dimensionless number is representative of lifetime reproductive allocation. Furthermore, mortality, M, at least in fishes, is linked to their size and their value of K (Pauly, 1982). Nonetheless, indeterminate, non-asymptotic growth has been documented in extensively in small fish (Depczynski and Bellwood, 2006; Hernaman and Munday, 2005a), and therefore other growth models will also be examined.

As such, in elucidating the relationships between size and life history patterns in small scorpaenoids, four primary goals are approached in this chapter. These are as follow:

1. Determine the growth patterns of small tropical scorpaenoids and the presence of sex-specific differences in growth rates.
2. Determine the maximum life spans of common tropical scorpaenoids.
3. Determine the age of initial sexual maturity in these scorpaenoids.

4. Determine the mortality rates and mean generational times of these scorpaenoids.

4.2 Material and Methods

Age estimation of scorpaenoids

Otoliths extraction and daily increment interpretation were based on methods described by Secor et al. (1991) and Campana and Neilson (1985). All otoliths were weighed using a Scaltec SBC-22 weighing scale (± 0.00001 g). To ensure that either sagittal otolith could be used during age estimates, weights of both left and right sagitta was recorded (with an accuracy of 0.00001 g) and compared using a *t*-test for paired comparisons for each species of fish as described by Sokal and Rohlf (1969). As no difference was found (Student's *t*-test, *P. longispinis* df = 172, $t = -0.217$, $p = 0.83$; *T. uranoscopus* df = 96, $t = -0.252$, $p = 0.80$; *S. horrida* df = 138, $t = 0.217$, $p = 0.83$) in all three species, the otolith for age examination was randomly selected during extraction, and was replaced by the remaining otolith in the event that one was damaged.

In most temperate fish species, the combination of each opaque and subsequent translucent zone is considered to be an *annulus*, as observed in other scorpaenids (La Mesa et al., 2005; Massutí et al., 2000). However, as *S. horrida*, *T. uranoscopus* and *P. longispinis* are all caught locally in tropical waters, the seasonal annulus were not visible under microscopic examinations and as such, daily growth rings (microincrements) were estimated and counted when otoliths were fully immersed in 70% ethanol and read under reflected light using a stereomicroscope at 25–40X magnification. Under reflected light, the nucleus and the opaque zones appeared as light rings and the translucent or hyaline zones as dark rings. Following other studies on scorpaenids (La Mesa et al., 2005; Massutí et al., 2000), we confirmed that rings were laid down daily by a 10 day validation using Oxytetracylcine marker in all three species (t-tests showed no significant difference in observed counts versus expected: *P. longispinis*, n = 5, t = 0.78, P>0.05; *T. uranoscopus*, n = 5, t = 1.63, P>0.05; *S. horrida*, n = 5, t = 1.5, P>0.05), providing the true age (in days) of aged specimens (Secor et al., 1991). These otoliths were hand ground evenly on both sides of the otolith using grinding paper ranging from 100, 200, 400, 800, 1200 and 2000 grit until the sagittal plane was reached. Digital pictures of the ground otoliths were then taken using the BK Plus Lab System (Visionary digital^{TM}) connected to a Canon 1DS Mark3, software used for rendering digital images included Lightroom 2, Helicon Focus and Adobe Photoshop CS4. As a rule, each otolith was read three times by the investigator, and reading for a given otolith was accepted only when two readings at least agreed. For this study, the maximum life span was defined as the age of the oldest fish collected.

Growth rates

Size-at-age plots were generated for each species where the age estimates (days) for each individual was plotted against its standard length (SL, mm). Growth trajectories from size-at-age plots were fitted against two growth models: the Von Bertalanffy growth function (VBGF) and a linear curve. The latter was selected based on evidence from literature that suggests indeterminate growth/growth in small fish (Depczynski and Bellwood, 2006; Hernaman and Munday, 2005a) was a better fit. The broken-stick model was not employed for the growth rates because no sharp breaks in plotted data were observed.

The Von Bertalanffy growth function is described by,

$$L_t = L_\infty\left(1 - e^{\left(-K(t-t_0)\right)}\right)$$

where L_t = length at age t, L_∞ = theoretical maximum length (asymptotic), K = growth coefficient, proportional to rate at which L_∞ is reached, t_0 = theoretical age at $L = 0$ (often negative, or zero). This was fitted to the age-length data using the program FISHPARM of the statistical package FSAS (Saila et al., 1988), which implements the Marquardt algorithm for non-linear least squares parameter estimation. The Von Bertalanffy growth parameters ($L\infty$, K and t_0) were calculated using the Ford-Watford plots for each species, and was employed to compare growth between all three species. To reduce the effect of noise estimators across daily growth, bin arrays for age were constrained to optimise smoothness of growth curves (Magnifico, 2007). For the linear curve, regression analyses were conducted in PASW ver. 18.0. Goodness of fit of each model was evaluated on the bases of residual sums of squares (RSS) and on the coefficient of determination (r^2). To test whether linear models were effective, the F-test for Lack-of-Fit was performed using PASW v18.

Length-weight relationships

To enable sex-specific and interspecific comparisons of growth properties, the relationship between fish length and fish weight was estimated by the allometric formula,

$$W = aL^b$$

where W is total body weight (g), L the standard length (mm), a and b are the coefficients of the functional regression between W and L (Ricker, 1973). By $\log_{10}$ transforming the weight data, the equation was log linearised to determine the regression parameters using PASW ver. 18.0. Where applicable, an ANCOVA (Zar, 1999) was used in order to confirm whether b values obtained in the linear regressions were significantly different from the isometric value (b=3), this comparison allowed for the determination of (statistical significance) the b-values, and their inclusion in the isometric range (b=3) or allometric ranges (negative allometric: b<3 or positive allometric: b>3). ANCOVAs were also used to compare linear regressions to determine if growth curves were different between the three species.

Comparison of size at maturity with life-history patterns

To determine whether the size at maturity of the three scorpaenoids was consistent with general life history theory, the timing of maturation was compared with the pattern reported by Charnov (1993), i.e. average size at maturity occurs at 65% of mean asymptotic size. For each species, the 'mean asymptotic size' was taken as the mean size of the largest 10% of individuals sampled (hereafter termed L_{10}). To examine the timing of maturation relative to the mean asymptotic size, the mean size at maturity was divided by the value of L_{10} and expressed as a percentage.

Lifespan

Maximum lifespan was defined as the oldest individual identified (in days) in each of the three species based on daily otolith counts as described by Secor et al. (1991).

Age at maturation

For all species, size and age at initial maturity were defined as the initial size or age at which developmental stage C (yolk vesicle) (Table 5.1) occurred in the species.

Mortality and mean generation time

Two indirect methods of estimating mortality, M was used because the key assumptions associated with the age- and length based catch curve methods, that all age and size groups had a similar abundance at recruitment and have been subjected to the same total mortality rate after recruitment (King, 1995), were not tested. Hoenig's equation (1983) was the first method used to provide estimates of instantaneous mortality rate (Z); this is based on observed maximum age (Hoenig, 1983). Hoenig's (1983) equation is:

$$\ln Z = 1.44 - 1.01 \ln t_{\max}$$

where $t_{\max}$ is the maximum observed age (in months). For each of the three study species, $t_{\max}$ was defined as the age of the oldest individual sampled, estimated from counts of otolith growth increments recorded during this study.

In addition, a new empirically derived method based on Hoenig's original equation was employed (Hewitt and Hoenig, 2005), which assumes that approximately 1.5% of the population is still alive at maximum age. Hewitt and Hoenig's equation is:

$$Z = 4.22/t_{max}$$

Where $t_{\max}$ is the age of the oldest individual sampled (in months).

Both methods were used as comparisons and confirmation for values of M. An estimate of the daily and yearly survival rate (S) was calculated by $S = e^{-Z}$ (Ricker, 1975), and both yearly mortality (M) was calculated from these survivorship values.

In addition, mean generational turnover (GT) was estimated using the formula,

$$(GT) = AM + [(T_{max} - AM)/2],$$

where AM = age at female maturation and T_{max} = maximum age. This gives a conservative averaged estimate for the time taken for a new generation to be generated, assuming that a stable population exists (Gaillard et al., 2005).

4.3 Results

A total of 305 specimens of *Paracentropogon longispinis* were sampled, but the gender for 25 specimens was not determinable due to their small size. Of the remaining 280 specimens, 36.8% were males and the rest females (177 specimens) (Figure 4.1). Age of sexual maturity occurred earlier in *P. longispinis* at around 30 mm SL (approximately 145 days)(Figure 4.1) and females of *P. longispinis* attained larger sizes than males, ranging from 20.5 to 67.4 mm and from 19.3 to 62.9 mm SL, respectively (Figure 4.1), the oldest specimen recorded was a female measuring 62.7 mm SL at about 14 months. Of the 105 specimens of *Trachicephalus uranoscopus* dissected, the gender for 13 was not determinable and only 13 males were found. Age of sexual maturity occurred at around 53 mm SL (approximately 320 days) for *T. uranoscopus*, the oldest specimen found was a female measuring 75.8 mm SL at about 22 months (Figure 4.2). Females ranged from 28.1 to 82.2 mm SL in *T. uranoscopus*, with males ranging between measuring 33 – 58.8 mm (Figure 4.2). There did not appear to be any sexual dimorphism in *P. longispinis* (Figure 4.1) while there were not enough male specimens to determine sexual dimorphism in *T. uranoscopus* (Figure 4.2).

Of the 82 specimens dissected, gender for eight *Synanceia horrida* was not confirmed. Of the remaining 74 specimens, the majority were females (79.7 %) with only 15 males. Specimens smaller than 119 mm SL were always male, with no males larger than 151 mm SL (Figure 4.3). As with the other two common species, females of *S. horrida* attained larger sizes than males, ranging from 119 to 247 mm SL and from 91 to 151 mm SL, respectively (Figure 4.3). At present it appears that *S. horrida* might display some sexual dimorphism, though few larger sized males were caught during the sampling period, which may be attributed to a lack of a larger sample size (Figure 4.3). However, the smallest size for *S. horrida* was a male measuring 48.3 mm SL (105 days) and age of first sexual maturity in females was 170 mm SL (approximately 1100 days). The oldest specimen found was a female measuring 211 mm SL at around five and a half years (Figure 4.3).

Based on the values at initial maturity, it was found that females of the three scorpaenoids matured between 46.7 to 77.8% asymptotic size. However, all three scorpaenoid species matured at sizes inconsistent with general life-history patterns for fishes (65% of mean asymptotic size; Charnov 1993). While *T. uranoscopus* (69%) and *S. horrida* (78%) matured much later with regards to asymptotic size, *P. longispinis* matured much earlier (47%)(Table 4-1). There appeared to be almost complete overlap in age-size structure between genders for *P. longispinis*. While it also appeared that *T. uranoscopus* and *S. horrida* had overlaps between genders, the low sample size of males made this difficult to confirm presently. As such, growth estimations in all three species were performed across pooled data regardless of gender.

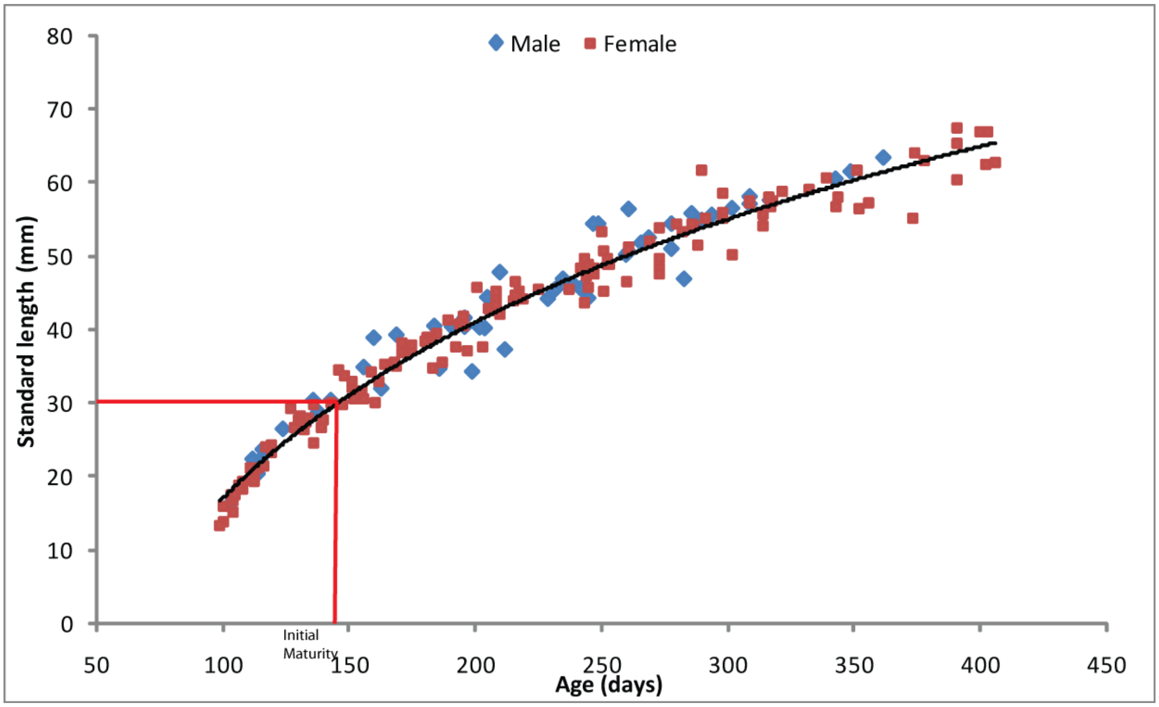

Figure 4.1 Age and size-based gender comparisons in *Paracentropogon longispinis* (n=280).

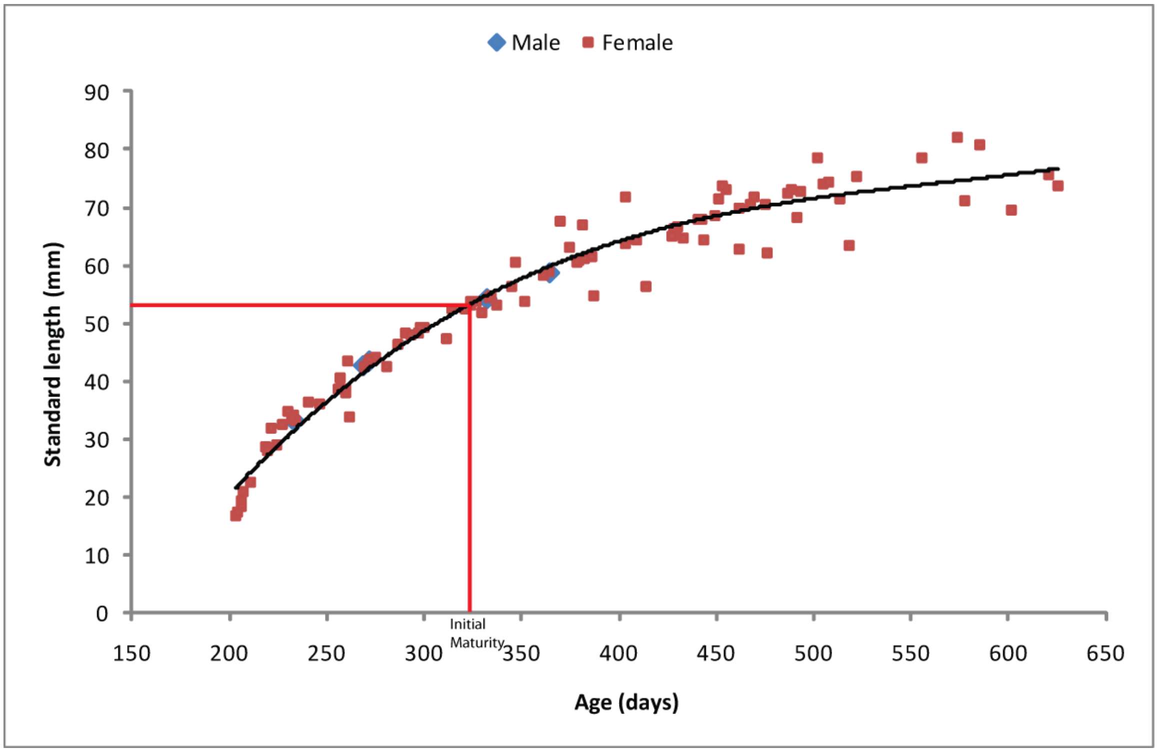

Figure 4.2 Age and size-based gender comparisons in *Trachicephalus uranoscopus* (n=92).

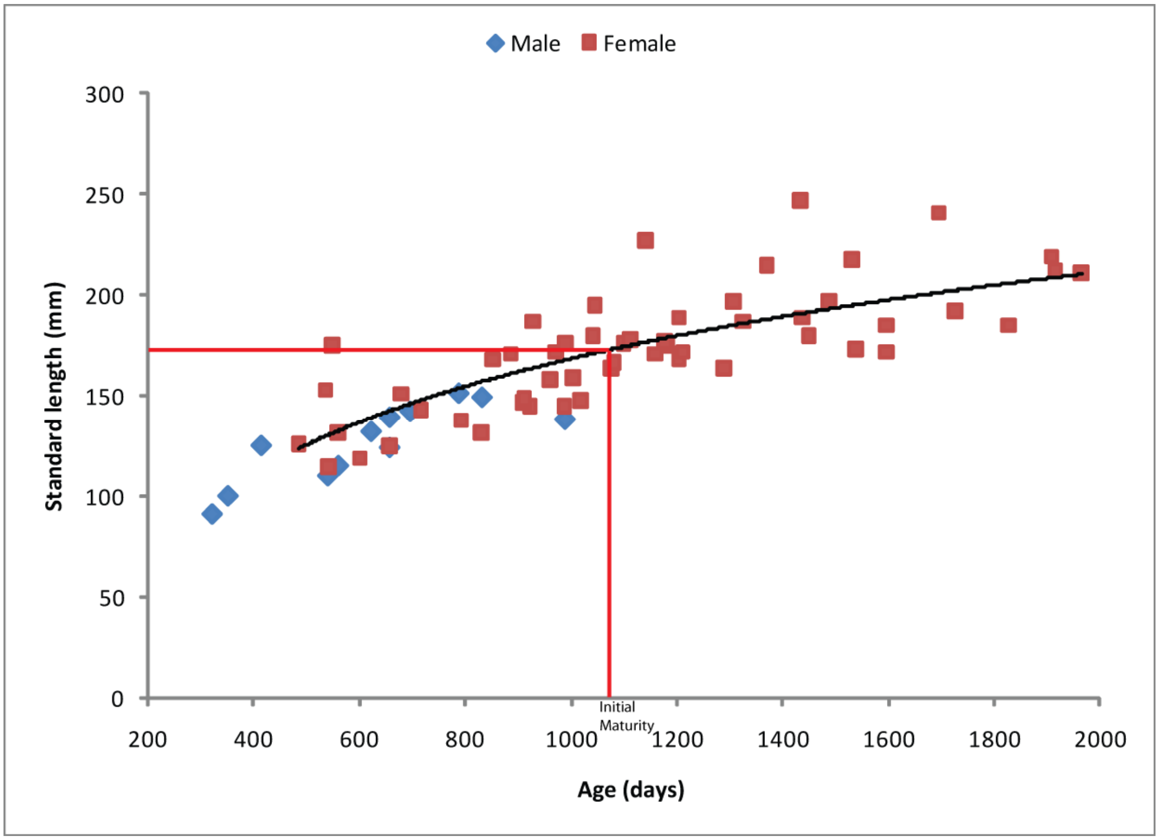

Figure 4.3 Age and size-based gender comparisons in *Synanceia horrida* (n=74).

Table 4-1 Relative size at maturity of females, defined as the percentage of the mean asymptotic size at which the mean size at maturity occurred, and calculated using: mean size at maturity/mean asymptotic size × 100. For fishes, mean size at maturity generally occurs at 65% of mean asymptotic size (Charnov, 1993). Mean asymptotic size (L_{10}) taken as the mean size of the largest 10% of individuals sampled for each species. Also provided is the maximum size attained for each species from this study and as recorded from the literature. SL = standard length.

Species	**Relative size at maturity (% of L_{10})**	**L_{10} (SL, mm)**	**Maximum size (SL, mm)**		
			This study	Recorded	Source
P. longispinis	46.7	64.3	67.4	80	Poss, 1999
T. uranoscopus	69.1	76.7	82.2	80	Poss ,1999
S. horrida	77.8	218.4	247	300	Randall et al, 1990

A total of 280 *P. longispinis*, 92 *T. uranoscopus* and 74 *S. horrida* (pooled across gender) were aged based on daily incremental ring counts. While the smaller scorpaenoids appeared relatively short-lived, the larger species lived much longer than both the smaller species (~four times more). Age estimates ranged from 0-15 months in *P. longispinis*, 0-22 months in *T. uranoscopus* and 0-5.5 years in *S. horrida*. Standard lengths of *P. longispinis* ranged from 13.4 to 67.4 mm (mean 42.1 mm), *T. uranoscopus* ranged from 16.8 to 82.2 mm (mean 54.4 mm), while *S. horrida* ranged from 48.3 to 247 mm (mean 160.2 mm) (Figure 4.4, 4.5 and 4.6).

F-tests for Lack-of-Fit indicated that linear models were not acceptable for explaining age-growth relationships in both *T. uranoscopus* ($F_{1, 91}$=7.67, P>0.05) and *S. horrida* ($F_{1, 73}$ =6.49, P>0.05), but the linear model was acceptable for *P. longispinis* ($F_{1, 279}$ = 3.37, P<0.05). Overall, growth in all three species was still best described by the Von Bertalanffy growth function (Figure 4.4, 4.5 and 4.6).

Comparisons between the growth curve of the three species indicate that both the smaller species of *T. uranoscopus* (*K* = 0.16) and *P. longispinis* (*K* = 0.17) had similar growth coefficients requiring almost double the time to reach maximum size as compared to faster growth rates in the larger *S. horrida* (*K* = 0.36) (Table 4-2). As expected asymptotic lengths were highest in *S. horrida*, followed by *P. longispinis* then *T. uranoscopus* (Table 4-2). Based on the length-age data, it took approximately 11-15 months for *P. longispinis* to reach maximum size, compared to 16-20 months for *T. uranoscopus* and four to five years in *S. horrida*. As such, it appeared that all three scorpaenoids invested a large proportion of their lifespan in somatic growth (though more for *T. uranoscopus* and *P. longispinis*), with growth occurring over much of their size range, with relatively little or no time spent at asymptotic size.

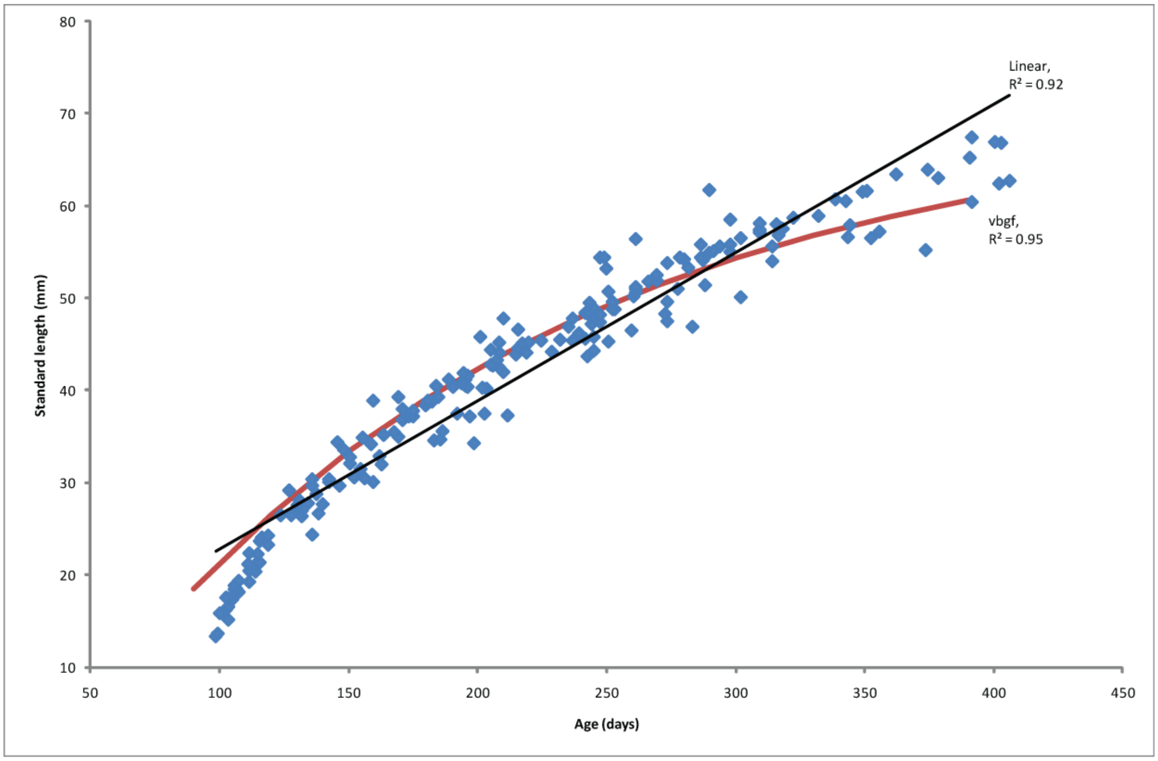

Figure 4.4 Von Bertalanffy growth curve in the long-spinned scorpionfish, *Paracentropogon longispinis* (n = 280).

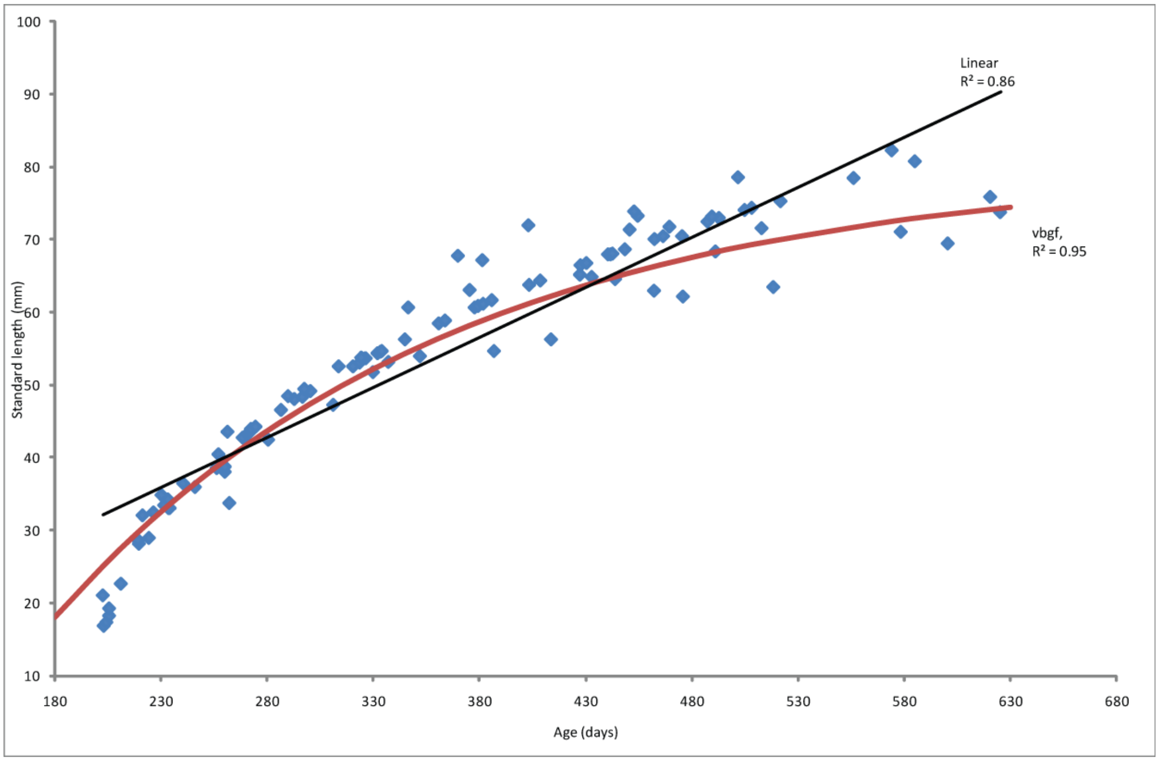

Figure 4.5 Von Bertalanffy growth curves in the stargazer waspfish, *Trachicephalus uranoscopus* (n = 92).

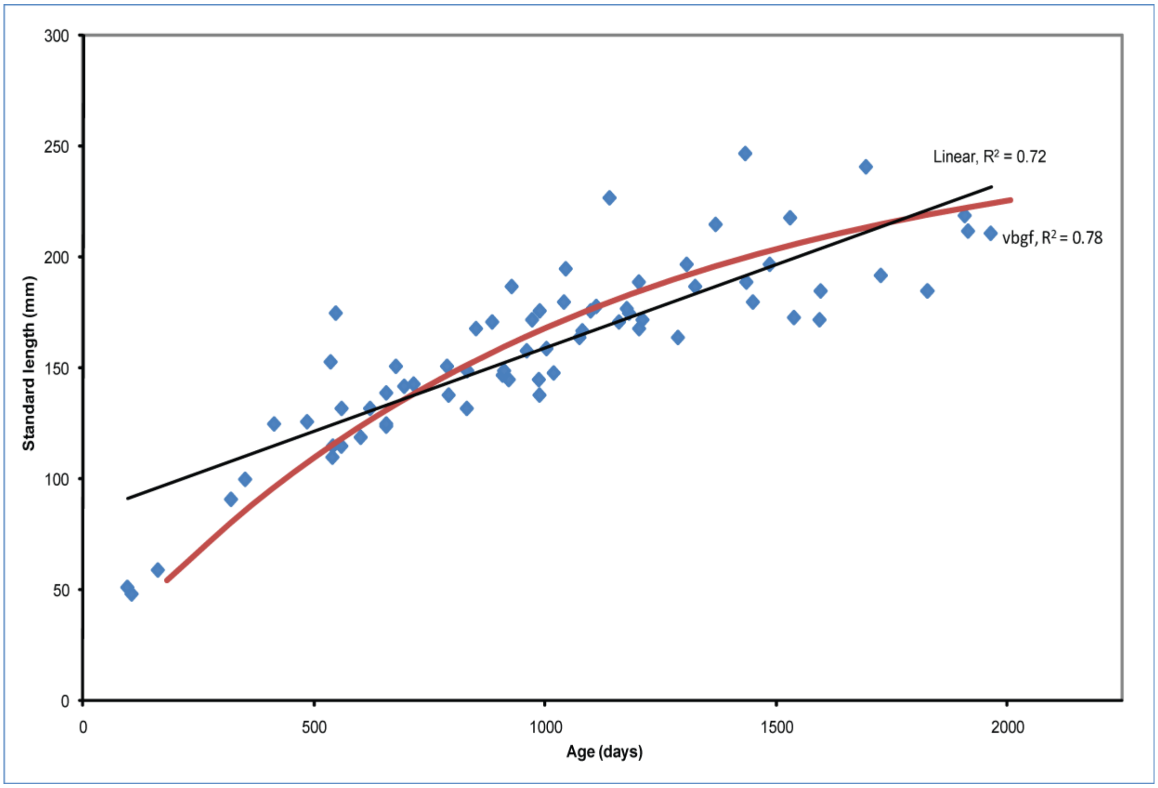

Figure 4.6 Von Bertalanffy growth curves in the estuarine stonefish, *Synanceia horrida* (n = 74).

Table 4-2 Growth parameters of the three common scorpaenoid species based on Ford-Walford plots where *a* and *b* = growth constants, used for calculating the Von Bertalanffy growth equation where *LINF* = theoretical maximum standard length in mm, *K* = growth curve and T_0 = theoretical age at length 0.

	Growth parameters				
Species	*a*	*b*	*LINF*	*K*	T_0
P. longispinis	11.19	0.84	70	0.17	2.39
T. uranoscopus	12.38	0.85	80	0.16	5.37
S. horrida	62.07	0.69	240	0.36	-0.58

The sample size ranged from 280 for *P. longispinis*, 92 for *T. uranoscopus* and 74 for *S. horrida*. All relationships were significant ($P<0.05$) with all r^2 values higher than 0.85. Length–weight relationships displayed predictable values, with *b* ranging from 3.64 to 4.89 (Table 4-3). For all species and genders, the relationship between total length and weight fit the relationship $W = aL^b$, where *W* = weight (g), *L* = total length (cm), and *a* and *b* are constants, with values determined by using $\log_{10}$ transformations and by fitting the values to a straight line by least squares. The length-weight relationships are presented for the three common scorpaenoid species found locally (Table 4-4). Females tended to be slightly larger and heavier than males in *P. longispinis* (Figure 4.7) and this difference in size was much more apparent in the two synanceids, *T. uranoscopus* (Figure 4.8) and *S. horrida* (Figure 4.9), but this could be due to the limited numbers of males collected in the present study. Sex ratios between each species varied, while *P. longispinis* was found at ratios of 1:1.72 (♂:♀), both *T. uranoscopus* and *S. horrida* were found to be dominated by females with ratios of 1:6.08 and 1:3.93 respectively. Such sex ratios coupled with varied length-weight relationships suggest possible hermaphroditism in *T. uranoscopus* and *S. horrida* but this seems unlikely as no gonads containing both male and female reproductive structures were ever identified in any specimen sampled (See Chapter 5).

If assuming that there is no difference between genders in the three species, then pair-wise comparisons based on ANCOVAs between each species (with data pooled across genders) indicated that all three had different growth rates as there were significant differences in length weight regressions between *P. longispinis* and *T. uranoscopus* ($F_{1,406}$ = 10.63, $P<0.05$), *P. longispinis* and *S. horrida* ($F_{1,372}$ = 140.83, $P<0.05$) and *T. uranoscopus* and *S. horrida* ($F_{1,171}$ = 106.49, $P<0.05$). The length-weight relationships (pooled across genders) also showed that positive allometric growth occurred for both *T. uranoscopus* and *S. horrida* whereas isometric growth occurred for *P. longispinis*. ANCOVAs comparing values of *b* against the hypothetical values of 3 (isometric) confirmed there were significant differences in regression slope values for *T. uranoscopus* and *S. horrida* but no significant differences for *P. longispinis* (Table 4-4).

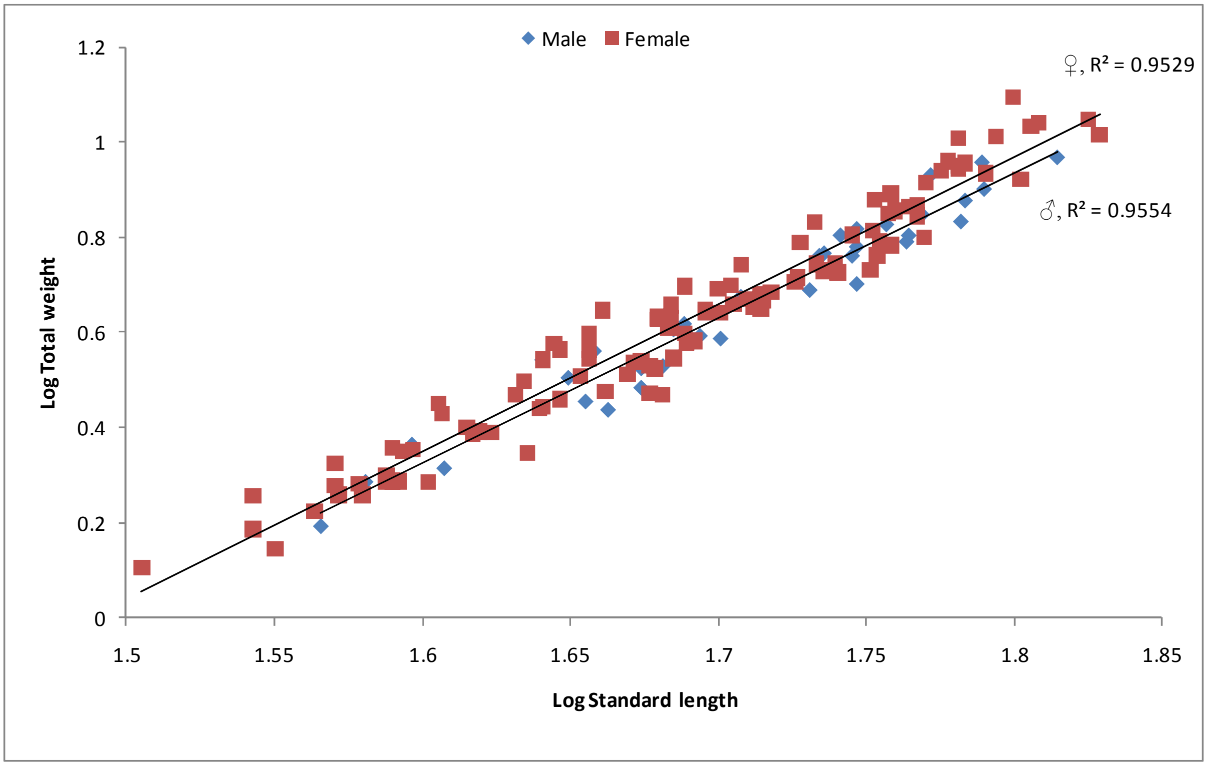

Figure 4.7 Linearised length-weight relationship in different genders of *Paracentropogon longispinis* caught from Changi Point Beach (n = 280).

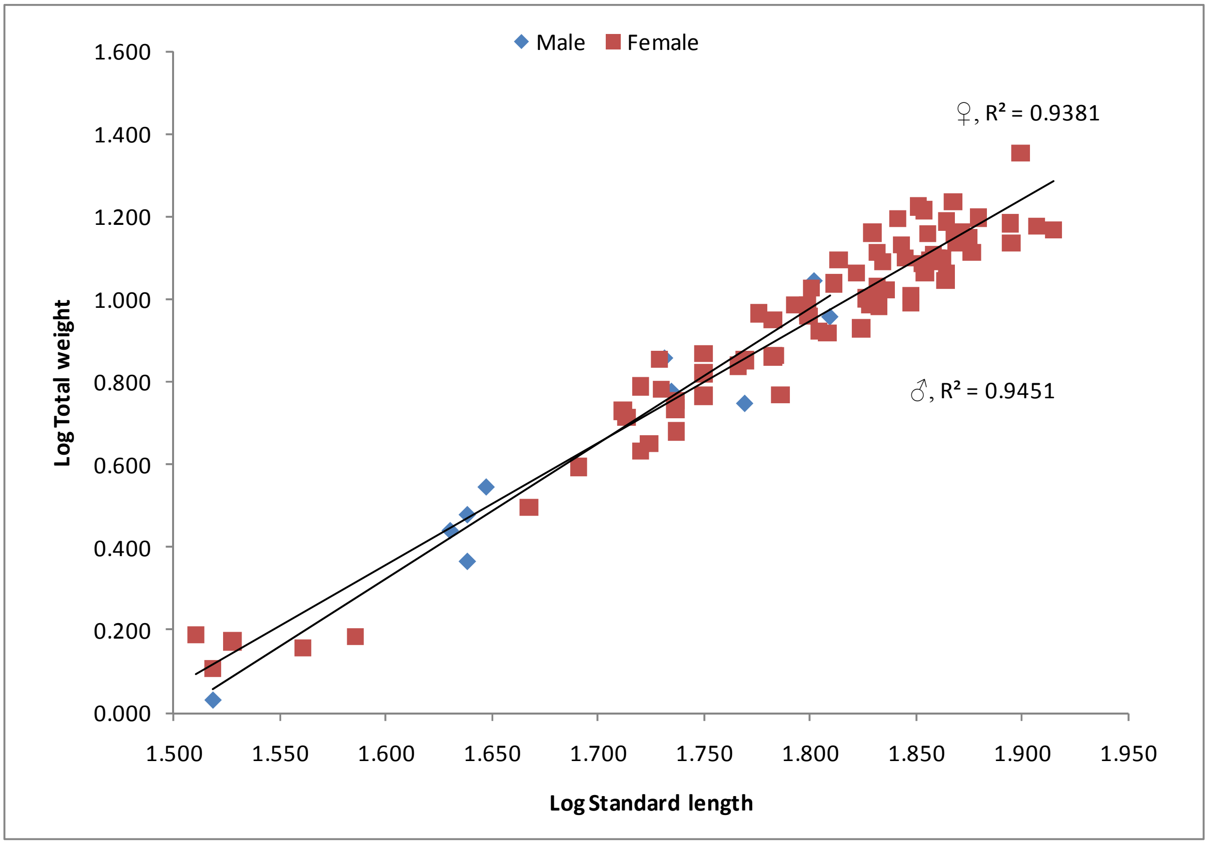

Figure 4.8 Linearised length-weight relationship in different genders of *Trachicephalus uranoscopus* caught from Changi Point Beach (n = 92).

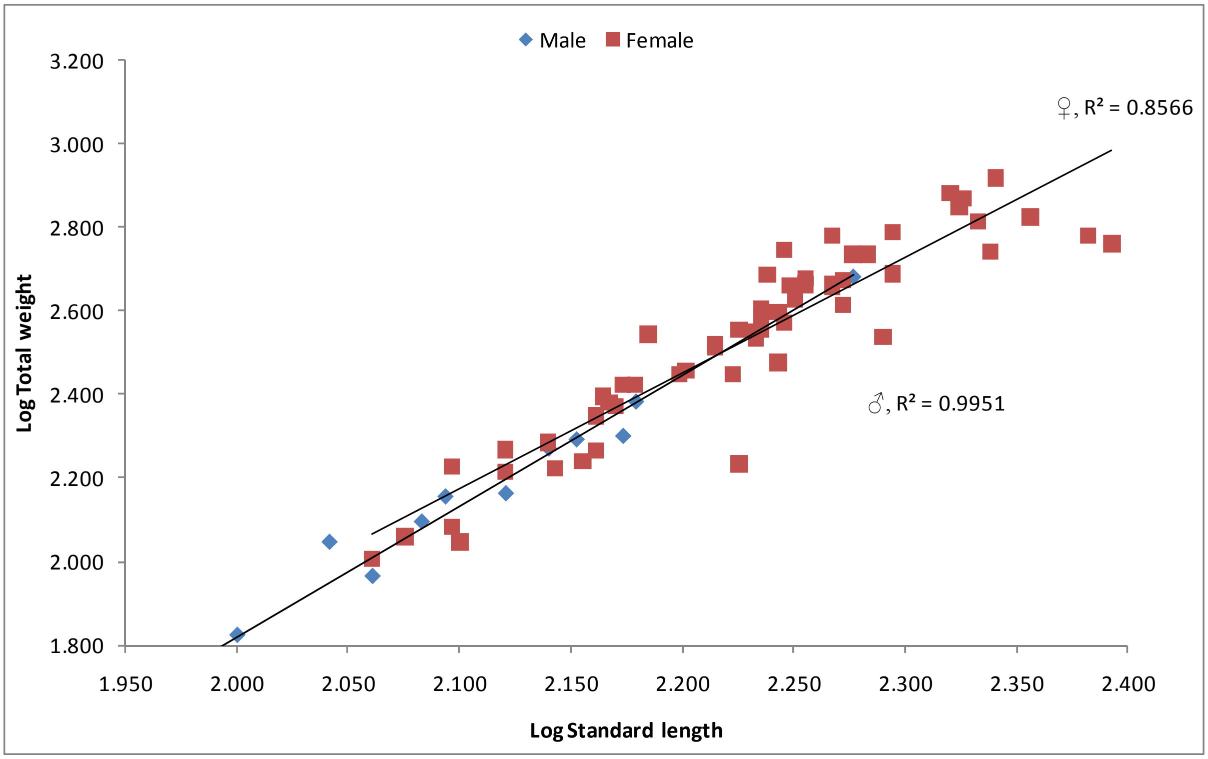

Figure 4.9 Linearised length-weight relationship in different genders of *Synanceia horrida* caught from Changi Point Beach (n = 74).

Table 4-3 Linearised relationships between standard length and total weight in male and females in three scorpaenoid species, where a and b are the coefficients of the functional regression $W = aL^b$. n = number.

Species	**Sex**	**Max SL (mm)**		**% size attained by half maximum life-span**	**LW relationship**		
			n		*a*	*b*	R^2
P. longispinis	♀	67.4	177	61.5	3.1	4.62	0.95
	♂	65.2	103	62.7	3.05	4.57	0.95
T. uranoscopus	♀	82.2	79	59.3	2.94	4.35	0.94
	♂	64.5	13	47.3	3.26	4.89	0.95
S. horrida	♀	247	59	67.8	2.77	3.64	0.86
	♂	189	15	67.4	3.13	4.45	0.99

Table 4-4 Length-weight relationships of common scorpaenoids (regardless of gender) with comparisons of slopes against theoretical values of *b* = 3 for determination of isometric or allometric growth patterns.

		Standard length (mm)	**Total weight (g)**				
Species	n	min-max	min-max	*a*	*b*	R^2	ANCOVA
P. longispinis	280	13.4-67.4	0.06-12.41	4.46	3.002	0.97	P>0.05
T. uranoscopus	92	16.6-82.2	0.16-15.73	4.58	3.039	0.98	P<0.05
S. horrida	74	48.3-247.0	6.61-827.5	4.21	3.021	0.96	P<0.05

Based on the indirect methods of Hoenig (1983) and Hewitt and Hoenig (2007), age-based estimates of *Z* gave high daily adult survivorship values all above 99% regardless of species (Table 4-5). Daily survivorships equated to very low daily mortalities for all three species. However, though mortality was low in general for these three species, daily mortality was found to be higher in the smallest species (~1.05% for *P. longispinis*), followed by *T. uranoscopus* (~ 0.85%) and lowest in the large *S. horrida* (~0.25%) (Table 4-5). There appeared to be little difference in survivorship or mortality between sexes in each species.

Mean generation turnover was relatively high in all three species of scorpaenoids. While the longer-lived *S. horrida* had turnover rates at about 1532 days (with T_{max} of 1965), generation turnover for the shorter-lived *P. longispinis* and *T. uranoscopus* were similarly high at 276 days (T_{max} of 406 days) and 473 days (T_{max} of 625 days) respectively (Table 4-6).

Table 4-5 Estimates of the instantaneous mortality rate, *Z*, and the corresponding daily survivorship, *S* and daily mortality rate *M*% based on indirect methods described by Hoenig (1983) and Hewitt and Hoenig (2007). n = number.

Species	**Sex**	**n**	**Age of oldest individual (days)**	**Instantaneous Mortality, *Z* (daily)**		**Survivorship, *S***		**Mortality, *M* % (daily)**	
				Hoenig	Hewiit & Hoenig	Hoenig,	Hewiit & Hoenig	Hoenig,	Hewiit & Hoenig
P. longispinis	♀	177	406	0.010	0.010	0.990	0.990	0.994	1.034
	♂	103	391	0.010	0.011	0.989	0.990	1.032	1.073
T. uranoscopus	♀	79	625	0.006	0.007	0.994	0.993	0.644	0.673
	♂	13	440	0.009	0.010	0.991	0.990	0.917	0.955
S. horrida	♀	59	1965	0.002	0.002	0.998	0.998	0.203	0.215
	♂	15	1204	0.003	0.004	0.997	0.997	0.333	0.350

Table 4-6 Mean generation turnover (*GT*) in females of *Paracentropogon longispinis*, *Trachicephalus uranoscopus* and *Synanceia horrida*, where *AM* = age at female maturation and T_{max} = maximum age.

Species	**Initial Maturity (days), *AM***	**Max age (days), T_{max}**	**$(T_{max}-AM)/2$**	**Generation turnover, *GT***
P. longispinis	145	406	130.5	275.5
T. uranoscopus	320	625	152.5	472.5
S. horrida	1100	1965	432.5	1532.5

4.4 Discussion

Life history patterns predict that small sized fish should display 1) low age at first maturity; 2) high value of *K* from the Von Bertalanffy growth function (VBGF); 3) small L_∞ from the VBGF; 4) high rates of instantaneous mortality (*M*) and 5) low maximum age (Adams, 1980). Although some of these characteristics were found in the small scorpaenoids *Paracentropogon longispinis* and *Trachicephalus uranoscopus*, two characteristics did not conform. This included a low growth rate (low *K*) and low mortalities (*M*). Conversely, the larger scorpaenoid *Synanceia horrida* had a higher age at first maturity, high *K* values, large L_∞, low rates of mortality and a high maximum age. As such, though it would appear that size does play an important part in affecting life history patterns in scorpaenoids, other factors such as taxonomic similarity could be important considerations for this group of fishes as well as potential reduced predation pressure due to venom or cryptic behaviour.

The findings of this study showed that the lifespan of both *P. longispinis* and *T. uranoscopus* were relatively short (approximately 1.5 years and 2.5 years, respectively) compared to longevities recorded in other temperate deepwater scorpaenoid species (Love et al., 1990b), but were similar to at least one species of shallow temperate scorpaenoid (the small *Scorpaena maderensis* compared to the large *S. horrida*). As such, it appeared that latitudinal variations in age occur in tropical scorpaenoids (in relation to higher latitude species) as previously discovered in some sebastids (Boehlert and Kappenman, 1980). However, among small tropical fish, lifespans were similar between the well-studied coral gobies (Hernaman and Munday, 2005a) and the small tropical scorpaenoids that were investigated during this project. Similar to coral gobies, both *P. longispinis* and *T. uranoscopus* (regardless of gender) attained short maximum lifespans and attained approximately 2⁄3 of their maximum size by half of their expected maximum life spans. Therefore, it appears that their patterns of growth and life-span conform to traditional concepts of life-history theory with regards to size. Growth patterns of the small scorpaenoids also differed from other relatively small but long-lived coral reef fishes, e.g., pomacentrids (Meekan et al., 2001), that were found to attain asymptotic size relatively quickly (2-6 years) and spend more of their lifespan at that size (>70%). However, there occurred similarities with other recently studied coral gobies that were found to invest in somatic growth throughout most of their lifespan and relatively little time at asymptotic size (Hernaman and Munday, 2005a; b).

Both *P. longispinis* and *T. uranoscopus* are presently the smallest adult species (approximately 60 mm and 70 mm SL for *P. longispinis* and *T. uranoscopus*, respectively) of scorpaenoids found in Singapore, and range amongst the smaller species in the Scorpaenoidei globally (Carpenter and Niem, 1999). The relatively short lifespans recorded in these scorpaenoids is plausible for these small sized tropical marine fish found inhabiting shallow waters of less than five meters depth, as several species of small marine gobies (e.g., *Trimma nasa*) have also been found to be short-lived (e.g., approximately 85 days at 18 mm SL) (Winterbottom and Southcott, 2008); with relatively small coral gobies like *Istigobius goldmanni*, *Asterropteryx semipunctatus, Amblygobius bynoensis*, *Amblygobius phalaena* and *Valenciennea muralis* which range between 55-113 mm in maximum length and 11-16 months in age also doing the same

(Hernaman and Munday, 2005a). The relatively larger tropical scorpaenoid *S. horrida* was found to live up to 5.5 years (approximately four times more than *P. longispinis* and *T. uranoscopus*), but this species was also approximately three times the size of the two smaller species (i.e. the largest specimen was found to be around 240 mm SL). Such variation in life span as a result of larger size has also been found in the temperate scorpaenoids such as the sebastids (Echeverria, 1987) and scorpaenids (La Mesa et al., 2010) (Figure 4.10).

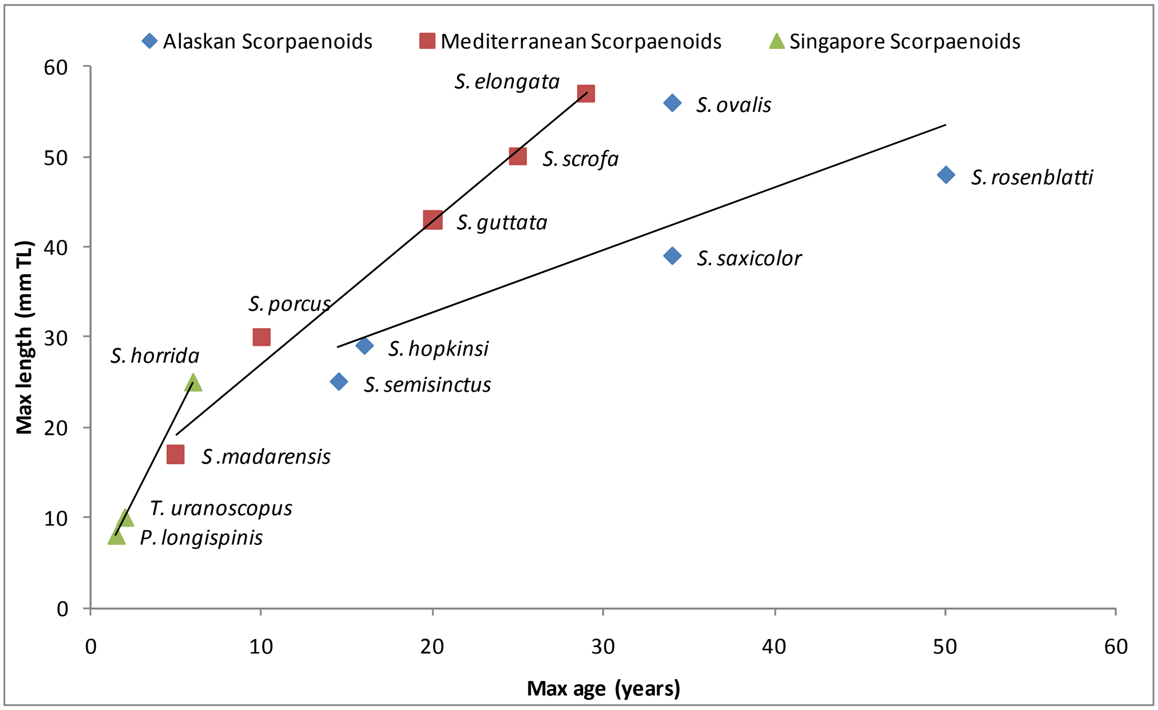

Figure 4.10 Length-age relationships between scorpaenoids found in temperate Alaskan (from Escheveria, 1987 and Love, 1990b), subtropical Mediterranean (from La Mesa et al., 2010) and tropical Singapore (present study).

Growth coefficients based on Von Bertalanffy equation varied between the three common tropical scorpaenoids. In these tropical scorpaenoids, *K,* the rate at which a species reaches maximum length, was low in both the smaller species (*P. longispinis* and

T. uranoscopus), while the larger *S. horrida* had much higher *K* values. Such variations in scorpaenoids inhabiting similar waters were also observed in the temperate sebastids, where *K* values varied between species and sex (Love et al., 1990b). Although most of these sebastids were found to grow more slowly than species of most other taxa, with *K* values ranging between 0.1 and 0.3 (Love et al., 1990b), some such as *Sebastes emphaeus* had growth rates in the higher range found in fishes (0.41), keeping with the widespread notion that small species quickly reach maximum lengths (Love et al., 1990b). Interestingly, this did not appear to be the case for the tropical scorpaenoids, with the opposite pattern of smaller species having slower growth rates compared to the larger species occurring here. This suggests that tropical scorpaenoids have very different life history strategies as compared to the temperate species, which might be attributed to many factors such as food habits and specialisations for feeding, metabolism rates and even the dynamics of muscle growth in each scorpaenoid species.

In addition, while higher L_{inf} values and lower *K* values were found in the Sebastids, studies by La mesa et al. (2005) have found relatively higher *K* values (0.29) in the relatively smaller *Scorpaena maderensis* (average 129 mm TL). Beverton and Holt (1960), comparing a broad range of taxa, discussed a widespread pattern among fish, in which maximum length *(L)* is inversely correlated with *K.* While this appeared true for very small and very large species within the genus *Sebastes,* it did not seem to hold for the majority of temperate rockfishes. It was also found that a low value of L_{inf} and a high value of *K* are usually correlated with a high environmental temperature, while high $\mathrm{L_{inf}}$ and low *K* indicate relatively lower temperature (Pauly, 1983). This however does not appear to be the case for the common tropical scorpaenoids found locally, which have low L_{inf} values and low K values (both *P. longispinis* and *T. uranoscopus*), or higher L_{inf} values and higher K values as in the case with *S. horrida*. Such low K values were similar to the small tropical coral gobies with K values ranging from 0.003 – 0.012 which was much lower than those recorded in either *P. longispinis* or *T. uranoscopus.* This could be attributed to the relatively smaller sizes attained by the coral gobies and potentially that there are more density-dependent interspecific interactions in the coral habitats where the gobies are found (Munday, 2000).

Contrary to other finding by Fisher et al. (2010), the large size of *S. horrida* (similarly sized to other temperate scorpaenoids such as *Sebastes hopkinsi*, *Sebastes jordani* and *Sebastes saxicola*) suggests that not all tropical scorpaenoids conform with current paradigms on maximum size with regards to latitude (the so-called Berman’s rule)(Figure 4.10). Possible explanations for this might again be related to the unique behavioural and development patterns that are displayed by this group of fishes (Wourms, 1991; Yang and Somero, 1993; Zimmermann and Kunzmann, 2001). It also appears that tropical scorpaenoids do not conform to general growth patterns in relation to environmental temperature, suggesting that scorpaenoids are unique group of fish with different life history strategies as compared to other fish families.

Results from this study also found that two species display similar positive allometric growth (*T. uranoscopus* and *S. horrida*), while the smallest and most common species, *P. longispinis*, displayed isometric growth. Such variations in allometry has also been found in the temperate scorpaenoids as well, with the small temperate scorpaenid, *Scorpaena* *porcus*, displaying positive allometric growth between size and weight (with an observed value of *b* = 3.0815 in all individuals) in the Black Sea (Bilgin and Celik, 2009), this was also similar to results reported by Erkoyuncu et al. (1994) (*b* = 3.0800) and Froese and Pauly (2007) (*b* = 3.0179). However, results by La Mesa et al. (2010) on this species along Adriatic Sea found that *S. porcus* displayed isometric growth instead. Such variations in allometric coefficients indicate that other factors may be important in determining the growth rates of this species. One possible important factor might be depth, as has been reported in sebastids (Cailliet et al., 2001) which might play a role in the temperate scorpaenids as well, as sampling depths varied slightly between both La Mesa et al. (2010) study who sampled from 8-75 m while Bilgin and Celik (2009) sampled in shallow waters ranging from 1-30 m depth. Studies in other temperate scorpaenoids have also found that the length-weight relationships in 19 sebastids differed as well, with 11 species showing positive allometric growth, while seven showed negative allometric growth and only one displaying isometric growth (Love et al., 1990b). The one species, *Sebastes semisinctus*, 25 cm TL, which was found to be similarly sized to *S. horrida* was not only one of the negatively allometric species, but also the sebastid species with the shortest lifespan (14.5 years) (Love et al., 1990b). Love et al. (1990) also found that benthic rockfishes were heavier over similar lengths when compared to the transitional or midwater species, with most benthic species thicker and deeper-bodied than midwater ones. This was similar to findings in this study with the more benthic *T. uranoscopus* and *S. horrida* being much more rotund than *P. longispinis*.

Results from this study also indicate that maturing gonads were only found in female *P. longispinis*, *T. uranoscopus* and *S. horrida* at standard lengths above 30 mm, 53 mm and 170 mm respectively. At these sizes, age at initial sexual maturity was approximated to be around five months for *P. longispinis*, 10 months for *T. uranoscopus* and three years for *S. horrida*. This was very different when compared to other scorpaenoids such as the Pacific ocean perch, *S. alutus* which was found to be sexually mature at the age of seven to ten years (Leaman, 1991). However, when viewed from the overall lifespan perspective, female *P. longispinis*, *T. uranoscopus* and *S. horrida* are reproductively active for approximately 47%, 69% and 78% of their lives respectively. With the exception of *P. longispinis*, such proportions were similar when compared to the longer lived temperate Sebastids which were generally found to be sexually active more than 70% of their lifespan (Wourms, 1991). The shorter reproductive periods found in the smallest tropical scorpaenoids suggests that more resources are directed to growth rather than reproduction, and may be a result of increased survivorship during development for such a short lived species (Leaman, 1991). As such, it would appear that scorpaenoids in general do not appear to conform to Charnov's (1983) predictions on mean age at sexual maturity (65%) regardless of whether the scorpaenoids are tropical or temperate species.

With shorter reproductive periods, there is a need to maximize and efficiently use energy between growth and reproduction (Leaman, 1991), which would affect the number and size of eggs produced during an animal's lifespan (Brooks et al., 1997). An important factor would be obtaining sufficient food resources with minimum competition with sympatric species, through either specialization of diet or broadening diet breadth

(Larson, 1991). Results from Chapter 3 have shown that both these scorpaenoid species have different dietary strategies (where *P. longispinis* is an amphipod specialist, while *T. uranoscopus* is a goby specialist). Although spawning during similar months, the different energy requirements appear to be reflected in the slight different reproductive strategies (i.e. size at sexual maturity) found in these scorpaenoid species, with scorpaenoids that consume lower energy food spending a shorter period of time developing gonads and a longer proportion of their lives growing.

So far, the differences in growth rates between the three species appear to be closely associated with lifespan. While the small short-lived isometrically inclined *P. longispinis* appears to allocate much of its resources to growth and sexual maturity in equal proportions, both the small short-lived allometric *T. uranoscopus* and large longer-lived allometric *S. horrida* appear to allocate more resources into growth initially followed by more into reproduction after attaining a certain size. These different strategies are likely to be related not only to longevity but also to the behavioural (prey capture techniques, active/sedentary lifestyles) differences between these species. Short-term observations on these species indicate that while both *T. uranoscopus* and *S. horrida* are sedentary "lie-in-wait" burying predators, *P. longispinis* adopts a more active foraging strategy constantly swimming diurnally and nocturnally (unpublished data). In the two synanceids, such sluggish behaviour could result in low baseline respiration rates which has been observed in other species of scorpaenoids (*Scorpaenopsis* and *Parascorpaena* species) (Zimmermann and Kunzmann, 2001) and could potentially have an effect on growth rates in warmer oxygen poorer waters as mentioned before. This initial faster growth followed by a slower growth with age was also supported in part by results in Chapter 3, which showed that *T. uranoscopus* displayed a shift in diet (low to high energy) at different stages of life history.

Compared to other small tropical fish such as gobies (*Eviota* spp.) which had daily mortalities ranging from 4-7% (Depczynski and Bellwood, 2006). Mortality was surprisingly low for all three scorpaenoid species regardless of size. Although it is generally assumed that smaller sized fish have higher mortalities due to increased predation pressure (Winterbottom and Southcott, 2008), this was not the case for small or large tropical scorpaenoids. One possible explanation for higher survivorship for these fishes could be either their highly toxic venom (Saunders et al., 1963; Schaeffer et al., 1971) or their cryptic behaviour (Ballantine et al., 2001; Grobecker, 1983), or in the case of these three species a combination of both these characteristics as defensive mechanism against predation. Although mortalities of these three species was low, it was surprising that generation turnover times are relatively high for the three scorpaenoids, with turnovers occurring at about 68% (~9 months), 76% (~16 months) and 78% (~51 months) of the maximum lifespan of *P. longispinis*, *T. uranoscopus* and *S. horrida* respectively. It is likely that the number of spawning periods will have an effect on this and will be covered in the following chapter.

In summary, the longevities of tropical scorpaenoids were much lower compared to the lifespan of similar sized temperate scorpaenoids but similar to other small-sized cryptic tropical coral reef gobies. It also appeared that while small scorpaenoid conformed to general life history paradigms with regards to size and age, there were differences in the growth patterns observed for each species. Moreover, strategies for growth in tropical scorpaenoids appeared to vary with relation to increasing size with smaller scorpaenoids with slower growths and shorter longevities (*T. uranoscopus* and *P. longispinis*) whereas growth curves and longevity of the larger *S. horrida* were much higher. Longevities and growth rates have both direct and indirect effects on the many other aspects of life history patterns in a fish species (e.g., ontogenetic diet shifts, reproductive patterns etc.), and the following chapters will reveal how these observed growth patterns affect these three species in greater detail.

Chapter 5. Reproductive biology of common coastal scorpaenoids of Singapore - reproductive output, seasonality and recruitment patterns

5.1 Introduction

The life histories of many organisms are constrained by trade-offs between mortality and reproduction yielding combinations that should maximise reproductive success (Roff, 1992; Stearns, 1992). Adaptations in relation to available energy and parental life expectancy (Pianka, 2000; Roff, 1992; Wootton, 1984), include changes in fecundity and size of eggs produced (Duarte and Alcaraz, 1989); egg dispersal methods (Fugita and Kohda, 1998; Hickford and Schiel, 2003); presence of parental care (Carlisle, 1985); spawning frequency and timing (Takano et al., 1991) and maternal age (Berkeley et al., 2004). A result of these trade-offs is that animals with “faster” life histories (e.g., early maturity, higher growth rates or smaller body size) tend to devote proportionally more of their resources to annual reproductive output than those with “slower” life histories (Gunderson, 1997; Read and Harvey, 1989).

With regard to body size and egg production, early stages (i.e. eggs and larvae) of teleostean fish are subject to great mortality (McGurk, 1986), such that very large investments in reproductive material (either number or size of eggs) are necessary to ensure the persistence of populations (this may be offset by investment into parental care). Fish reproductive effort can be measured as the egg mass (or volume) produced per female, and is therefore the product of fecundity (number of eggs produced per female) and egg size. Fecundity alone may not be related to the probability of survival of the individual eggs because egg mortality is usually scaled to egg size (e.g., McGurk 1986). Therefore, a given reproductive effort allocated to many small, or to few large eggs may yield vastly different recruitment to juveniles (Ware, 1975). While it is generally accepted that fish fecundity and egg size increase with body size (Blueweiss et al., 1978), there are many large fish that spawn small eggs (e.g., *Mola mola* and *Thunnus thynnus*). Under such circumstances, the hypothesis that egg size increases with increasing body size remains controversial (Hislop, 1984), and will be interesting to see if comparison in egg size between small and larger tropical scorpaenoids conform to either possibility.

In relation to egg mass and body mass, condition and tissue-somatic indices (such as the gonado-somatic index (GSI)) are a general measure of the overall condition of the fish or growth status of a specific tissue. Tissue somatic indices are commonly utilised in studies because of the relative ease of determination and the general belief that certain indices can be an excellent predictor of adverse health in fish (Adams and McLean, 1985). In particular, the GSI is a useful tool that is also frequently reported as a general measure of gonad maturation and spawning readiness, and is based on the broad assumption that proportionally larger gonads indicate greater development (West, 1990).

The spawning seasons of marine fishes are characteristically longer at lower latitudes (Munro et al., 1973; Quasim, 1955). A number of authors have given as a reason for long tropical spawning seasons the fact that the lower the latitude, the longer the season when temperature and food conditions favour the survival of juveniles (Harden Jones, 1968;

Quasim, 1955). This explains why long breeding seasons can occur in the tropics, but it does not explain why they do occur. There must be some selective pressure favouring long breeding seasons, otherwise they would presumably not exist. For many temperate species, a longer lifespan is necessary since there is usually often only a short period in any one year suitable for reproduction. The same relationship between life span and spawning frequency does not hold in the tropics; where spawning can simply occur more frequently rather than over a longer life span.

Results from Chapter 4 demonstrate the possibility that tropical scorpaenoids may lean towards the equilibrium category of life history as defined by Winnemiller and Rose (1992), where small fish were found to display characteristics often associated with traditional *K*-strategists adapting to life in resource-limited or density-environments. For fish inhabiting an environment with pronounced seasonal variability, the breeding seasons are invariably confined to a brief and specific period of the year (Bye, 1984). Although seasons are not as pronounced in the tropics; with monsoonal seasons replacing the four seasons that are found in higher and lower latitudes, and little variations in day length from seasonal changes (Johannes, 1978), predictable and restricted spawning periods are also found to occur (Lowe-McConnell, 1979). In addition, records of tropical fish displaying monsoonal breeding seasons (i.e. spawning periods during either the tropical southwestern or northeastern monsoon seasons) are limited with most records involving freshwater fish such as the cyprinids (Ahyaudin and Bat-Kamaruzaman, 1996; Hussain et al., 2003) and bagrids (Khan et al., 1990). Coincidentally, two families of tropical marine fish (siganids and pomacentrids) studied were also found to display monsoonal breeding patterns both locally (Lam, 1974; Low et al., 1997) as well as in Indonesia (Susilo et al., 2009). Although temperature fluctuations may not be as distinct in the tropics, the effects of heavy rainfall can change salinity in estuaries by a substantial degree in Singapore waters (Tham, 1953). As changes in salinity can influence the spawning behaviours in fish (Vlaming, 1971), variations in salinity during monsoon periods may influence spawning periods in the tropical scorpaenoids that inhabit these very shallow estuarine habitats (< 2 m depth) (Kwik et al., 2010).

Variations to environmental conditions through seasonality can also influence the annual timing of recruitment, as the timing of reproduction may also be adapted to match oceanographic conditions that are favourable to the survival of larvae (Cushing, 1987; Johannes, 1978). As pelagic larvae recruiting to demersal habitats often do so in pulses, this can influence the structure of juvenile and adult populations in different coastal habitats (Doherty and Fowler, 1994; Roughgarden et al., 1988). Moreover, regular patterns in recruitment may reflect the timing and strength of earlier spawning events (Carr, 1991; Robertson, 1991), which can be synchronised with lunar, tidal and seasonal cycles (Abesamis and Russ, 2010; Forward, 1998; Robertson, 1992; Rothlisberg et al., 1995). Surprisingly, there is little known about the spawning and recruitment patterns of tropical fishes at lower latitudes in the Indo-Pacific region and the extent to which monsoonal conditions influence these patterns.

Results from Chapter 4 provide interesting insights into the reproductive biology of scorpaenoids inhabiting shallow coastal waters in Singapore that warrant further investigation. Firstly, the sex ratios and size distributions are suggestive of protandrous hermaprhoditism as per criteria set up by Sadovy and Shapiro (1987). Sex allocation theory predicts that sex change is favoured when fertility increases more rapidly with age in one sex than the other (Ghiselin, 1969). Given that stronger relationships between body size and fecundity are more pronounced in females than males (see Avise and Mank 2009) and that predation risk is generally greater in small fish, protandry potentially confers significant advantages. While population parameters have been used to suggest hermaprhoditism, sex ratios are also biased by mating system (Avise and Mank, 2009), and true assessment should be based on examination of gonadal material (Sadovy and Shapiro, 1987).

Secondly, of the three species examined, *Trachicephalus uranoscopus* (maximum 82.2 mm SL) and *Synanceia horrida* (160.2 mm SL) were found to have determinate growth (although neither spent much time at asymptotic size) while the other small species, *Paracentropogon longispinis* (67.4 mm SL) appeared to have indeterminate growth. Relative benefits between determinate and indeterminate growth have been extensively discussed and disputed in resource allocation models (Engen and Sæther, 1994; Kozlowski, 1992; Perrin and Sibly, 1993); basically, organisms with indeterminate growth face a life-history trade-off in resource allocation between reproduction and growth throughout their entire life (Stearns, 1992). Resource allocation theory suggests that indeterminate growth is only optimal if both production and mortality rates increased with body size (Taylor and Gabriel, 1993), and, perhaps perversely, if both production and mortality decrease with size (Perrin and Sibly, 1993; Perrin et al., 1993). Seasonality of resource acquisition and reproduction may also support indeterminate growth in perennial species, so long as growth occurs almost immediately prior to reproduction so that benefits are tangible without loss to mortality (Doebeli and Blarer, 1997).

This chapter therefore examines, through gonad histology, sexual pattern (i.e. hermaphroditism), size-dependent reproductive output (number and quality) and patterns of annual reproduction in *P. longispinis*, *T. uranoscopus* and *S. horrida*. Results will be discussed in relation to life-history strategies. Specific aims are to:

1. Confirm/reject hermaphroditism in *P. longispinis* and *T. uranoscopus*
2. Determine the effects of body size on reproductive effort of these small tropical scorpaenoids (with a larger species used for comparison)
3. Determine if tropical scorpaenoids display an annual or seasonal patterns of reproduction. This will be done by looking at temporal changes in a) the GSI and b) the size-structure distribution of tropical scorpaenoids.

5.2 Materials and Methods

Please refer to general materials and methods for detailed description on monthly collections of *Paracentropogon longispinis*, *Trachicephalus uranoscopus* and *Synanceia horrida* (see 1.2.2).

Gonad assessment of **P. longispinis, T. uranoscopus** *and* **S. horrida**

To assess whether the sex patterns of *P. longispinis*, *T. uranoscopus* and *S. horrida*, gonad tissue from males, females and indeterminates were examined histologically (see appendix A for histology protocol). For each gonad sample, assessment of hermaphroditism was based on gonadal structures defined by Sadovy and Shapiro (1987), where hermaphroditism could be determined by structural changes to gonads and their associated ducts. This included the presence of three possible types of germinal tissue configuration:

1. delimited type, a membrane of connective tissue separates male from female tissues;
2. undelimited type, male and female tissues are separate when they occur together in the gonad, but are not divided by a connective tissue boundary;
3. undelimited type, male and female tissues are mixed.

For estimates of reproductive output, only female gonads were sampled, as it is assumed that egg production rather than sperm production has a greater effect on offspring production (Helfman et al., 1997). In addition, females contribute nourishment to the developing embryo and this maternal role is more likely to have an influence on development during early life stages of progeny (Murua and Saborido-Rey, 2003). Gonad samples collected during dissections were initially preserved in 10% Bouin's solution for 72 hours and stored in 70% ethanol. Two sub-samples (approx 5% each) of these gonads were cut out for *S. horrida*, *T. uranoscopus* and *P. longispinis*. One batch of gonad sub-samples was dehydrated and embedded in paraffin wax in preparation for histological examinations (see appendix for histology protocol). 5-10 um sections of samples were performed and the gonads were stained using Mayer's haemotoxylin-eosin. The developmental stages of the oocytes were categorised according to Yoneda et al. (2000) with a few modifications appropriate to the *S. horrida*, *T. uranoscopus* and *P. longispinis* oocytes and are shown in Table 5-1. All oocyte sections were viewed in the compound microscope under 40X magnification and used to confirm gross maturity stages. For all scorpaenoid species, four gross maturity stages of eggs were identified and used to differentiate the different developmental stages of oocytes. This included the immature stage which was defined from the chromatin nucleus stage to the peri-nucleus stage, Maturing stage which was from the yolk vesicle stage to the late vitellogenic stage, Ripe stage when oocytes were mature and the Resting stage when oocytes were atretic (Table 5-2). Based on these categories, embryos of the second sub-sample of gonad material were gently teased apart, with the proportion of embryos in each gross maturity category enumerated using a dissecting microscope. Between 100 and 200 oocytes from each ovarian stage in each specimen was examined, to determine the frequency distribution of different staged oocytes within each species over different months. The gonado-somatic index (GSI) was calculated by using the formula;

GSI (%) = wet weight of gonads (g) / Total wet weight of specimen x 100

2-way nested design ANOVAs were used to compare the GSI values during the 2-year period (months nested in years). Prior to the ANOVAs, the data for each taxon were tested for homogeneity of variances using Levene's test, and all data became homogeneous when $\log_{10}(x + 1)$ transformed. Tukey's honest significant difference (HSD) tests were used for post-hoc comparisons of means. The nested ANOVA, Levene's test, Tukey HSD tests were carried out using Statistica ver. 8 (Statsoft, 2007).

Reproductive effort of **P. longispinis, T. uranoscopus** *and* **S. horrida**

The total reproductive effort (TRE) in scorpaenoids was calculated based on a recently developed relationship between the Von Bertalanffy growth equation (VBGF) with the reproductive-allocation growth (RAG) equation (Charnov, 2008). Charnov's formula states that the VBGF growth function $K = 0.55*\text{TRE}$. Using this formula, it is possible to calculate the reproductive effort based on:

$$\text{TRE} = K/0.55$$

Where TRE is total reproductive effort and K is the VBGF growth coefficient obtained from Chapter 4. In addition, to assess if gonado somatic indices changed with size, the relationship between GSI and body length (both log transformed) were examined. For the linear curve, regression analyses were conducted in PASW ver. 18.0. Goodness of fit of each model was evaluated on the bases of residual sums of squares (RSS) and on the coefficient of determination (r^2). In addition, to obtain an indication of reproductive output as a relation to size in each species, RO_{size} was calculated based on:

$$\text{RO}_{\text{size}} = \text{Maximum egg size recorded /Maximum size of female fish (SL mm)}$$

As body size is related to capacity for egg capacity in fish (Hislop, 1988), higher body mass in relation to size should be indicative of greater egg production. One reflection of increased size is the use of the body condition factors where better "condition" (nutritional and health status) are usually more full-bodied and therefore heavier at a given length. Fish condition has therefore been traditionally estimated by the equation proposed by Fulton (1911) and was used as a method for comparing the maximum body condition (in relation to higher reproductive potential) between the three scorpaenoid species. To account for allometry, the formula used was modified (Bagenal and Tesch, 1978) and described as:

$$BC_{max}= 100 \text{ x } M_{max}/L_{max}b$$

where BC_{max} is the maximum body condition in females, M_{max} is the maximum weight of a female observed in grams, L_{max} is the longest attained length of a female in cm (SL) and b is the constant determined by the length-weight relationship in females obtained from Chapter 4 (See Table 4-3).

***Seasonal patterns of* P. longispinis, T. uranoscopus *and* S. horrida**

For this part of the study, two types of data were collected (size and abundance of species during each sampling period as variables), allowing tests on the temporal distribution of individual species. I used 3-way nested ANOVAs, with size class, month and year as factors (months nested in years) to compare the abundance per size class of the three occurring taxa between sampling months. Prior to the ANOVAs, the data for each taxon were tested for homogeneity of variances using Levene's test, and all data became homogeneous when $\log_{10}(x+1)$ transformed. Tukey's honest significant difference (HSD) tests were used for post-hoc comparisons of means. The nested ANOVA, Levene's test, Tukey HSD tests were carried out using Statistica ver. 8 (Statsoft, 2007).

Table 5-1 Histological characteristics of *Paracentropogon longispinis*, *Trachicephalus uranoscopus* and *Synanceia horrida* at different developmental stages.

Species	Egg size (um)	Developmental stage of oocyte	Description
P. longispinis	<10	chromatin nucleus (a)	Nucleus has one large nucleolus.
	15-50	peri-nucleus (b)	Multiple nucleoli are seen at the periphery of the nucleus; follicle cells surrounding the oocyte form a narrow layer.
	70-100	yolk vesicle (c)	Small yolk vesicles appear in the peripheral region of the cytoplasm.
	150-250	early vitellogenic (d)	Yolk globules fill the ooplasm; ranulose (yolked) and thecal cell layers are clearly observed.
	250-350	late vitellogenic (e)	Yolk globules become larger; yolk continues to accumulate.
	>350	Mature (f)	Breakdown of germinal vesicle; yolk globules fuse with each other and form a single mass.
	-	Atretic (g)	Disintegration of the nucleus and yolk globules; disorganization of the follicular cell layers.
T. uranoscopus	<25	chromatin nucleus (a)	As above
	25-150	peri-nucleus (b)	
	200-330	yolk vesicle (c)	
	350-520	early vitellogenic (d)	
	600-850	late vitellogenic (e)	
	>900	Mature (f)	
	-	Atretic (g)	
S. horrida	<50	chromatin nucleus (a)	As above
	10-200	peri-nucleus (b)	
	200-400	yolk vesicle (c)	
	500-750	early vitellogenic (d)	
	750-900	late vitellogenic (e)	
	>950	Mature (f)	
	-	Atretic (g)	

Table 5-2 Gross morphological descriptions of maturity stages in common scorpaenoids.

Characteristics of gross maturity stages	
Maturity stage	**Description**
Immature	Thin threads and contained within a transparent membrane (a,b)
Maturing	Ovary gets larger, orange or yellow eggs may be visible to naked eye, later stages ovary becomes gelatinous (c, d, e)
Ripe	Ovary is a large gelatinous mass with hydrated eggs suspended at the outer edges (f)
Resting	Ovary appears firm and pink with no eggs visible (g)

5.3 Results

In all three species of scorpaenoids, histological examinations of males and females as well as indeterminates across all sizes revealed that no gonads ever contained male or female reproductive tissues concurrently. This strongly suggests that hermaphroditism does not occur in the three scorpaenoid species.

The reproductive output (as a function of the gonado somatic index) varied in size depending on species. While *Paracentropogon longispinis* displayed no significant difference in GSI among size classes ($R^2 = 0.001$) (Figure 5.1). The linear regression indicated that there was a moderate increase in GSI values with increasing size in *T. uranoscopus* ($R^2 = 0.24$) (Figure 5.2), which was also similar in *Synanceia horrida* ($R^2 = 0.18$) (Figure 5.3).

Comparisons of reproductive effort of the three scorpaenoids species indicate that similar total effort was allocated to reproduction in the two small species (*P. longispinis* and *Trachicephalus uranoscopus*), whereas the larger *S. horrida* displayed almost double the amount of effort into reproduction (Table 5-3). This higher effort also appeared to be related to a higher body condition which might support the extent of positive allometry that occurs in S. *horrida* (See chapter 4). Not surprisingly, the maximum number and size of eggs was highest in the largest sized *S. horrida* as well (Table 5-3). However, it was surprising how much larger and abundant eggs were in *T. uranoscopus* compared to *P. longispinis*. Also surprising was the size of eggs in relation to body length, where *T. uranoscopus* actually produced the largest eggs among the three scorpaenoids (Table 5-

3). As a result of such relatively large eggs in the small sized *T. uranoscopus*, its GSI values were the highest found among all the three scorpaenoids (Table 5-3).

Table 5-3 Reproductive characteristics and effort of *Paracentropogon longispinis*, *Trachicephalus uranoscopus* and *Synanceia horrida*.

Species	**Max GSI (%)**	**Max size of eggs (um)**	**Max no. of eggs**	**Max size of eggs / Max body size (mm), RO_{size}**	**Total reproductive effort, TRE**	**Body condition, BC_{max}**
P. longispinis	1.92	400	7000	5.93	0.31	3.4
T. uranoscopus	22.11	1350	35000	16.42	0.29	4.6
S. horrida	14.17	2100	700000	8.50	0.65	11.5

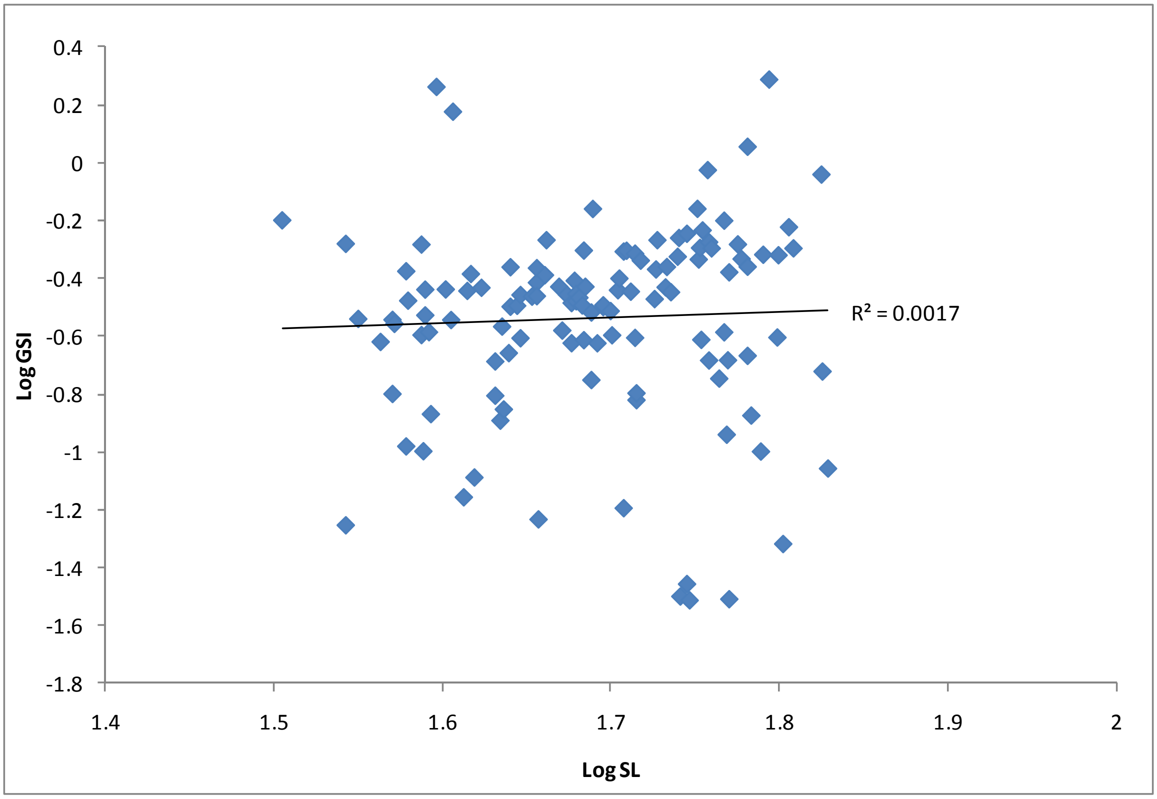

Figure 5.1 Linear relationship between the gonado-somatic index and size in mature female *Paracentropogon longispinis* (n= 122).

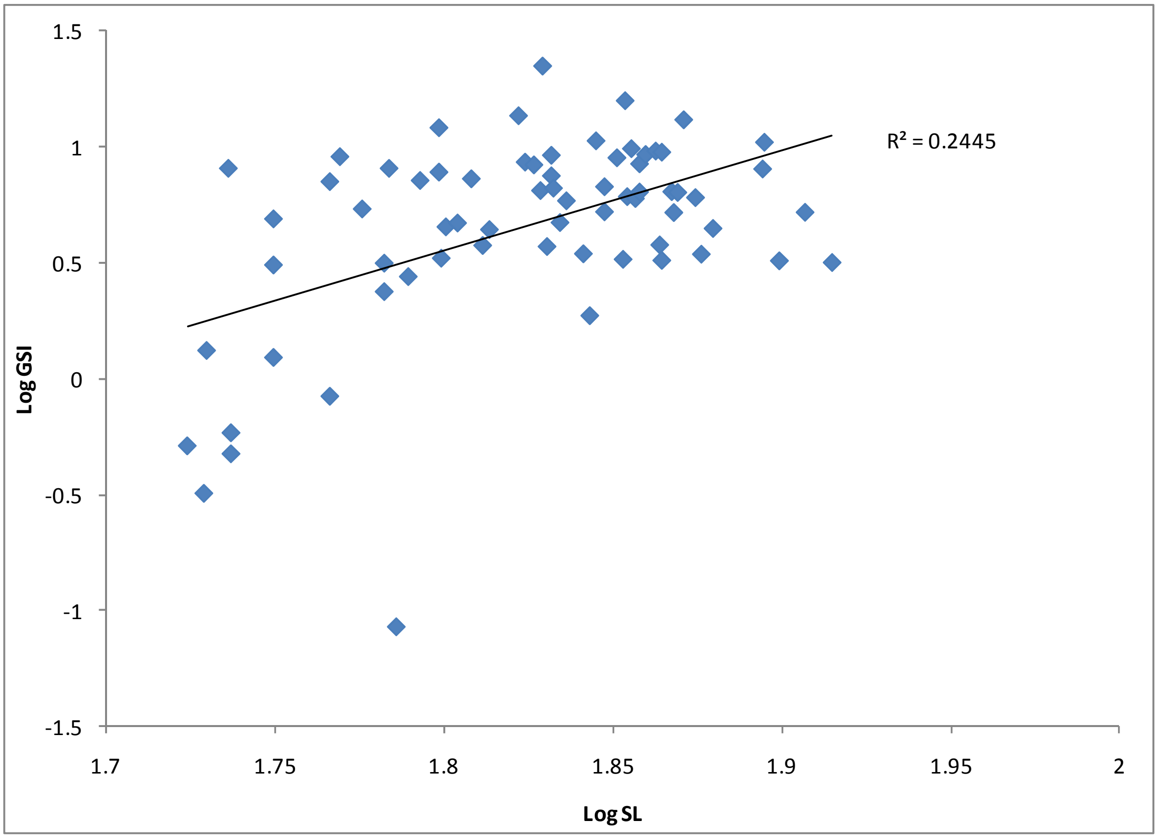

Figure 5.2 Linear relationship between the gonado-somatic index and size in mature female *Trachicephalus uranoscopus* (n=68).

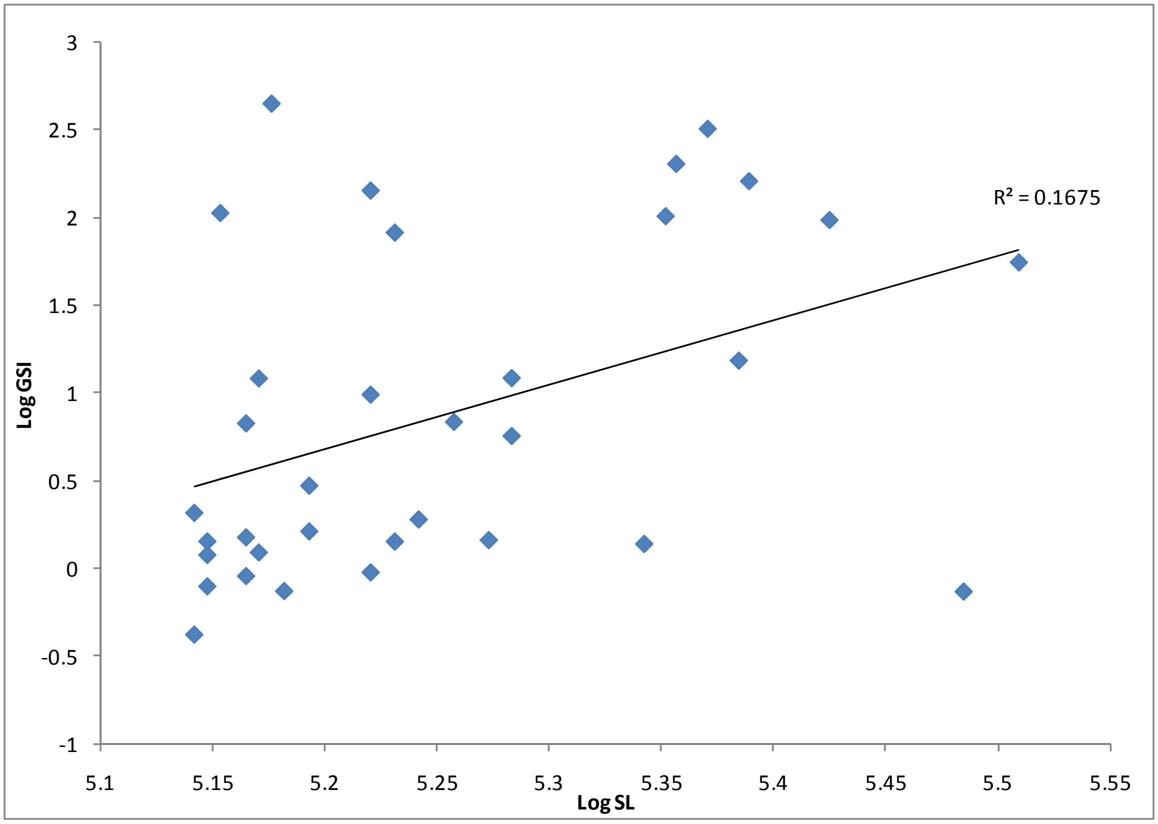

Figure 5.3 Linear relationship between the gonado-somatic index and size in mature female *Synanceia horrida* (n=36).

A similar trend was observed in all the three scorpaenoid species where peaks in GSI occurred during the latter part of the year, especially between the months of September to November (Figure 5.4, Figure 5.6 and Figure 5.8). This period of time coincides with the north-east monsoonal period that usually begins around November and lasts till around January (Tham, 1953). The 2-way nested ANOVA on looking at temporal variation in GSI values in *P. longispinis* indicated that there was no difference between the years ($F_{1,22}$=0.43, P>0.05) but there was a difference between the months ($F_{22,135}$=2.73, P<0.05) and the post-hoc Tukeys indicated that the month of November had significantly higher GSIs compared to other months (Figure 5.4). These peaks in GSI during the months of

November were also reflected in the higher proportions of ripe eggs during this month. It also appeared that the spawning period for *P. longispinis* started around September and lasted till around December based on proportion of ripe eggs and higher GSI values (Figure 5.5).

In *T. uranoscopus*, peaks in GSI were observed only during September of the second year with potentially similar peaks occurring during the first year, as there appeared to be increasing GSI values in August in both years (Figure 5.6). Analysis using the 1-way nested ANOVA indicated that there was a significant difference in GSI between years ($F_{1,22}$=7.65, $P<0.05$) as well as between months ($F_{22,78}$=1.93, $P<0.05$). However, this was only due to the lack of mature females captured during the months of September and December in the first sampling year. Evidence for spawning occurring during the last quarter to support GSI peak values obtained during the second year was reflected by higher proportions of ripe eggs during September, with proposed spawning periods starting from about August till October (Figure 5.7). Like *T. uranoscopus*, the GSI values and proportions of ripe eggs occurred during similar periods for *S. horrida*. Peaks in GSI values occurred in September in both years, with similarly high proportions of ripe eggs occurring during this month (Figure 5.8). Spawning periods also appeared to occur between September to November in *S. horrida* (Figure 5.9), but unfortunately the lack of mature female captures during certain months made temporal comparisons of GSI values using the nested ANOVAs unacceptable. Evidence for a single extended spawning period at the end of the year for the three common scorpaenoids was further supported by the presence of small sized recruits, occurring approximately three to six months after the peak GSI periods in all three species (Figure 5.10, 5.11 and 5.12), with the youngest specimens of *P. longispinis*, *T. uranoscopus* and *S. horrida* found to range between four to six months of age (based on ageing in Chapter 4). Spikes in juvenile numbers during these months were found to occur over both years and is a strong indication that recruitment processes are occurring between January to April in the three species (Figure 5.10, 5.11 and 5.12). Larval durations also appear to be quite short, which may explain the lack of settlement check marks in the otoliths.

In terms of overall abundance of the three scorpaenoids, *P. longispinis* was the most commonly caught species at Changi Point Beach and was consistently caught every month during the two years of sampling (Figure 5.10). There also appeared to be two peaks in abundance of *P. longispinis*, one in April 2006 and again in February 2008 (Figure 5.10), both coinciding with spawning events that may have occurred around September in 2005 and 2006. The nested 1-way ANOVA indicated that though there was no significant difference between two years sampled ($F_{1,22} = 0.001$, $P>0.05$), but there was a difference between months ($F_{22,120} = 1.64$, $P<0.05$). Post hoc Tukeys indicated that abundances in April of the first year of sampling were significantly higher than other sampling months. Although not as abundant as *P. longispinis*, *T. uranoscopus* was also caught consistently at Changi Point Beach with the exception for the month of September 2006 (Figure 5.11). Higher capture rates occurred during April and August 2006 with a peak in January 2007 (Figure 5.11). Similar to *P. longispinis*, the nested ANOVA also indicated that there was no significant difference in abundances between both years ($F_{1,22} = 1.73$, $P>0.05$) but there was a difference between the months ($F_{22,144} = 1.94$, $P<0.05$) in

T. uranoscopus. In comparison, *S. horrida* was caught during most of the two years sampling period with the exception of July to August 2008 (Figure 5.12). The highest catch rates for *S. horrida* occurred during March 2007 and February 2008 (Figure 5.12). However, the nested ANOVA indicated that there was a significant difference between the two years sampled ($F_{1,22}$ = 4.98, $P<0.05$) but there was no significant difference between the months ($F_{22,120}$ = 0.59, $P>0.05$).

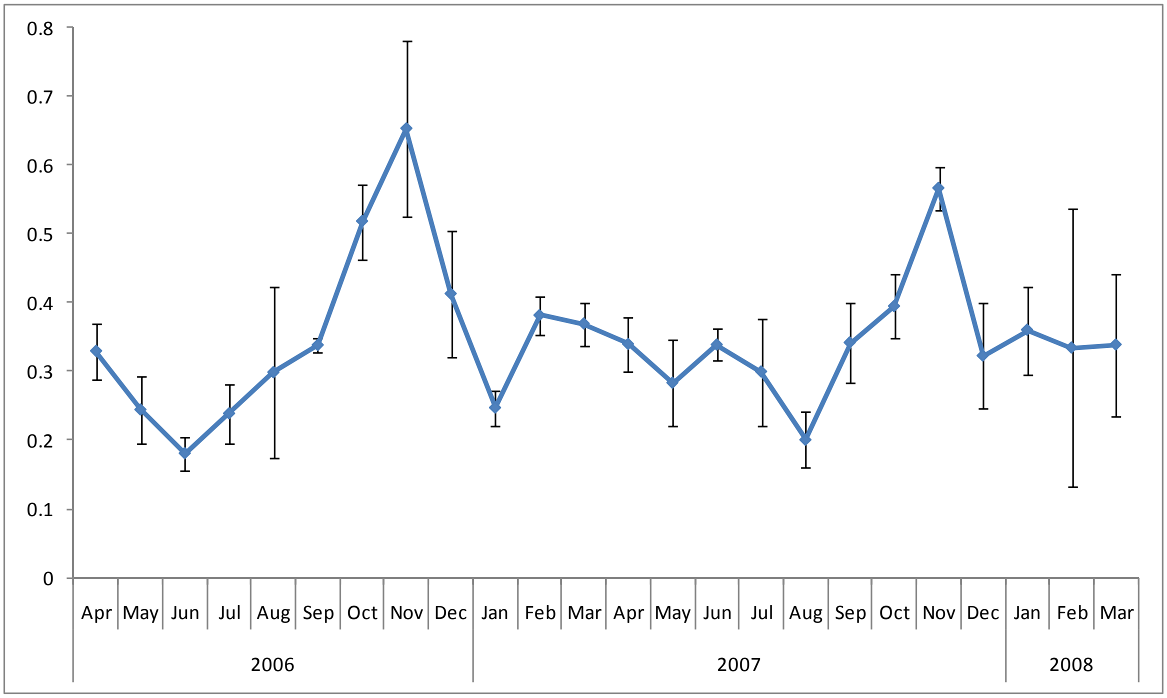

Figure 5.4 Average gonado-somatic index of *Paracentropogon longispinis* caught monthly at Changi Point Beach between April 2006 and March 2008 (n = 159, error bars are average GSI ± s.e.).

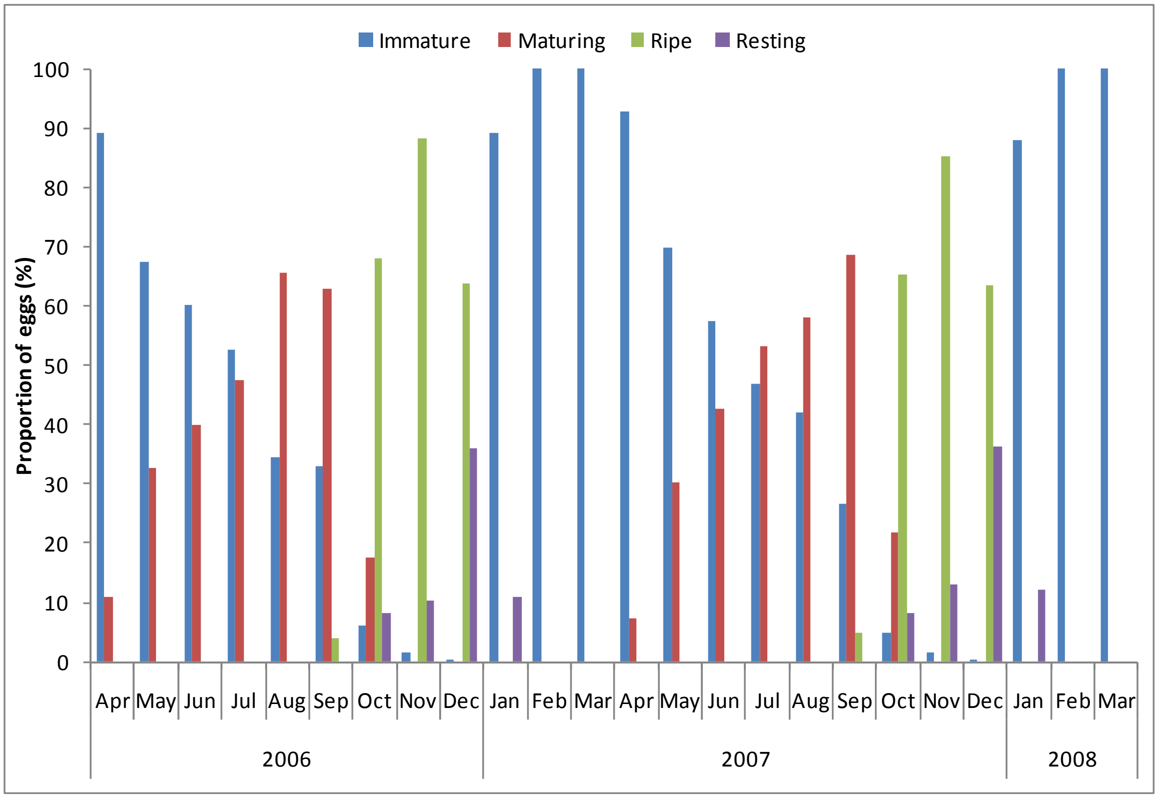

Figure 5.5 Proportion of primary and secondary eggs found in *Paracentropogon longispinis* during each month between April 2006 and March 2008 (n = 159).

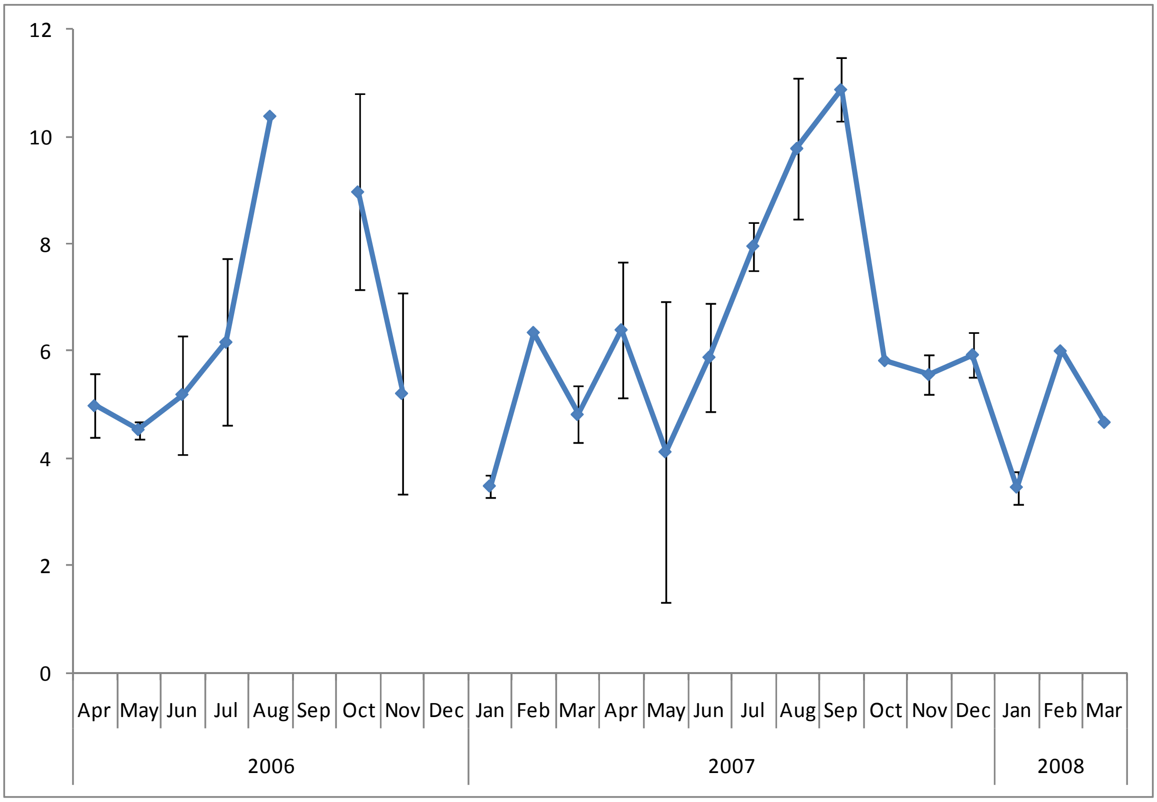

Figure 5.6 Average gonado-somatic index of *Trachicephalus uranoscopus* caught monthly at Changi Point Beach between April 2006 and March 2008 (n = 100, error bars are average GSI ± s.e.).

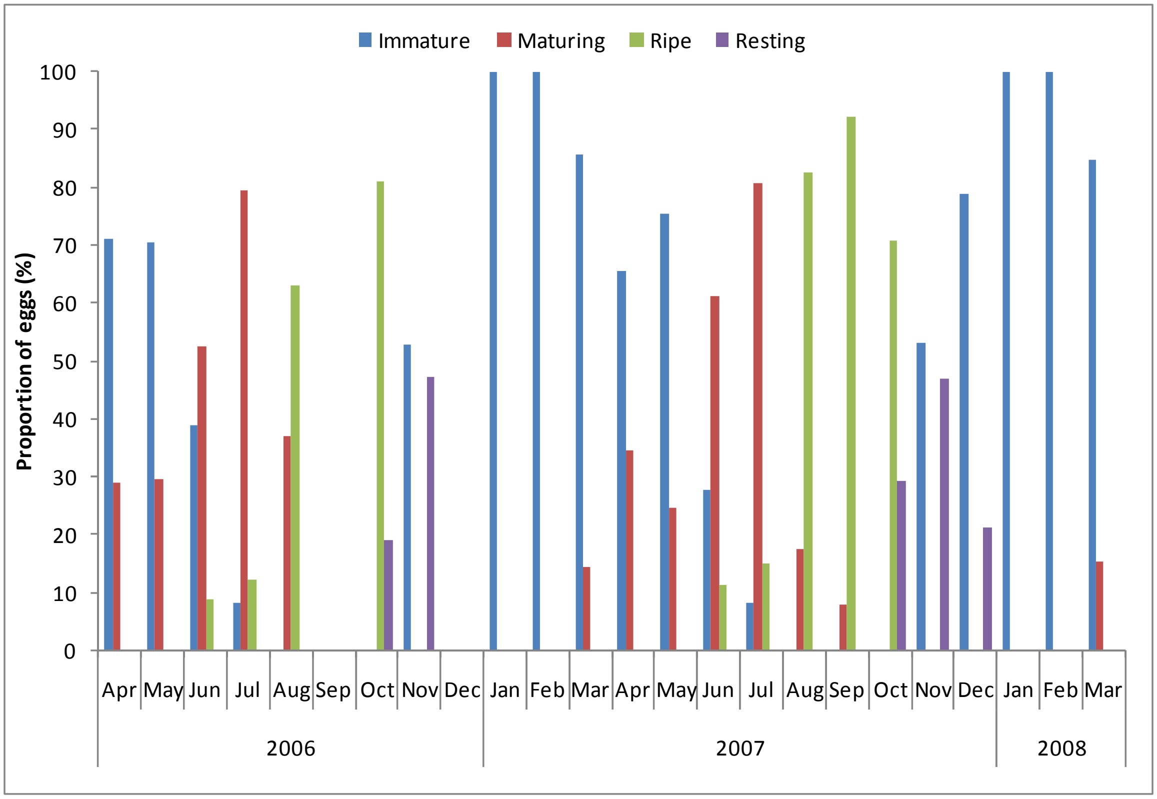

Figure 5.7 Proportion of primary, secondary and tertiary eggs found in *Trachicephalus uranoscopus* during each month between April 2006 and March 2008 (n = 100).

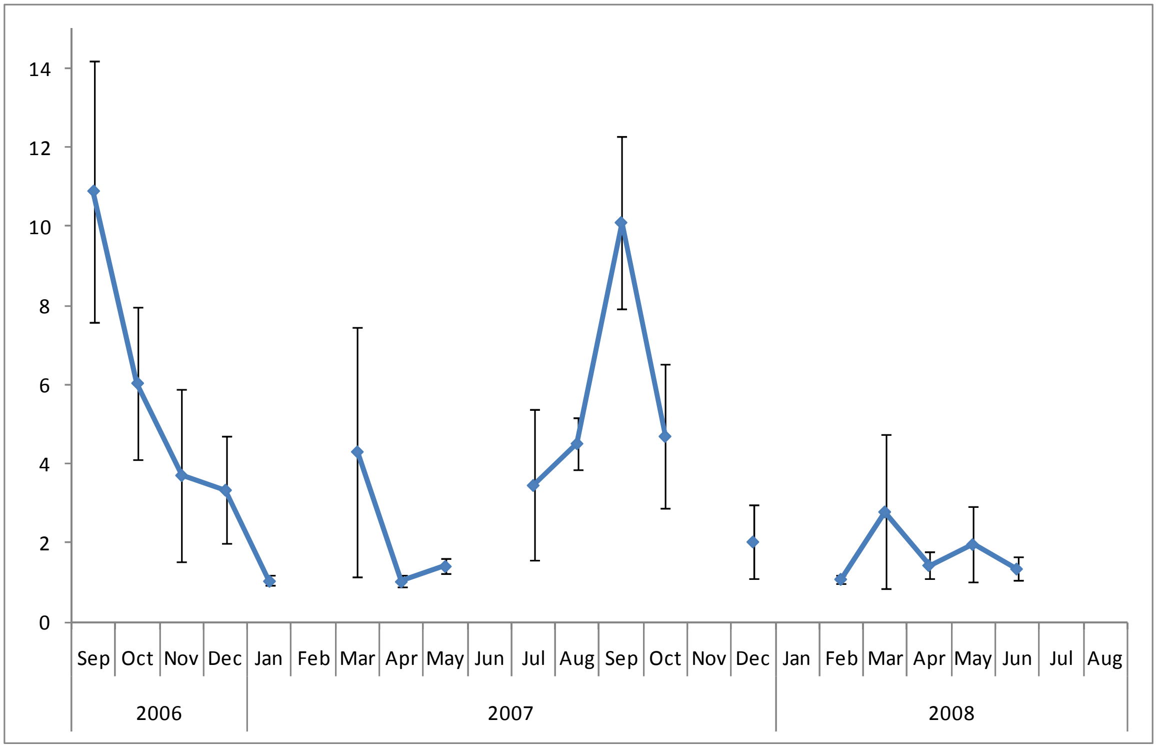

Figure 5.8 Average gonado-somatic index of *Synanceia horrida* caught at Sentosa Island between September 2006 and August 2008 (n = 54, error bars are average GSI ± s.e.).

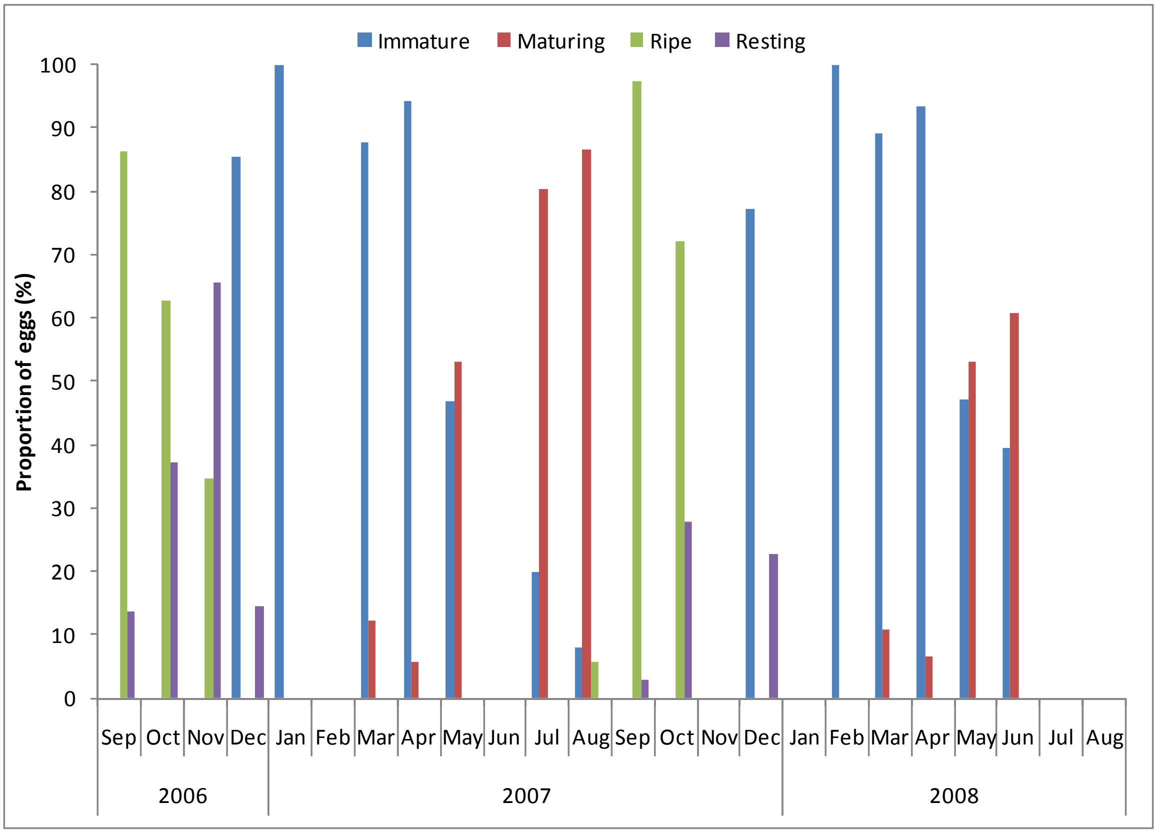

Figure 5.9 Proportion of primary, secondary and tertiary eggs found in *Synanceia horrida* during each month September 2006 and August 2008 (n = 54).

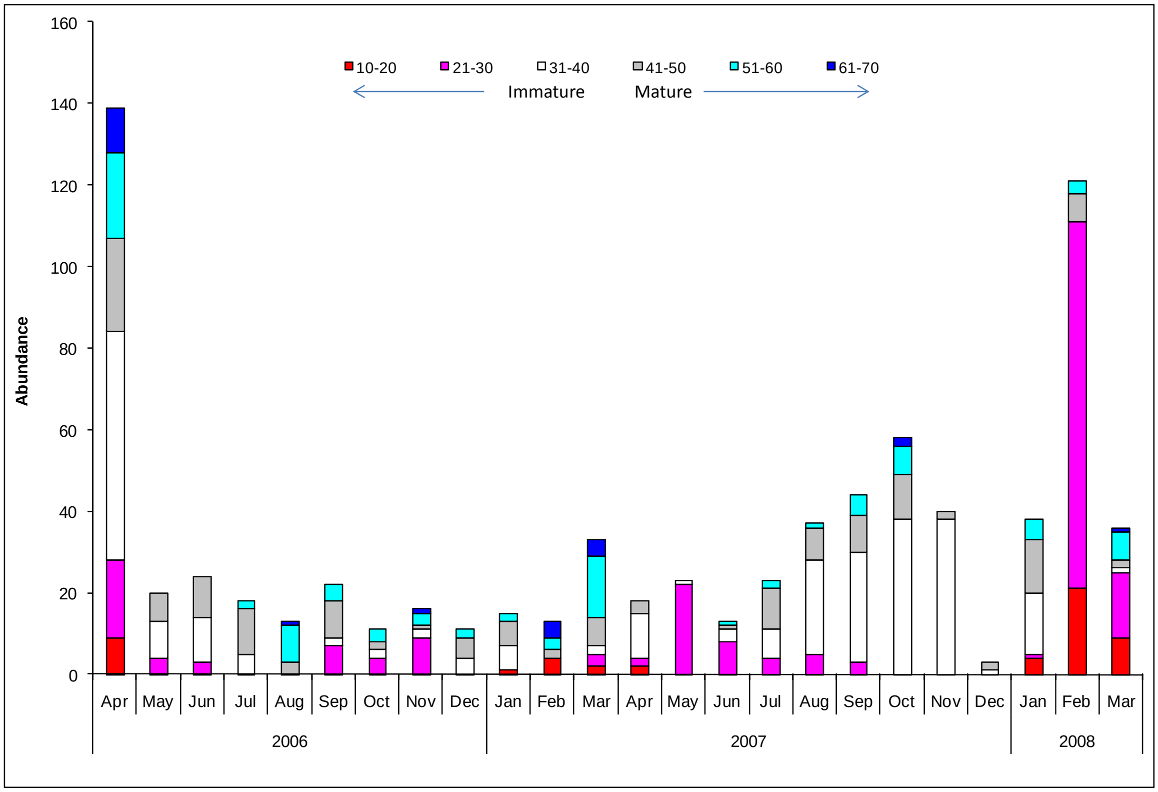

Figure 5.10 Size distribution frequency of *Paracentropogon longispinis* caught between April 2006 and March 2008 along three sampling sites at Changi Point Beach (n = 780).

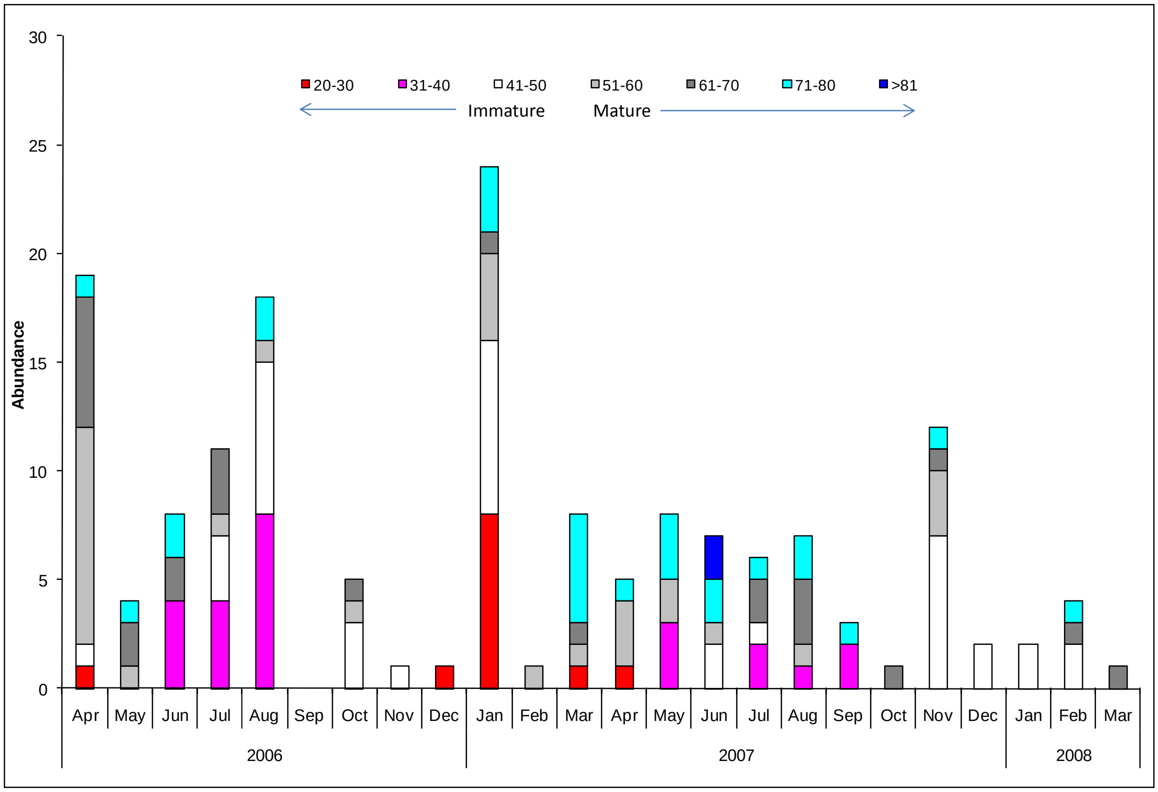

Figure 5.11 Size distribution frequency of *Trachicephalus uranoscopus* caught between April 2006 and March 2008 along three sampling sites at Changi Point Beach (n =158).

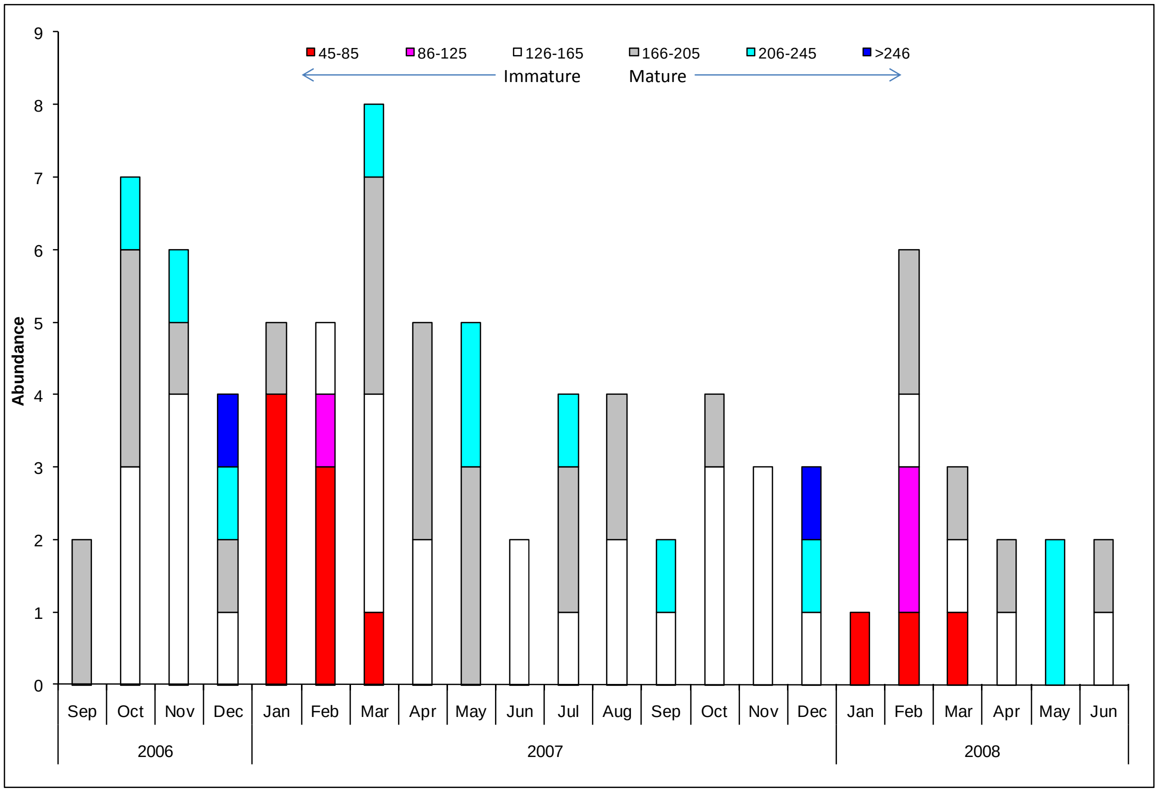

Figure 5.12 Size distribution frequency of *Synanceia horrida* caught between September 2006 and August 2008 along three sampling sites at Sentosa Island (n = 85).

5.4 Discussion

Sex patterns in scorpaenoids

Although not fully measured in any species, the nature and costs/benefits of female-to-male sex reversal can usually be outlined in fishes (Jones, 1980; Munday et al., 2010; Robertson and Choat, 1974; Warner and Hoffman, 1980). Benefits usually relate primarily to the opportunity for males to mate with multiple females over their lifespan (Avise and Mank, 2009; Munday et al., 2010). Whereas, females can spawn once daily or less, males may spawn up to 100 times a day, and even relatively disadvantaged secondary males spawn more frequently than females (Munday et al., 2010; Warner and Hoffman, 1980).

The absence of sex change in *Paracentropogon longispinis*, *T. uranoscopus* and *Synanceia horrida* might be indicative of a strategy to avoid expending energetic costs towards sex reversal. This would involve, at a minimum, 1) a metabolic expenditure of energy to alter gonadal cell types (Brusle et al., 1989; Reinboth, 1962), inducing new enzyme systems for the biosynthesis of different steroid hormones (Baroiller et al., 1999; Yeung et al., 1985), a change in the bodily mosaic of colour pigments (Shapiro, 1981c), alternating types and frequencies of behavioural activities (Rodgers et al., 2005; Shapiro, 1981a; b; Warner and Hoffman, 1980) and probably an increase in body size and change in body composition (Rodgers et al., 2005; Shapiro, 1981d) ; 2) the loss of reproductive time during sex reversals occurring in the breeding season (especially in short-lived fish such as *P. longispinis* and *T. uranoscopus*); and 3) an increased risk of mortality during sex change (exacerbated in small sized fish), resulting from either a) predation from individuals made temporarily more conspicuous than normal males or females by transitional alteration in colouration (Shapiro, 1981c) or behaviour (Rodgers et al., 2005; Shapiro, 1981a; b), or b) disease in individuals weakened temporarily by the energy demands of sex change. Finally, differential mortality rates between sexes may serve either as an advantage or a disadvantage of sex reversal, depending on the size and direction of the difference.

It has been suggested that the potential for sex change can be derived from size-age frequency and sex ratios (Sadovy and Shapiro, 1987). Sadovy and Shapiro (1987) found that protogyny was characterised by higher female biased ratios, with older or larger males found. Conversely, protandry could be characterised by male biased ratios, with larger and older females (Sadovy and Shapiro, 1987). More recently, it was also found that bi-directional hermaphroditism (e.g., coral dwelling gobies) can also occur and was characterised by equal sex ratios with overlapping size-age frequency (Munday et al., 2010). All the common scorpaenoids found in Singapore appear to display sexual dimorphism with larger specimens dominated by females. However, as no specimens were ever found to display hermaphroditic characteristics in their gonads (Sadovy and Liu, 2008), it is likely that *Paracentropogon longispinis* is gonochoristic. For *Trachicephalus uranoscopus* and *Synanceia horrida*, sex structure appeared to be characterised by female biased ratios with older and larger females, which does not conform to either definition of protogyny or protandry. However, due to the lack of male captures in *S. horrida* and *T. uranoscopus* at present, a gonochoristic strategy could only be substantiated in *P. longispinis* that had similar ratios for both male and female captures. In addition, the low numbers of male *T. uranoscopus* might also indicate that separation of sexes may occur in this species as found in other scorpaenoids such as *Sebastes marinus* (Sorokin, 1961) and *Sebastes alutus* (See Gunderson, 1974), and that both sexes aggregate during reproductive events. The presence of larger females in relation to males has been observed in some viviparous sebastids such as *S. flavidus*, *S. melanops, S. mystinus* and *S. serranoides* (Echeverria, 1986). In these cases of size sexual dimorphism, the presence of smaller males might indicate early sexual maturation of males where energy is invested to reach initial growth of sexual maturity which slows down for sperm production (Echeverria, 1986), and the presence of larger females could also be a means of increasing reproductive success by having larger bodies to produce and accommodate either large numbers of embryos or just large embryos (Echeverria, 1986).

Spawning patterns and reproductive effort

Cole (1954) designated as "semelparous" those life histories involving only a single reproductive event, followed by death, and as "iteroparous" those in which reproduction occurs on more than one occasion during lifespan. Results from this study suggest that *T. uranoscopus* and *P. longispinis* appear to have only one spawning cycle (possibly semelparous) during their short lifespan (see Figure 5.5, 5.7 and 5.9), while *S. horrida* is likely to be iteroparous with multiple spawning periods over its 6-year lifespan (see Chapter 4 for longevities). Semelparity as a strategy is relatively uncommon in fish, but it appears that it is size independent, with large fish (e.g., salmonids) displaying single breeding cycles even with relatively long lifespans (Crossin et al., 2009), as well as small sized gobies (e.g., *Crystallogobius linearis*, 35 mm SL) with short lifespans (~12 months) also displaying semelparity (Caputo et al., 2003). In addition, studies on small sized coral dwelling gobies (i.e. *Eviota* sp. in Depczynski & Bellwood (2006) and the small Mediterranean goby *Aphia minuta* (Caputo et al., 2000), have also found that both these small gobies displayed multiple spawning periods upon attaining maturity over their short lifespan.

The majority of scorpaenoids (at least in sebastids and scorpaenids in subtropical and temperate regions) are potentially iteroparous (Bilgin and Celik, 2009; Fewings and Squire, 1999; Leaman, 1991; Munoz et al., 2005; Pavlov and Emel'yanova, 2007; Ruiz-Carus et al., 2006) but display a range in length of reproductive life (Leaman, 1991; Love et al., 1990b; Takahashi et al., 1991). Two kinds of iteroparity may be recognised in species whose reproduction is seasonal, and those can be termed “abbreviate” or “protracted” (Miller, 1984). Abbreviate iteropares display a long breeding season with several to many spawnings by individual fish but adult lifespans are usually short and cover only one to a few breeding seasons. The protracted iteropares are longer-lived species, with frequently not more than two spawnings in a season, at up to 60 day intervals. They may, however, participate in two to over ten seasons. Repeat spawning, over a more or less extended breeding season is believed to have originated in relation to the availability of plankton in warmer seas for most of the year (Qasim, 1956). This pattern of productivity would support not only planktotrophic offspring but also adult dietary needs for repeated gametogenesis and secondary reproductive activities (e.g. egg size or fecundity) (Miller, 1984). As such, it is conceivable that both *P. longispinis* and *T.*

uranoscopus inhabiting tropical estuarine habitats are likely to be abbreviate iteropares spawning over extended an extended period of time annually.

With so many strategies occurring in small sized fishes, there must be other compelling factors that result in such variation in spawning patterns. Two important considerations that can affect life history patterns are resource allocation and mortality (Kozlowski and Teriokhin, 1999), both of which have direct affects on reproductive patterns. Resource-dependent growth rates could not only determine age of maturity (Roff et al., 2006) but also the reproductive output (e.g., fecundity, egg size etc) due to allocation of resources from growth to reproduction. This might be especially critical in fish that display indeterminate growth (as found in *P. longispinis* and *T. uranoscopus*, see Chapter 4), where growth appears to continue even after attaining sexual maturity compared to most other fishes that reach asymptotic lengths after maturity.

While size-dependent mortality (due to primarily predation or unstable environmental conditions) is likely to select for semelparity (Cole, 1954) as would be expected in small fish inhabiting estuarine habitats, results from Chapter 4 indicate that both *P. longispinis* and *T. uranoscopus* were iteropares with relatively low mortality rates. It is likely that these low mortality rates might be a result of resource trade-offs between increased defensive mechanisms (i.e. venomous spine and cryptic colouration) with either growth or reproduction (Steiner and Pferffer, 2007). However, it must be noted that both *P. longispinis* and *T. uranoscopus* are found inhabiting shallow coastal estuarine habitats which can undergo drastic fluctuations in environmental conditions (e.g., salinity, temperature and turbidity), which in itself could be a driving factor for the single spawning pattern observed during the monsoon season with regards to higher survivorship or optimal dispersal of larvae.

Reproductive effort was found to be much higher in *T. uranoscopus* and *S. horrida* compared *to P. longispinis*. This was likely to be associated with the growth patterns observed in these scorpaenoids. While *P. longispinis* produced fewer and smaller eggs, both *T. uranoscopus* and *S. horrida* produced larger egg masses and much larger eggs. This corresponds with the length-weight relationships recorded where *P. longispinis* was found to display isometric growth while both *T. uranoscopus* and *S. horrida* displayed positive allometric growth (Chapter 4), which resulted in bigger body masses and larger body cavities for gonad production. In addition, the increased allocation of resources towards reproduction in *T. uranoscopus* and *S. horrida* was supported by significantly higher GSI values with increasing body lengths, which is contrary to Roff's (1992) suggestion that the GSI in most fish should be constant or only increase slightly with size. While energetically costly, the benefit of larger egg size should increase the potential for survival of the individual fish, because the larger larvae produced are subject to lower mortality (McGurk, 1986), are able to feed on greater size range of prey, and swim faster; and because longer yolk duration should increase larval resistance to starvation and, thereby, increase its probability of encountering a favourable environment.

Comparisons with reproductive strategies of other temperate scorpaenoids indicate that while most sebastids are viviparous (Wourms, 1991), most demersal cottoids (in which *P.*

longispinis is a member) are oviparous, and either spawn demersally in masses or exhibit parental care. Other members of the scorpaenids and pteroids are also thought to be oviparous but extrude gelatinous floating egg masses during spawning events (Wourms, 1991; Yoneda et al., 2000). Additionally, though no *in situ* spawning events were observed for both species, observations on the morphology of eggs masses produced by both species indicate that while egg masses of *T. uranoscopus* and *S. horrida* are partially covered in a gel matrix (which has been found to be an egg predator deterrent in pteroids (Moyer and Zaiser, 1981)), no such gel was found in egg masses produced by *P. longispinis* (unpubl. data.). Evidence from other observations on *S. horrida* (which is behaviourally and morphologically similar to *T. uranoscopus*) and comparisons of eggs from this study suggest that *T. uranoscopus* is likely to be a demersal spawner with negatively buoyant eggs, similar to *S. horrida* (Fewings and Squire, 1999), while *P. longispinis* may be a broadcast pelagic spawner. In either species, further investigations into spawning behaviour are required to confirm these suspicions.

Seasonality in scorpaenoids

Peaks in the GSIs and ripe eggs of all three species indicate that spawning periods for *P. longispinis*, *S. horrida* and *T. uranoscopus* appeared to occur during the last quarter of the year (around September to November). The peaks in GSIs and ripe eggs during these months also coincided with periods just before the onset of the northeast monsoonal period in Singapore which occurs around November to January (Tham, 1953). As the monsoon period begins, the increased rainfall causes decreases in both salinity and temperature (Tham, 1953), both factors of which have been known to affect survivorship of not only larval fish (Brain et al., 1996) but also the zooplankton which are an important food source for larval fish (Mallin, 1991). It has also been determined that during changes between the southwest and northwest monsoon seasons, ocean conditions can become static and water movement is due mainly to tides and is less affected by prevailing winds, resulting in weaker currents and drifts along the coastal shores (Tham, 1953). As such, a possible strategy for the common scorpaenoids is to spawn when weaker tidal currents and winds occur at just before and at the start of the northwest monsoon, reducing transport of larvae long distances from where they originated and while water conditions are still optimum for larval survivorship (Johannes, 1978), coinciding with periods of higher zooplankton abundance for consumption during hatching. This strategy might also explain the presence of anti-predatory gel matrices which have been found in other scorpaenoids (Deblois and Leggett, 1991; Dulcic et al., 2007), and possibly in *T. uranoscopus* (present data) and *S. horrida* (Fewings and Squire, 1999) which also have very large gel matrices.

Based on the peaks in GSI (which can be assumed to be related to spawning periods), it was expected that spawning aggregations or recruitment events would be observed during monthly seines. However, though adults were frequently found during the entire year, larger individuals of all three species were not dominant during the months of October to November. It is possible that the spawning adults of both species migrate from the shallow habitats (< 2 m) to deeper waters (i.e. channel that occurs 100 m offshore and reaches depths of 20 m) to spawn. Such displays of migratory spawning behaviours have been found to favour transport of pelagic eggs and pelagic larvae offshore where predation is reduced, as compared to predation pressures that can be found in the adult habitats (Johannes, 1978). This migratory breeding strategy has been observed in many estuarine fish (both demersal and pelagic spawners) from the east coast of South Africa, which spawn in the vicinity of estuary mouths (Dando, 1984), thus increasing the chances of post-larvae or juveniles migrating back to the nursery grounds.

Interestingly, although larger adults were not observed during peak GSI periods, there appeared to be an increase in the abundance of recruits over the months following the spawning periods from January to about May. There have been arguments about the presence of true seasons in the tropics and consequently that tropical fish should not display distinct seasonal breeding patterns. The results from this study show that tropical scorpaenoids do indeed display monsoonal seasonal spawning patterns. This is likely to be associated to changes in environmental conditions (similar to higher latitudes) brought about by the effects of the monsoon period which prevail over the tropics, and successful adaptations of reproductive strategies and tactics by these tropical fish under these environmental conditions.

In general, it would appear that differences in the reproductive strategies of small tropical scorpaenoids occurred more as a result of taxonomic relations rather than size. While both the synanceids (*T. uranoscopus* and *S. horrida*) appear to have similar strategies regardless of size differences between them, differences in strategies occurred when comparing the small sized scorpaenoids (*P. longispinis* and *T. uranoscopus*). Possible explanations are that both *T. uranoscopus* and *S. horrida* have similar resource allocation strategies which could be due to these two species having similar morphological and behavioural traits (e.g., benthic lie-in-wait predatory piscivores) compared to *P. longispinis* which is quite different.

Chapter 6. General Discussion

Implications of small body size on life history patterns of fish

Among life-history characteristics, organism body size is thought to be a key characteristic which influences a slew of other traits (Ricklefs and Finch, 1995). Body size is a major constraint on energy assimilation and metabolic rates (limitations of mouth and stomach size) (Kozlowski, 1992; Schmidtt and Holbrook, 1984), and therefore limits growth, reproduction (limitations of egg number and size due to body cavity constraints) (Munday and Jones, 1998) and survival (Calder, 1985; Reiss, 1989; Rochet, 2000). In general, larger bodied organisms tend to have slower growth, lower mortality and greater longevity (Calder, 1984; Roff, 1992), with the converse true in smaller organisms.

A major implication of being smaller sized is the increased risk of higher mortality through higher predation pressure (Mittelbach and Chesson, 1992; Scharf et al., 2000; Ware, 1975). While little is known about small equatorial estuarine fish, short life expectancies are thought to be a result of higher predation rates in small-sized reef fish (Munday and Jones, 1998). This is especially true of the well studied small coral-dwelling gobies, with documented daily mortality rates of 7.8% in *Eviota sigillata* (see Depczynski and Bellwood, 2005), 4.3-5.6% for *E. melsama* and *E. queenslandica* (see Depczynski and Bellwood, 2006), 4.7% for *Trimma nasa* (see Winterbottom and Southcott, 2008). This is further supported by cases in which removal of predation pressure resulted in unexpectedly high longevities. For example, captive *Prionolepis nocturna* (Gobiidae) persisted beyond 3.25 years at the Waikiki Aquarium (Randall and

Delbeek, 2009), and *Asterropteryx semipunctata* (Gobiidae) for 11 years at the Hawaii Institute of Marine Biology (Randall and Delbeek, 2009). Although this may not be entirely due to changes in mortality due to captivity; tagged coral gobies of the genus *Gobiodon* (maximum length <40 mm) were resampled in the field over a period of three years, providing a minimum life span of four years (Randall and Delbeek, 2009). *Paragobiodon encephalatus*, another coral-dwelling goby, was also found to persist for over 3 years using tagging and release methods (Kuwamura et al., 1994). In such small coral dwelling fishes, deviations from the body-size-short lifespan relationship may be affected by lowered mortality. *Gobiodon* is believed to have a skin-toxin in their skin mucus which renders them unpalatable to predators (Schubert et al., 2003). Both *Gobiodon* and *Paragobiodon* live amongst the branches of live coral, which could also offer additional protection against predation (Patton, 1994).

Rapid linear growth in the early life-history of fishes is viewed as a means to decrease size-dependent predation (Anderson, 1988). However, the relative value of this while a fish's maximum size remains within the limits for high predation risk is debatable. High extrinsic mortality has been shown to favour rapid growth (Arendt, 1997), earlier maturation (Reznick and Endler, 1982) and shorter intrinsic life spans (Williams, 1957; but see Resnick et al. 2004). This can also affect resource allocation in terms of somatic repair (disposable soma theory, Kirkwood 1981). As such, resource allocation towards repair can be greatest early in life, decreasing rapidly towards the end of lifespan but such investment in repair is non-optimal when extrinsic mortality is high (Cichoń and Kozlowski, 2000). When costs exceed tangible benefits, investment in soma ceases

(Perrin and Sibly, 1993) and resources are allocated towards reproduction rather than somatic maintenance (Cichoń and Kozlowski, 2000). However, trade-offs between fecundity and reproductive output may also offer a better explanation, as the increase is theoretically volumetric (Wootton, 1990). For fish, many life history traits (e.g. growth, lifespan, age of sexual maturity) are closely associated with environmental conditions. Longevity is thought to be enhanced by increased depth, lower water temperature, high pressure, low oxygen levels and relatively limited food supply may slow metabolic rate and life processes (Cailliet et al., 2001). In situations where environmental conditions are in opposition to supposedly more stable deep water environments (e.g. shallow estuarine habitats), we would expect different life history strategies and adaptations to account for these different and varying conditions.

Implications for small fish living in impacted shallow estuarine habitats

In general, estuaries worldwide are well known to be highly variable environments where conditions such as salinity, temperature, turbidity and oxygen concentration can fluctuate rapidly, both temporally and spatially (Dando, 1984; Schelske and Odum, 1959; Selleslagh and Amara, 2008). This is particularly true in shallow estuaries where greater temperature extremes can occur compared to adjacent coastal waters. Drought, rain and flood conditions can also greatly alter the character of estuaries. Besides the obvious effects on temperature and salinity, river spates can cause displacement of sediment from the upper reaches and its deposition into the middle and lower reaches when the estuary broadens and the current slackens (Dando, 1984; Prandle, 2009; Van Rijn, 2004). Conversely low river run-off results in increased tidal scour and the sediment is transported back to the upper reaches.

It is not surprising that mass mortalities of estuarine fish, especially juveniles, are common after sudden changes in water conditions (Bongersma-Sanders, 1957). Abrupt decreases in temperature have been reported to cause larval and juvenile mortalities in many species and may result in the loss of a complete year-class (Dey, 1981; Joseph, 1972; Pepin, 1991; Pihl and Rosenberg, 1982; Sponaugle et al., 2006). Sudden salinity changes can also cause mortalities on estuarine young (Bennett, 1985). Low oxygen levels are another major cause of heavy mortalities in eggs, larvae and juveniles (Bejda et al., 1992; Kohler, 1981; Miller et al., 2002), and is often associated with higher levels of suspended matter in the water and siltation of the benthos.

In Singapore estuaries, small fish (not restricted to just scorpaenoids) inhabiting these shallow (<2 m) tropical habitats face many challenges surviving in this environment. This includes the physical depth-dependent size limitations that are generally imposed on fishes inhabiting such shallow habitats (Ellis and Bell, 2004; Morrison et al., 2002; Schlosser, 1987); the increased variability in temperature, salinity and turbidity through increased outflow from adjacent terrestrial runoff during heavy rainfall (especially along the equator, see Tham 1953); an increased turbidity that is exacerbated by wave action along the littoral zones stirring up the fine sediment (a characteristic of Singapore coastal shores, see Dikou and Woesick 2006). Another important factor that can affect fish communities (regardless of size) is the high amount of reclamation that occurs along the shores of Singapore (Chou, 2011; Dikou and van Woesick, 2006; Glaser et al., 1991; Hilton and Manning, 1995; Tan et al., 2010), which not only causes the loss of marine habitats (e.g. coral reefs and seagrass beds) through smothering (Al-Mandany et al., 1991; Fabricius and Wolanski, 2000; Ralph et al., 2006; Rogers, 1990), but also increases turbidity-related stressors in fish and other organisms (Amesbury, 1981; Cyrus and Blaber, 1992; Fabricius and Wolanski, 2000).

In spite of these challenges, there are small fish species (from juvenile to adult stages) that successfully inhabit these habitats (e.g. small scorpaenoids and small gobies)(Hajisamae and Chou, 2003; Kwik et al., 2010). A possible advantage of living in this highly variable and potentially more stressful environment is the size-related restriction of larger predators (Patterson and Whitfield, 2000) and of other species of fish that could potentially be competitors for resources (Hajisamae et al., 2003; Schlosser, 1987; Whitfield, 1980). Furthermore, the primary productivity in tropical shallow estuarine habitats is high (Qasim, 1973; Schelske and Odum, 1959), resulting in high biomass of zooplankton and other meiobenthos (Burchmore et al., 1984; Dittman, 2000, 2001; Nicolas et al., 2007; Reise, 1991). As such, successful adaptation, potentially through plasticity in life history patterns, by any small fish to this variable habitat, gives access to a highly productive area that is also inaccessible to larger fish (predatory or otherwise).

Conflicting evidence for the extinction of small sized fish in relation to habitat has recently been raised. While a recent meta-analysis of size-dependent extinction in fish by

Olden (2007) has suggested that only freshwater small fish are more at risk of extinction due to anthropogenic effects. Evidence from studies of small coral reef gobies by Munday (2004) has shown that small fish further offshore are just as susceptible to extinction due to habitat loss. In either case, the fact that small tropical estuarine scorpaenoids inhabit an area which is located between habitats investigated by both Olden (2007) and Munday (2004), suggest that small estuarine fish are just as likely (if not more) to be affected by anthropogenic effects and are at higher risk of extinction.

Reclamation in Singapore has occurred at an astounding rate (Hilton and Manning, 1995), with an almost 25% increase in land mass over the last 50 years (Yong et al., 1991). It is likely that this will continue as both the human population and the demands for habitable land increase (Glaser et al., 1991). Results from Chapter 2 suggest that at least four small scorpaenoid species (*Cocotropus echintatus*, *Inimicus brachyrhynchus*, *Inimicus cuvieri* and *Scorpaenodes guamensis*) may have become locally extinct or now occur in much lower abundances presently, and it is uncertain if reclamation might be a factor. However, in spite of all the reclamation and the other environmental changes associated with reclamation (e.g. increased turbidity, loss of habitats, etc.), at least two species of small tropical scorpaenoids still appear to be resilient. Results from Chapter 3 have found that *Paracentropogon longispinis* and *Trachicephalus uranoscopus* are among the most abundant small sized fish inhabiting shallow coastal habitats (from juvenile to adult) that have either been previously reclaimed or are in close proximity to reclaimed areas (Figure 6.1). In many instances of species loss (due to anthropogenic effects), fish (small or large) are known to migrate relatively far away when conditions become intolerable (Childs et al., 2008; Whitfield, 1994). This suggests that small scorpaenoids such as *P. longispinis* and *T. uranoscopus* may be more tolerant to reclamation impacts than expected, as these small scorpaenoids are unlikely to move far from their associated habitats (pers. obs.); this was also observed in a tagging study of a related scorpaenoid species *Synanceia horrida* (unpubl. data). Alternatively, it is also possible that these small scorpaenoids move away during reclamation events and recolonise these soft sediment habitats once conditions have stabilised (to be verified in potential future tagging experiments). It is also possible that anthropogenic effects could reach a critical point where the potential loss of these species could occur (either directly from physiological stressors or indirectly through loss of prey or habitat).

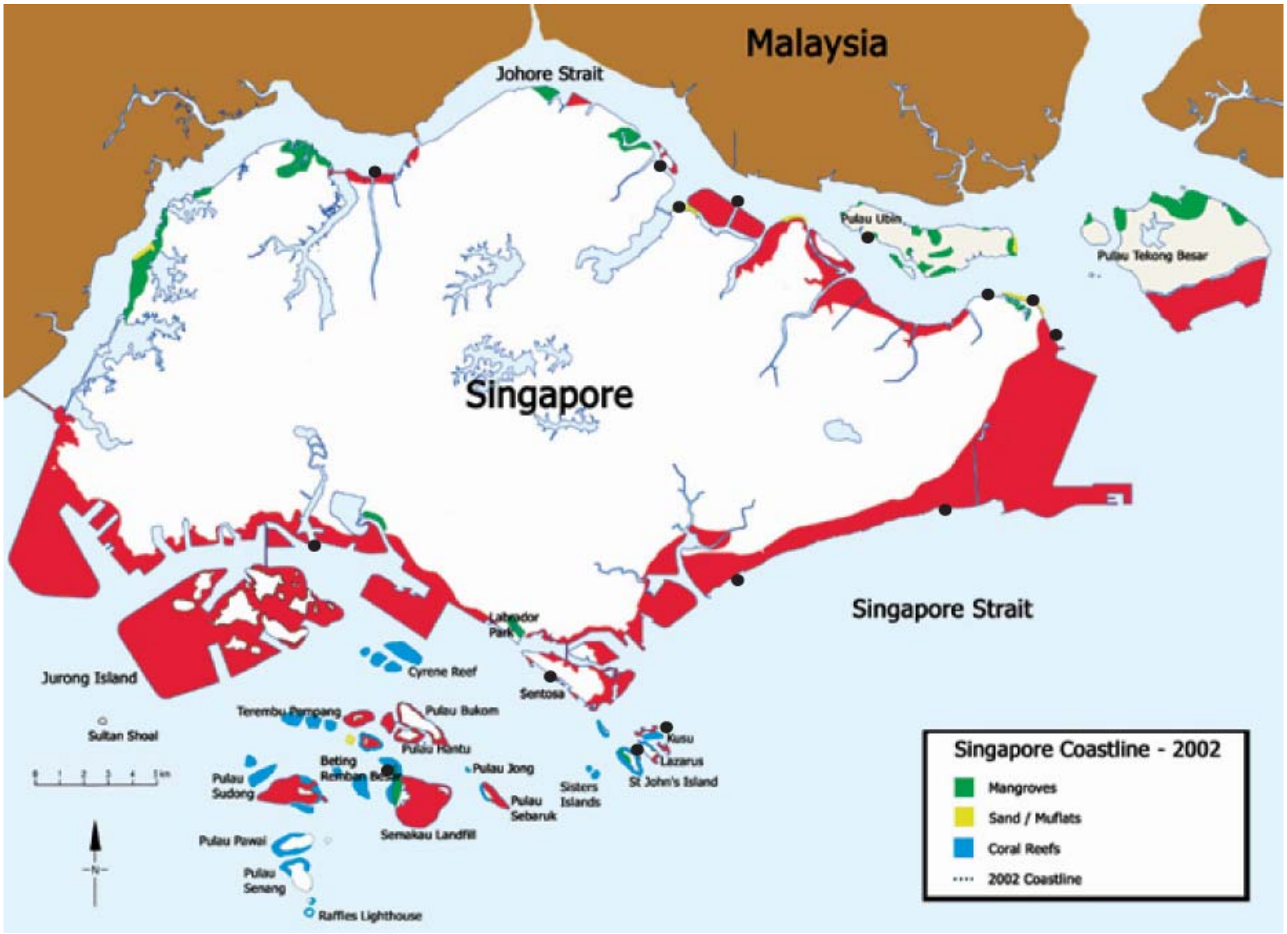

Figure 6.1 Map of Singapore indicating reclamation and changes in general size as of 2002 (where red indicates increase in land mass through reclamation; ● indicates records of small scorpaenoid captures since mid 1990s, map obtained from Singapore Waters: Unveiling our seas by Nature Society of Singapore 2003).

Variations in life history patterns of small tropical scorpaenoids

Successful adaptation or resilience of fishes in an impacted habitat is dependent on trade-offs between nutrients, life history patterns (e.g. growth and reproductive strategies) (Kozlowski, 1992; Kozlowski and Teriokhin, 1999), physiological (Lam et al., 2005; Zimmermann and Kunzmann, 2001) and behavioural traits (Post and Parkinson, 2001; Sargent and Gross, 1993). Moreover, a balanced energy budget is even more important when fish (e.g. scorpaenoids) require resources for investments into morphological or behavioural defences (Steiner and Pferffer, 2007). As such, understanding the types of dietary resources these small scorpaenoids utilised was an important link to how these small fishes survived in these impacted areas.

Both the diets and dietary habitats of both the small scorpaenoids differed greatly in this study. While *P. longispinis* fed primarily on amphipods and other small crustaceans (low energy yield), *T. uranoscopus* fed primarily on the star goby, *Yongeichthys nebulosus* (high energy yield). While feeding behaviour between both small scorpaenoids were different (active foraging versus ambush predation), prey availability for both *P. longispinis* and *T. uranoscopus* was high, either due to high prey abundance (e.g. meiobenthic fauna in soft sediment habitats, see Mallin, 1991; Moller and Rosenberg, 1982) for *P. longispinis*, or reduced competition due to a specialised diet on a poisonous prey item (Brodie and Brodie, 1999) in *T. uranoscopus*. In addition, there appeared to be no clear ontogenetic dietary shifts in the smaller *P. longispinis*, while *T. uranoscopus* appeared to feed on amphipods for a very short period of time after settlement then shifting to fish at a very early stage. In either scorpaenoid species, it appeared that dietary resources were not a limiting factor when living in this shallow estuarine habitat. As such, any life history patterns that are observed are likely to be a good indication of how both these small scorpaenoids have adapted to this environment.

In trying to understand how life history patterns in small scorpaenoids such as *P. longispinis* and *T. uranoscopus* improve resiliency in estuarine habitats, the first question would be how different or similar life history patterns are for *P. longispinis* and *T.*

uranoscopus compared to general life history characteristics found in other fishes. The second would be how such differences might help in improving resiliency of these scorpaenoids in their impacted habitats. Comparisons against the popular *r*- and *K*-selected life history patterns defined by MacArthur and Wilson (1967) indicate that while both *P. longispinis* and *T. uranoscopus* had generally similar characteristics between each other, both these small scorpaenoids did not conform to either *r*- or *K*- selected strategies (Table 6-1). With the exception of egg size and sexual maturity, both the small scorpaenoids appeared to have similar combinations of both *r*- and *K*- selected characteristics (Table 6-1). It is likely that the differences in egg size and age at sexual maturity are associated with the different resource allocation budgets (due to the different diets and behaviour) observed in both *P. longispinis* and *T. uranoscopus*.

Table 6-1 General characteristics of *r*-selected and *K*-selected populations as defined by MacArthur and Wilson (1967) compared to characteristics displayed by the small scorpaenoids *Paracentropogon longispinis* and *Trachicephalus uranoscopus*.

Parameter	***r*-selected**	***K*-selected**	***P. longispinis***	***T. uranoscopus***
Environment	variable and/or unpredictable	constant and/or predictable	variable and/or unpredictable (r)	variable and/or unpredictable (r)
Lifespan	short	long	short (r)	short (r)
Growth rate	fast	slow	slow (k)	slow (k)
Fecundity	high	low	low (k)	low (k)
Natural mortality	high	low	low (k)	low (k)
Population dynamics	unstable	stable	unstable (r)	unstable (r)
Sexual maturity	early	late	early (r)	late (k)
Offspring survival (size at birth)	low	high	low (r)	high (k)
Parental Care	low	high	low (r)	low (r)

While the *r*- and *K*-selected life history strategies defined by MacArthur and Wilson (1967) have generally been accepted as a relatively dependable predictor for life history patterns in fish, there have been arguments if the relationships within each strategy may be more variable and that more strategies may occur (Kozlowski, 1996; Roff et al., 2006; Winnemiller and Rose, 1992). A recent study by Winnemiller and Rose (1992) found that life history strategies were more complex and that three general life history strategies (periodic, opportunistic and equilibrium) could be identified amongst fishes in north America (Table 6-2). To further support observations with regard to previous differences in life history characteristics (against *r*- and *K*- selection), further comparisons were done comparing life history strategies defined by Winnemiller and Rose (1992) to *P. longispinis* and *T. uranoscopus*.

Comparisons in life history strategies between the small scorpaenoids and the three pre-defined strategies by Winnemiller and Rose (1992) indicate that while *T. uranoscopus* leaned towards the equilibrium strategy, *P. longispinis* appeared to lie between both the opportunistic and equilibrium strategy (Table 6-2). Similar to the *r*- and *K*- strategies, the key differences based on the strategies defined by Winnermiller and Rose was age at sexual maturity and egg size. It would appear that both *P. longispinis* and *T. uranoscopus* display life history strategies which are intermediates of general strategies pre-defined by either MacArthur and Wilson (1967) or Winnemiller and Rose (1992). Such intermediate strategies are likely to be associated with the different resource allocation budgets that occur within each scorpaenoid species. In addition, as the feeding niche (including morphological features required for trophic function) probably determines a large proportion of the total environmental variance experienced by an organism (Winnemiller and Rose, 1992), we should expect a variety of fish with divergent life-history strategies to coexist in the same habitat, as seen in *P. longispinis* and *T. uranoscopus*.

Table 6-2 General life history strategies identified as end-points of a trilateral continuum as defined by Winnemiller and Rose (1992) compared to characteristics displayed by the small scorpaenoids *Paracentropogon longispinis* and *Trachicephalus uranoscopus*.

Parameters	**Periodic**	**Opportunistic**	**Equilibrium**	***P. longispinis***	***T. uranoscopus***
Maturation	late	early	late	early	late
Size at maturation	large/intermediate	small	small/medium	small	small
Clutch size	large	small	small	small	small
Egg size	small	small	large	small	large
Growth rates	fast	fast	slow	slow	slow
Reproductive season	short	long	long	long	long
Parental care	-	-	possible	unknown	unknown

For any organism to survive and adapt to an environment, tradeoffs often need to take place within life history strategies (Roff et al., 2006; Roff, 1992; Stearns, 1992). The plasticity of such life history strategies are themselves dependent on the availability and subsequent allocation of resources that contribute towards competing life history traits such as growth, maintenance, reproduction, and storage (Angilletta et al., 2003; Perrin and Sibly, 1993). Moreover, for any organism that has to adapt to variable environmental conditions (such as small estuarine fish), there exists energy expenditures towards physiological tolerances (Wendelaar Bonga, 1997), and this energy comes in the form of nutrition combined with life history strategies that optimise tolerance (Claireaux and Lefrancois, 2007).

While both *P. longispinis* and *T. uranoscopus* have slight differences in reproductive strategies (primarily egg size), other life history traits are relatively similar (lifespan, growth rates, maximum size, low mortality). As such, it is likely that the similar life history traits observed in small scorpaenoids might explain how they have adapted to shallow estuarine habitats. It is also likely that the resource allocation towards surviving in these variable habitats is an important factor. So how might these small scorpaenoids balance resources budgets? A brief overview of life history characters from the various chapters provides some possible ways in which these small scorpaenoids could optimise energy. This include having 1) optimised foraging and predation strategies depending on prey energy costs (low foraging for high energy prey in *T. uranoscopus* versus increased foraging on low energy foods in *P. longispinis*) as observed in Chapter 3; 2) slower, almost linear indeterminate growth as observed in Chapter 4 (balancing both growth and reproduction); and 3) reduced predation pressure from increased defensive mechanisms as observed in low mortalities also in Chapter 4 (energy tradeoffs between defence and survivorship); and 4) limited reproduction (seasonal spawning) under optimal conditions for larval survival (larval dispersal, food for larvae and recruitment) as observed in Chapter 5.

Based on life history strategies, we would expect a short lived organism to spawn almost continuously after reaching sexual maturity (Balon, 1984; Kozlowski, 1992); this was not the case for either *P. longispinis* or *T. uranoscopus*. Although both had different reproductive strategies with regard to egg size and age at maturity, both still spawned during the northeast monsoon period when higher productivity occurred, resulting in higher larval survivorship (Kumari et al., 2002; Pradeem Ram et al., 2003). The shorter lived *P. longispinis* appeared to be semelparous (having only one breeding cycle in its lifetime), and *T. uranoscopus* appeared to be iteroparous with potentially up to two cycles in its lifetime. It is more likely that both these species are abbreviate iteropares (Miller, 1984) as reproductive characteristics in both species lean towards iteroparity (Table 6-3), with extended breeding seasons (almost 3 months in both species). As the environmental variations can be extreme in estuaries, and survivorship of larvae is critical for small species producing few eggs, then this strategy of "saving" energy for egg production during optimum conditions appears to be an effective and feasible strategy along estuarine waters of Singapore.

Table 6-3 General characteristics of life history trade-offs for reproductive strategies as defined by Cole (1954).

Factor	Semelparity	Iteroparity	*P. longispinis*	*T. uranoscopus*
Young survival	Constant or predictable	Variable or unpredictable	Variable or unpredictable	Variable or unpredictable
Adult survival	low	high	high	high
Reproductive behaviour	high energetic cost	low energetic cost	low energetic cost	low energetic cost

Additional adaptations for increased survivorship in small scorpaenoids

Another factor that played an important role in the adaptability of both *P. longispinis* and *T. uranoscopus* was their relatively low mortality rates (Chapter 4). Such low mortalities go against the general paradigm that smaller fish should be subject to higher mortalities due to higher predation pressure, begging the question as to why these fish have such high survivorship? One possibility is the high defensive potential of these fishes (in some respects, similar to the poisonous *Gobiodon* (see Schubert et al., 2003)). While all scorpaenoids are venomous to varying degrees (Austin et al., 1962; Balasubashini et al., 2006; Schaeffer et al., 1971), the role of venom in the ecology of these fish is not well understood. Moreover, almost all (and definitely in *P. longispinis* and *T. uranoscopus*) display cryptic colourations or behaviour, adding to their defensive capabilities (Pers. Obs.). Such investments toward defence must come at high energetic costs, but this could result in the high survivorship observed in juveniles and adults of these tropical scorpaenoids (Steiner and Pferffer, 2007). An unpublished study by Kwik (2011, unpubl. data) found that venom in *S horrida* is more effective against terrestrial animals and less effective against marine animals (e.g. sharks, groupers and snappers). However, there are few records of predators feeding on scorpaenoids, including predation on the red lionfish, *Pterois volitans* by the tiger grouper, *Mycteroperca tigris*, in the Bahamas (Maljkovic et al., 2008); predation of another small lionfish, *Pterois miles*, by the pacific cornetfish, *Fistularia commerson* in Israel (Bernadsky and Goulet, 1991); and the presence of unidentified scorpaenids in the gut contents of Australian fur seals, *Arctocephalus pusillus doriferus* (Hume et al., 2004). Although similar studies on the venom effects of *P. longispinis* and *T. uranoscopus* on marine organisms would have been useful, the small size of both these small scorpaenoids made venom collection difficult. What is clear is that they have relatively well developed spines and venom glands (unpubl. data), and it is with certainty that the venom of juveniles and adult *P. longispinis* and *T. uranoscopus* is painful to human beings (J. Kwik, pers. obs.), and that it is likely that predation on these scorpaenoids (and even perhaps other species) is reduced by their defensive capabilities.

Fishes have evolved physiologically to live within a specific range of environmental variation, and existence outside of that range can be stressful or fatal (Barton et al., 2002). These ranges can coincide for fishes that evolve in similar habitats (Attrill, 2002). The high numbers of small scorpaenoids (both at juvenile and adult sizes) in shallow estuarine habitats suggests that while subject to fluctuating environmental conditions, these small fish have adapted remarkably. This is also seen in another family (i.e. Gobiidae) that also utilise this habitat throughout their lifetime, while the numerous other families found inhabiting this area consist of juveniles to sub-adults only (Kwik et al., 2010). Life history characteristics of these small scorpaenoids appear to have intermediate strategies based on the general characteristics that are commonly defined in most other fishes. As these characteristics are associated with environmental conditions, then it is likely that small scorpaenoids may have adapted to this environment through the evolution of certain life history traits over successive generations.

The life history characteristics displayed by both *P. longispinis* and *T. uranoscopus* occur through tradeoffs between resource allocation and increased survivorship (either through increased physiological tolerances or increased defensive capabilities). The low competition for food resources either between these two species or between other sympatric species, and specific spawning periods allows both species to optimise energy budgets for adaptations to this environment. It is also possible that the challenging nature (affecting both physiological and physical limits of fish) of this habitat, also provides both these two small scorpaenoids a niche habitat which cannot be utilised by many other fishes. However, it is uncertain if there is a critical point at which environmental conditions could be too drastic for these fishes to survive due to increased anthropogenic affects.

Implications and future studies

Many small fish in tropical estuarine habitats remain unstudied. Results from this study so far indicate that small tropical scorpaenoids are unique as they do not conform entirely to general life history patterns found in many other taxa. Due to the paucity of information regarding small tropical fish in estuarine habitats, increased studies in other small tropical fish (e.g. small estuarine gobies) may help to increase present understanding of life history patterns of small tropical estuarine fishes. Furthermore, environmental conditions along the equator are very different from those seen in the majority of studies performed in higher latitudes, which may also help to account for the different life history patterns observed in these small estuarine fish.

In trying to confirm that life history patterns can affect tolerances of small tropical fish, comparative life history studies into another large group of fish (i.e. gobies) is highly recommended, as estuarine gobies have similar characteristics compared to the tropical scorpaenoids investigated during this study (e.g. small size, juvenile to adult sizes inhabiting the same area throughout lifespan, relatively abundant, potentially poisonous, variable diets etc). Assuming that both these groups of fishes are similarly resilient in impacted habitats, then they should display some level of similarity with regards to life history strategies.

Other studies that would also help answer questions of the resilience of small scorpaenoids in these habitats would be studies elucidating the ecological significance of their venom. This may explain how defensive mechanisms may increase survivorship at various developmental stages in these fishes and as a result of resource allocation variations, affect life history strategies or tactics. Moreover, there has been evidence of toxins being sequestered from prey items. With the poisonous *Y. nebulosus* as a prey item for *T. uranoscopus*, there exist the possibility that prey selection for this goby could not only reduce competition with other predators, but might also confer greater defensive potential. This would have to be tested using biochemical and molecular techniques on both the flesh and toxin found in *T. uranoscopus* and *Y. nebulosus*.

Conservation issues of the large scorpaenoid *Synanceia horrida*

Although not the primary study species, *S. horrida* is unique as it has not only been identified as one of the most venomous marine fish in the world (Cooper, 1991; Lee et al., 2004; Ngo et al., 2009) but is also the largest species found in abundance locally (Chapter 2). It is also the one of only tropical species that is known to be commercially harvested (Fewings and Squire, 1999; Richards, 1993) and is marketed relatively widely in Singapore (pers. obs.).

According to anecdotal reports and personal communications, several species of scorpaenoids are targeted for human consumption in countries such as the United States, Italy, Taiwan, Malaysia, Hong Kong, China, Indonesia, Japan and Singapore (Key et al., 2005; La Mesa et al., 2005; Sadovy, 1999). Other species which are collected include the lionfish (Pteroidae) and some other species of scorpionfish for the ornamental aquarium trade (Schofield, 2009). Although frequently collected, there are no data indicating harvest rates or tonnage per annum of these fishes. As little is understood on the population ecology, reproductive biology and growth rates of these fishes, it is difficult to determine the effects of removing these scorpionfish from the ecosystem, especially if the harvest rates cannot be confirmed or controlled at present. In Southeast Asia, some people traditionally believe that there are medicinal benefits in consuming synanceids (Richards, 1993). Although harvesting numbers are uncertain, records from fisheries reports have indicated local extinctions of *S. horrida* in Papua New Guinea where these fish were overharvested to supply not only markets in Southeast Asia (Richards, 1993) but also to supply anti-venom production in other countries (Brown and Fielder 1991).

In addition to harvesting *S. horrida* for food and anti-venom production, *S. horrida* is also collected and culled for public safety in Singapore (pers. obs.). Due to the high volume of tourists attracted to the popular beaches of Singapore and the potential risks of litigation through envenomation events, certain beaches are patrolled and cleared of *S. horrida* in the hopes of reducing envenomation incidences. However, with limited information regarding site fidelity and spawning or recruitment aggregation events of *S. horrida*, it will be interesting to see if the continuous removal of *S. horrida* will actually make a difference to the number of incidences at these beaches.

Conclusion

In general, life history patterns (e.g. growth and reproduction) of organism are limited by nutrient uptake and allocation of resources. For small tropical scorpaenoids such as *Paracentropogon longispinis* and *Trachicephalus uranoscopus*, inhabiting variable environments (such as estuaries) coupled with specialised dietary habits and behaviours, grants access to abundant dietary resources with lower inter- and intraspecific competitive interactions. As a result, growth and reproductive strategies are unlikely to be limited by resources for these small tropical scorpaenoids. However, physiological (variable water conditions) and physical (shallow depths) constraints that occur in tropical estuarine environments, restrict the maximum size to which these fishes can attain. But the advantages of living in this variable habitat (e.g. reduced predation, high productivity) are likely to outweigh such constraints to growth and increased physiological tolerances. In order to survive successfully in this habitat, life history strategies must be "evolved" so that fitness in both species is optimised, regardless of the variable environmental conditions. For both species, this appears to be primarily in the form of reduced growth rates (i.e. balance of resources between growth and reproduction) and restricted spawning periods (i.e. increased survivorship of young during optimum periods). Assuming that dietary resources are not a limiting factor, then it is possible that resources could also be allocated towards 1) physiological tolerances to the variable environmental conditions that occur in tropical estuarine habitats, and also towards 2) increased defensive capabilities which though energetically costly, increases the overall survivorship of both juvenile and adult fishes. Through such adaptations in either life history patterns or resource allocation, it appears that both these species have adapted successfully to this environment, as they have remained resilient and abundant throughout the constant coastal development that occurs in Singapore. This however, may change if environmental stressors reach a critical level beyond the capabilities for these fishes to survive.

Expected Papers from thesis

Kwik J.T.B, Chen P.Z., Sin T.M. & P.K.L. Ng (2010) Diel variations and diversity of fish communities along the unreclaimed shallow coastal of coastal habitats of Changi Point Beach, Singapore. The Raffles Bulletin of Zoology **58(1)**:125-135.

Kwik, J.T.B., Ng, K.L.P. and Sin, T.M. (submitted to Nature in Singapore) Annotated species list of scorpaenoids inhabiting coastal waters of Singapore.

Kwik, J.T.B., Ng, K.L.P. and Sin, T.M. (In prep for The Raffles Bulletin of Zoology) Arms race in stonefish – Evolutionary Redundancy.

Kwik, J.T.B & Yau, Y.H. (in prep for Toxicon) Ecological perspectives of venom from the estuarine stonefish, *S. horrida*.

Kwik, J.T.B., Ng, K.L.P. and Sin, T.M. (in prep for Journal of Fish Biology) Reproductive biology of tropical scorpaenoids of Singapore.

Kwik, J.T.B., Ng, K.L.P. and Sin, T.M. (in prep for Journal of Fish Biology) Growth patterns of tropical scorpaenoids inhabiting estuarine waters of Singapore.

Kwik, J.T.B., Ng, K.L.P. and Sin, T.M. (in prep for Marine Ecology Progress Series) Trophic ecology of small tropical scorpaenoids inhabiting impacted shallow soft sediment estuarine habitats of Singapore.

References

Abesamis RA, Russ GR. 2010. Patterns of recruitment of coral reef fish in a monsoonal environment. Coral reefs 29:911-921.

Adams PB. 1980. Life history patterns in marine fishes and their consequences for fisheries management. Fishery Bulletin 78(1):1-12.

Adams SM, McLean RB. 1985. Estimation of Largemouth Bass, *Micropterus-salmoides* Lacepede, Growth Using the Liver Somatic Index and Physiological Variables. Journal of Fish Biology 26(2):111-126.

Adrim M, Chen IS, Chen ZP, Lim KKP, Tan HH, Yusof Y, Jaafar Z. 2004. Marine fishes recorded from the Anambas and Natuna Islands, South China Sea. Raffles Bulletin of Zoology 11:117-130.

Ahyaudin AB, Bat-Kamaruzaman AK. 1996. The reproductive biology of the cyprinid, *Thynnichthys thynnoides* (Bleeker), in the Chenderoh Reservoir - a small tropical reservoir in Malaysia. hydrobiologia 318:139-151.

Al-Mandany IM, Abdalla MA, Abdu SE. 1991. Coastal zone management in Bahrain: An analysis of social, economic and environmental impacts of dredging and reclamation. Journal of Environmental Management 32(4):335-348.

Alfred ER. 1966. The fresh-water fishes of Singapore. Zoologische Verhandelingen 78:3-77.

Ali TS, Saleh JH, Jabir AA. 2002. Growth oscillation of some Iraqi marine fishes northwest Arabian gulf. Marina Mesopotamica 17(1):13-21.

Allen GR, Adrim M. 2003. Coral reef fishes of Indonesia. Zoological Studies 42(1):1-72.

Allen GR, Erdman MV. 2009. Reef fishes of the Bird's Head Peninsula, West Papua, Indonesia. Check List 5(3):587-628.

Allen GR, Randall JE. 1977. Review of the sharpnose pufferfishes (subfamily Canthigasterinae) of the Indo-Pacific. Records of the Australian Museum 30:475-517.

Allen GR, Swainston R. 1988. The marine fishes of north-western Australia. A field guide for anglers and divers. Western Australian Museum, Perth. 1-70 p.

Amesbury SS. Effects of turbidity on shallow-eater reef fish assemblages in Truk, eastern Caroline Islands; 1981; Manila. p 155-200.

Anderson JT. 1988. A review of size dependent survival during pre-recruit stages of fishes in relation to recruitment. Journal of Northwest Atlantic Fishery Science 8:55-66.

Angel A, Ojeda FP. 2001. Structure and trophic organization of subtidal fish assemblages on the northern Chilean coast: the effect of habitat complexity. marine ecology progress series 217:81-91.

Angilletta MJ, Wilson RS, Navas CA, R.S. J. 2003. Tradeoffs and the evolution of thermal reaction norms. Trends in Ecology & Evolution 18:234-240.

Arendt JD. 1997. Adaptive instrinsic growth rates: an integration across taxa. Quarterly Review of Biology 72:149-177.

Arendt JD, Wilson DS. 1997. Optimistic growht: Competition and Ontogenetic niche-shift select for rapid growth in pumpkinseed sunfish (*Lepomis gibbosus*). Evolution 51(6):1946-1954.

Arul A, Myint Win B, Hamid N. Case study of the Changi east land reclamation project, Singapore; 2008 11-16 August; Arlington, Virginia, United States.

Attrill MJ. 2002. Community-level indicators of stress in aquatic ecosystems. In: Adams SM, editor. Biological Indicators of Ecosystem Stress. Bethesda, MD: American Fisheries Society. p 473-508.

Austin L, Cairncross KD, McCallum IAN. 1962. Some pharmacological actions of the venom of the stonefish, *Synanceja horrida*. Toxicon 1(1):45-45.

Avise JC, Mank JE. 2009. Evolutionary perspectives on hermaphroditism in fishes. Sexual Development 3:152-163.

Bagenal TB, Tesch FW. 1978. Age and growth. In: Bagenal T, editor. Methods for the assessment of fish production in fresh waters 3rd ed: Blackwell Scientific Publications. p 365.

Bakay YI, Mel'nikov SP. 2008. Biological and Ecological Characteristics of Deepwater Redfish *Sebastes mentella* (Scorpaenidae) at Different Depths in the Pelagial of the Irminger Sea. Journal of Ichthyology 48(1):68-80.

Baker R, Sheaves M. 2005. Redefining the piscivore assemblages of shallow estuarine nursery habitats. Marine Ecology Progress Series 291:197-213.

Baker R, Sheaves M. 2006. Visual surveys reveal high densities of large piscivores in shallow estuarine nurseries. Marine ecology progress series 323:75-82.

Balasubashini MS, Karthigayan S, Somasundaram ST, Balasubramanian T, Viswanathan P, Menon VP. 2006. In vivo and in vitro characterization of the biochemical and pathological changes induced by lionfish (*Pterios volitans*) venom in mice. Toxicology Mechanisms and Methods 16(9):525-531.

Ballantine DL, Navarro JN, Hensley DA. 2001. Algal colonization of Caribbean Scorpionfishes. Bulletin Of Marine Science 69(3):1089-1094.

Balon EK. 1984. Patterns in evolution of reproductive styles in fishes. In: Potts GW, Wootton R, J, editors. Fish reproduction: strategies and tactics. New York: Academic Press. p 35-53.

Barbour AB, Montgomery ML, Adamson AA, Diaz-Ferguson E, Silliman BR. 2010. Mangrove use by the invasive lionfish *Pterois volitans*. Marine Ecology Progress Series 401:291-294.

Baroiller JF, Guigen Y, Fostier A. 1999. Endocrine and environmental aspects of sex differentiation in fish. Cellular and Molecular Life Sciences 55:910-931.

Barton BA, Morgan JD, Vijayan MM. 2002. Physiological and condition-related indicators of environmental stress in fish. In: Adams SM, editor. Biological Indicators of Ecosystem Stress. Bethesda, MD: American Fisheries Society. p 111-148.

Beerkircher L, Arocha F, Barse A, Prince E, Restrepo V, Serafy J, Shivji M. 2009. Effects of species misidentification on population assessment of overfished white marlin *Tetrapturus albidus* and roundscale spearfish *T. georgii*. Endagered Species Research 9:81-90.

Bejda AJ, Phelan BA, Studholme AL. 1992. The effect of dissolved oxygen on the growth of young-of-the-year winter flounder,*Pseudopleuronectes americanus*. Environmental Biology of Fishes 34(3):321-327.

Bennett BA. 1985. A mass mortality of fish associated with low salinity conditions in the Bot river estuary. Transactions of the Royal Society of South Africa 45(3-4):437-447.

Bennett P. *Pterois russellii novi* species. 1831. p 128.

Berkeley S, Chapman C, Sogard SM. 2004. Maternal age as a determinant of larval growth and survival in marine fish, *Sebastes melanops*. Ecology 85(5):1258-1264.

Bernadsky G, Goulet D. 1991. A Natural Predator of the Lionfish, *Pterois miles*. Copeia 1:230-231.

Beverton RJH, Holt SJ. 1960. A review of the life span and mortality rates of fish in nature and their relation to growth and other physiological characteristics. In: Wolstenholme GEW, Connor MD, editors. Ciba Foundation Colloquia on Ageing, The Lifespan of Animals. Boston: Lillie, Brown and Co. p 142-177.

Bilgin S, Celik ES. 2009. Age, growth and reproduction of the black scorpionfish, *Scorpaena porcus* (Pisces, Scorpaenidae), on the Black Sea coast of Turkey. . Journal of Applied Icthyology 25:55-60.

Blaber SJM, Brewer DT, Salini JP. 1995. Fish Communities and the Nursery Role of the Shallow Inshore Waters of a Tropical Bay in the Gulf of Carpentaria, Australia. Estuarine and Coastal Marine Science 40:177-193.

Blackburn TM, Gaston KJ. 1994. Animal body size distributions: Patterns, mechanisms and implications. Trends in Ecology & Evolution 9:471-474.

Blackburn TM, Gaston KJ, Loder N. 1999. Geographic gradients in body size: a clarification of Bergmann's rule. Divers Distribution 5:165-174.

Bleeker ET. 1849. Bijdrage tot de kennis der Scleroparei van den Soenda-Molukschen Archipel. Verhandelingen van het Bataviaasch Genootschap van Kunsten en Wettenschappen 22(1-10).

Bleeker ET. 1859. Nat. Tyds. Ned. Indie.

Bleeker ET. 1861. Akad. Wet. Amsterdam, Verslag.

Bleeker ET. 1874. Révision des espèces insulindiennes de la famille des Synancéoïdes. Natuurkundige Verhandelingen van de Hollandsche Maatschappij der Wetenschappen te Haarlem 2(3):1-22, Pls 21-24.

Bleeker ET. 1876a. Akad. Wet. Amsterdam. Verslag. 16(2):p25, pl.22, fig.22.

Bleeker ET. 1876b. Mémoire sur les espèces insulindiennes de la famille des Scorpénoïdes. Verslagen en Mededeelingen der Koninklijke Akademie van Wetenschappen. . Afdeling Natuurkunde v 16:1-100, Pls. 101-105.

Bleeker P. 1852. Nieuwe bijdrage tot de kennis der ichthyologische fauna van Ceram. Natuurkundig Tijdschrift voor Nederlandsch Indië v. 3: 689-714.

Bloch ME. 1787. Naturgeschichte der ausländischen Fische. Berlin. Naturgeschichte der Ausländischen Fische 3(i-xii):1-146, Pls. 181-216.

Bloch ME, Schneider JG. 1801. M. E. Blochii, Systema Ichthyologiae iconibus cx illustratum. Post obitum auctoris opus inchoatum absolvit, correxit, interpolavit Jo. Gottlob Schneider, Saxo. Berolini. Sumtibus Auctoris Impressum et Bibliopolio Sanderiano Commissum. Systema Ichthyologiae i-lx:1-584, Pls. 581-110.

Blueweiss L, Fox H, Kudzma V, Nakashima D, Peters R, Sams S. 1978. Relationships between body size and some life history parameters. Oecologia 37:257-272.

Bo MW, Chu J, Choa V. 2005. Chapter 9 The Changi east reclamation project in Singapore. 247-276 p.

Boehlert GW, Kappenman RF. 1980. Variation of growth with latitude in two species of Rockfish (*Sebastes pinniger* and *S. diploproa*) from the Northeast Pacific Ocean. Marine Ecology Progress Series 3:1-10.

Bongersma-Sanders M. 1957. Mass mortality in the sea. In Treatise on Marine Ecology and Paleoecology. Memoirs of the Geological Society of America 67:941-1010.

Brain M, St John M, Wieland K. 1996. Eastern Baltic cod: perspectives from existing data on processes affecting growth and survival of eggs and larvae. Marine Ecology Progress Series 134:265-281.

Brenneke F, Hatz C. 2006. Stonefish envenomation--a lucky outcome. Travel Med Infect Dis 4(5):281.

Brewer DT, Blaber SJM, Salini JP, Farmer MJ. 1995. Feeding Ecology of Predatory Fishes from Groote Eylandt in the Gulf of Carpentaria, Australia, with Special Reference to Predation on Penaeid Prawns. Estuarine, Coastal and Shelf Science 40(5):577-600.

Brickle P, V. Laptikhovsky V, Pompert J, Bishop A. 2003. Ontogenetic changes in the feeding habits and dietary overlap between three abundant rajid species on the Falkland Islands' shelf. Journal of the Marine Biological Association of the UK 83:1119-1125.

Brodie ED, Brodie EDJ. 1999. Costs of exploiting poisonous prey: evolutionary trade-offs in a predator-prey arms race. Evolution 53(2):626-631.

Brooks S, Tyler CR, Sumpter JP. 1997. Egg quality in fish: What make a good egg? Reviews in Fish Biology and Fisheries 7:387-416.

Brown IW, Fielder DR. 1991. The Coconut Crab: Aspects of *Birgus latro* biology and ecology in Vanuatu. ACIAR Monograph No , Canberra 1991 8.

Brusle S, Debas L, Cauty C. Morphological and cytological aspects of sex inversion in a protogynous hermaphrodite *Epinephelus microdon* (Teleostei, Serranidae); 1989; Tahiti. p 559-562.

Bulman C, Althaus F, He X, Bax NJ, Williams AJ. 2001. Diets and trophic guilds of demersal fishes of the south-eastern Australian shelf. Marine and Freshwater Research 52:537-548.

Burchmore JJ, Pollard DA, Bell JD. 1984. Community structure and trophic relationships of the fish fauna of an estuarine *Posidonia Australis* seagrass habitat in port hacking, new South Wales. Aquatic Botany 18(1-2):71-87.

Burrows MT. 1994. An optimal foraging and migration model for juvenile plaice. Evolutionary ecology 8(2):125-149.

Butcher JG 2004. The closing of the frontier: a history of the marine fisheries of Southeast Asia c. 1850–2000. Pasir Panjang, Singapore, Institute of Southeast Asian Studies.

Bye VJ. 1984. The role of environmental factors in the timing of reproductive cycles. In: Potts GW, Wootton RJ, editors. Fish reproduction: Strategies and tactics. London: Academic Press. p 410.

Cabral HN. 2003. Differences in growth rates of juvenile *Solea solea* and *Solea senegalensis* in the Tagus estuary, Portugal. Journal of the Marine Biological Association of United Kingdom 83(3944):1-8.

CAFS. 2007. Database of genetic resources of aquatic organisms in China (as of January 2007). Chinese Academy of Fishery Science.

Cailliet GM, Andrews AH, Burton EJ, Watters DL, Kline DE, Ferry-Graham LA. 2001. Age determination and validation studies of marine fishes: do deep-dwellers live longer? Experimental Gerontology 36(4-6):739-764.

Calder WA. 1984. Size, function, an life history. . Cambridge Massachussetts USA: Harvard University Press.

Calder WA. 1985. Size and metabolism in natural systems. In: Ulanowicz RE, Platt T, editors. Ecosystem Theory for Biological Oceanography. Department of Fisheries and Oceans, Ottawa. 260 pp.: Canadian Bulletin of Fisheries and Aquatic Sciences. p 65-75.

Campana SE, Neilson JD. 1985. Microstructure of fish otoliths. Canadian Journal of Fisheries and Aquatic Sciences 42:1014-1032.

Cantor TE. 1849. Catalogue of Malayan fishes. Journal and Proceedings of the Asiatic Society of Bengal 18(2):i-xii + 983-1443, Pls. 1441-1414.

Caputo V, Candi G, La Mesa M, Arneri E. 2000. Pattern of gonad maturation and the question of semelparity in the paedomorphic goby *Aphia minuta*. Journal of Fish Biology 58:656-669.

Caputo V, M.L. M, Candi G, Cerioni PN. 2003. The reproductive biology of the crystal goby with a comparison to that of the transparent goby. Journal of Fish Biology 62:375-385.

Carlisle TR. 1985. Parental response to brood size in a cichlid fish. Animal Behaviour 33(1):234-238.

Carpenter KE, Niem VH. 1999. FAO species identification guide for fishery purposes: The living marine resources of the western central pacific. Rome.

Carr MH. 1991. Habitat selection and recruitment of an assemblage of temperate zone reef fishes. Journal of Experimental Marine Biology and Ecology 146:113-137.

Chabanet P, Ralambondrainy H, Amanieu M, Faure G, Galzin R. 1997. Relationships between coral reef substrata and fish. Earth and Environmental Sciences 16(2):93-102.

Charnov EL. 1993. Life-history invariants: some explanations of symmetry in evolutionary ecology: Oxford University Press.

Charnov EL. 2008. Fish growth: Bertanlanffy k is proportional to reproductive effort. Environmental Biology of Fishes 83:185-187.

Chen Y, Jackson DA, Harvey HH. 1992. A comparison of Von Bertanlanffy and polynomial functions in modelling fish growth data. Canadian Joural of Fisheries and Aquatic Science 49:1228-1235.

Cheong L. 1996. Overview of the current international trade in ornamental fish, with special reference to Singapore. Reviews in Science and Technology 15(2):445-481.

Chia LS, Khan H, Chou LM. 1988. The coastal environmental profile of Singapore. Manila, Phillipines: International Center for Living Aquatic Resources Management. 92 p.

Chidester FE. 1922. Studies on fish migration II. The influence of salinity on the disperal of fishes. The American Naturalist 56(645):373-380.

Childs AR, Cowley PD, Næsje TF, Booth AJ, Potts WM, Thorstad EB, Økland F. 2008. Do environmental factors influence the movement of estuarine fish? A case study using acoustic telemetry. Estuarine, Coastal and Shelf Science 78:227-236.

Choat JH, Robertson DR. 2002. Age-based studies. In: Sale PF, editor. Coral reef fishes: dynamics and diversity in a complex ecosystem. San Diego: Academic Press. p 57-80.

Chou LM. Importance of Southeast Asian marine ecosystems in biodiversity maintenance. In: Turner IM, Diong CH, Lim SSL, Ng PKL, editors; 1996. p 227–235.

Chou LM. 2011. Coastal Ecosystems. In: Ng PKL, Corlett RT, Tan HTW, editors. Singapore Biodiversity: An encyclopaedia of the natural environment and sustainable development. Singapore: Didier Millet. p 76-87.

Chuang SH. 1961. On Malayan Shores. Singapore: Muwu Shosa. 225 p.

Chuang SH. 1973. Animal life and nature in Singapore. Singapore: Singapore University Press. 320 p.

Cichoń M, Kozlowski J. 2000. Ageing and typical survivorship curves result from optimal resource allocation. Evolutionary Ecology Research 2:857-870.

Claireaux G, Lefrancois C. 2007. Linking environmental variability and fish performance: integration through the concept of scope for activity. Philosophical Transactions of the Royal Society B 362:2031-2041.

Clarke KR. 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18:117-143.

Clarke KR, Warwick RM. 2001. Changes in marine communities: an approach to statistical analysis and interpretation. . Plymouth, United Kingdom. 172 p.

Cole LC. 1954. The population consequences of life history phenomena Quarterly Review of Biology 29:103-137.

Connell SD. 1998. Patterns of pisciviory by resident predatory reef fish at One Tree Reef, Great Barrier Reef. Marine and Freshwater Research 49:25-30.

Cooper NK. 1991. Historical vignette--the death of an Australian army doctor on Thursday Island in 1915 after envenomation by a stonefish. Journal Of The Royal Army Medical Corps 137(2):104.

Coull BC. 1999. Role of meiofauna in estuarine soft-bottom habitats. Australian Journal of Ecology 24(4):327-343.

Crossin GT, Hinch SG, Cooke SJ, Cooperman MS, Patterson DA, Welch DW, Hanson KC, Olsson I, English KK, Farrell AP. 2009. Mechanisms influencing the timing and success of reproductive migration in a capital breeding semelparous fish species, the Sockeye Salmon. Physiological and Biochemical Zoology 82(6):635-652.

Cushing DH. 1987. Population biology and the management of fisheries. Trends in Ecology & Evolution 2:138-139.

Cuvier G, Valenciennes A. 1829. Tome quatrième. Livre quatrième. Des acanthoptérygiens à joue cuirassée. . Histoire naturelle des poissons 4(i-xxvi (2)):1-518, Pls. 572-599, 597 bis.

Cyrus DP, Blaber SJM. 1992. Turbidity and Salinity in a Tropical Northern Australian Estuary and their Influence on Fish distribution. Estuarine and Coastal Marine Science 35:545-563.

Dando PR. 1984. Reproduction in estuarine fish. In: Potts GW, Wootton RJ, editors. Fish reproduction: Strategies and tactics. London: Academic Press. p 410.

De la Paz RM, Aragones N, Agulto D. 1988. Coral-reef fishes off western Calatagan, Batangas (Luzon Island, Philippines) with notes on new and rare captures and controversial taxa. Philippine Journal of Science 117:237-318.

de Medeiros PR, Costa Ramos RT. 2007. Prediciting ecomorphological patterns from morphology of a tropical estuarine fish assemblage. Biociencias 15(1):40-46.

Deblois EM, Leggett WC. 1991. Functional response and potential impact of invertebrate predators on benthic fish eggs: analysis of the *Callioius laeviusculus*-capelin (Mallotus villosus) predator-prey system. Marine Ecology Progress Series 69:205-206.

Deng D-F, Koshio S, Yokoyama S, Bai SC, Shao Q, Cui Y, Hung SSO. 2003. Effects of feeding rate on growth performance of white sturgeon (*Acipenser transmontanus*) larvae. Aquaculture 217(1-4):589-598.

Depczynski M, Bellwood DR. 2005. Shortest recorded vertebrate lifespan found in a coral reef fish. . Current Biology 15(8):288-289.

Depczynski M, Bellwood DR. 2006. Extremes, plasticity, and invariance in vertebrate life history traits: insights from coral reef fishes. Ecology 87(2):3119-3127.

Dey WP. 1981. Mortality and growth of young-of-the-year striped bass in the Hudson River Estuary. Transactions of the American Fisheries Society 110:151-157.

Dikou A, van Woesick R. 2006. Survival under chronic stress from sediment loads: Spatial patterns of hard coral communities in the southern islands of Singapore. Marine Pollution Bulletin 52(1):7-21.

Dittman S. 2000. Zonation of benthic communities in a tropical tidal flat of north-east Australia. Journal of Sea Research 43:33-51.

Dittman S. 2001. Abundance and distribution of small infauna in mangroves of Missionary Bay, North Queensland, Australia. Revista de Biologia Tropical 49(2).

Doebeli M, Blarer A. 1997. A note on the timing of tradeoffs in discrete life history models. Journal of Evolutionary Biology 10:107-120.

Doherty P, Fowler A. 1994. An empirical test of recruitment limitation in a coral reef fish. Science 263:935-939.

Doherty PJ. 1983. Diel, lunar and seasonal rhythms in the reproduction of two tropical damselfishes: *Pomacentrus flavicauda* and *P. wardi*. Marine Biology 75(2-3):215-224.

Duarte CM, Alcaraz M. 1989. To produce many small eggs or few large eggs: a size dependent reproductive tactic of fish. Oecologia 80:401-404.

Duarte DW, Moreno CA. 1981. The specialized diet of *Harpagifer bispinis*: its effect on the diversity of Antarctic intertidal amphipods. Hydrobiologia 80:241-250.

Dulcic J, Jug-Dujakovic J, Bartulovic V, Glamuzina B, Haskovic E, Skaramuca B. 2007. Embryonic and larval development of largescaled scorpionfish *Scorpaena scrofa* (Scorpaenidae). Cybium 31(4):465-470.

Duncker A. 1903. Naturh. mus. Hamburg, mitteil.

Echeverria TW. 1986. Sexual dimorphism in four species of rockfish genus Sebastes (Scorpaenidae). Environmental Biology of Fishes 15:181-190.

Echeverria TW. 1987. Thirty-four species of california rockfishes: maturity and seasonality of reproduction. Fishery Bulletin 85(2):229-250.

Ellis WL, Bell SS. 2004. Conditional use of mangrove habitats by fishes: Depth as a cue to avoid predators. Estuaries and Coasts 27(6):966-976.

Endean R. 1962. A study of the distribution, habitat, behaviour, venom apparatus, and venom of the stonefish. Toxicon 1(1):43-44.

Engen S, Sæther BE. 1994. Optimal allocation of resource to growth and repdocution. Theoretical Population Biology 48:126-171.

Erkoyuncu I, Erdem M, Samsun O, zdamar E, Kaya Y. 1994. A research on determination of meat yield, chemical structure, and length-weight relationship of some fish caught in the Black Sea. Istanbul University Journal of Fish and Aquatic Science 8:181-191.

Eschmeyer WN. 2010. Catalog of Fishes electronic version.

Eschmeyer WN, Rama-Rao KV, Hallacher LE. 1979. Fishes of the scorpionfish subfamily Choridactylinae from the western Pacific and the Indian Ocean. Proceedings of the California Academy of Sciences 41(21):475-500.

Fabricius KE, Wolanski E. 2000. Rapid smothering of coral reef organisms by muddy marine snow. Estuarine, Coastal and Shelf Science 50:115-120.

Feary DA, Almany GR, Jones GP, McCormick MI. 2007. Coral degradation and the structure of tropical reef fish communities.

Ferraris CJ, McGrouther MA, Parkinson KL. 2000. A critical review of the types and putative types of southern Asian marine and freshwater fish species in the Australian Museum named by Francis Day. Records of the Australian Museum 52:289-306.

Fewings DG, Squire LC. 1999. Notes on the reproduction of estuarine stonefish *Synanceia horrida*. 31-33 p.

Fishelson L. 1997. Experiments and observations on food consumption, growth and starvation in *Dendrochirus brachypterus* and *Pterois volitans* (Pteroinae, Scorpaenidae). Environmental Biology of Fishes 50:391-403.

Fisher JAD, Frank KT, Leggett WC. 2010. Global variation in marine fish body size and its role in biodiversity–ecosystem functioning. Marine ecology progress series 405:1-13.

Fonseca VF, Cabral HN. 2007. Are fish early growth and condition patterns related to life-history strategies? Reviews in Fish Biology and Fisheries 17:545-564.

Forward RB, Tankersley, R. A., and Reinsel, K. A. 1998. Selective tidal stream transport of spot (*Leistomus xanthurus* Lacepède) and pinfish (*Lagodon rhomboides* Linneaus) larvae: contribution of circatidal rhythms in activity. Journal of Experimental Marine Biology and Ecology 226:19-32.

Foster SA, Baker JA. 1995. Evolutionary interplay between ecology, morphology and reproductive behavior in threespine stickleback, *Gasterosteus aculeatus.* Environmental Biology of Fishes 44:213-223.

Fowler HW. 1938. A list of the fishes known from Malaya. Singapore: Kelly and Walsh Ltd.

Fricke R. 1999. Fishes of the Mascarene Islands (Réunion, Mauritius, Rodriguez): an annotated checklist, with descriptions of new species. . Koenigstein: Koeltz Scientific Books. 31:759 p.

Fricke R. 2005. Types in the fish collection of the Staatliches Museum für Naturkunde in Stuttgart, described in 1845-2004. Stuttgarter Beiträge zur Naturkunde Serie A (Biologie) 684(1-95).

Froese R, Pauly D. 2010. FishBase. World Wide Web electronic publication.

Fugita H, Kohda M. 1998. Timing and sites of parturition of the viviparous scorpionfish, *Sebastiscus marmoratus*. Environmental Biology of Fishes 52(1-3):225-229.

Fujita H, Kohda M. 1996. Male mating effort in the viviparous scorpionfish, *Sebastiscus marmoratus*. Ichthyological Research 43(3):247-255.

Fulton TW. 1911. The sovereignity of the sea. London, Edinburgh. 799 p.

Gadgil M, Bossert WH. 1970. Life historical consequences of natural selection. American Naturalist 104:1-24.

Gadgil M, Solbrig OT. 1972. The concept of r- and K- selection: evidence from wild flowers and some theoretical considerations. American Naturalist 106:14-31.

Gaillard JM, Yoccoz NG, Lebreton JD, Bonenfont C, Devillard S, Loison A, Pontier D, Allaine D. 2005. Generation time: a reliable metric to measure life-history variation among mammalian populations. American Naturalist 166:119-123.

Galis F, de Jong PW. 1988. Optimal foraging and ontogeny; food selection by *Haplochromis piceatus*. Oecologia 75:175-184.

Garcia AM, Bemvenuti MA, Vieira JP, Motta Marques DML, Bums MDM, Moresco A, Vinicius M, Condini L. 2006. Checklist comparison and dominance patterns of the fish fauna at Taim Wetland, South Brazil. Neotropical Ichthyology 4(2):261-268.

Gaston KJ. 1996. The multiple forms of the interspecific abundance-distribution relationship. Oikos 76:211-220.

Gatz AJ. 1979. Community organization in fishes as indicated by morphological features. Ecology 60(4):711-718.

Gelwick FP, Matthews WJ. 2007. Trophic Relations of Stream Fishes. Methods in Stream Ecology (Second Edition). San Diego: Academic Press. p 611-635.

Gerking SD. 1994. Feeding ecology of Fish. San Diego, California: Academic Press. 416 p.

Ghiselin MT. 1969. The evolution of hermaphroditism among animals. Quarterly Review of Biology 44:189-208.

Glaser R, Haberzett P, Walsh RPD. 1991. Land reclamation in Singapore, Hong Kong and Macau. Geojournal 24(4):365-373.

Gosline WA. 1996. Structures associated with feeding in three broad-mouthed, benthic fish groups. Environmental Biology of Fishes 47:399-405.

Grandcourt EM, Al Abdessalaam TZ, Francis F, Al Shamsi AT. 2004. Biology and stock assessment of the Sparids, *Acanthopagrus bifasciatus* and *Argyrops spinifer* (Forsskål, 1775), in the Southern Arabian Gulf. Fisheries Research 69(1):7-20.

Gratwicke B, Petrovic C, Speight MR. 2006. Fish distribution and ontogenetic habitat preferences in non-estuarine lagoons and adjacent reefs. Environmental Biology of Fishes 76(2-4):191-210.

Gray CA, Kennelly SJ. 2003. Catch characteristics of the commercial beach-seine fisheries in two Australian barrier estuaries. Fisheries Research 63(3):405-422.

Gray JE. 1830-1835. Illustrations of Indian zoology; chiefly selected from the collection of Major-General Hardwicke, F.R.S. p Pls. 1-202.

Grobecker D. 1983. The "lie-in-wait" feeding mode of cryptic teleost, *Synanceia verrucosa*. Environmental Biology of Fishes 8(3):191-202

Grossman GD, Coffin R, Moyle PB. 1980. Feeding ecology of the Bay Goby (Pisces: Gobiidae). Effects of behavioral, ontogenetic, and temporal variation on diet. Journal of Experimental Marine Biology and Ecology 44(1):47-59.

Grzimek B. 2003. Fishes. In: Schlager N, editor. Grzimek's Animal Life Encyclopedia. 2 ed. Farmington Hills, MI The Gale Group.

Guest MA, Connolly RM, Loneragan NR. 2003. Seine nets and beam trawls compared by day and night for sampling fish and crustaceans in shallow seagrass habitat. Fisheries Research 64(2-3):185-196.

Guidetti P, Fanelli G, Fraschetti S, Terlizzi A, Boero F. 2002. Coastal fish indicate human-induced changes in the Mediterranean littoral. Marine Environmental Research 53(1):77-94.

Guidetti P, Terlizzi A, Fraschetti S, Boero F. 2003. Changes in Mediterranean rocky-reef fish assemblages exposed to sewage pollution. Marine Ecology Progress Series 253:269-278.

Gunderson DR. 1974. Availability, size composition, age composition. and growth characteristics of Pacific ocean perch (*Sebastes alutus*) off the northern Washington coast during 1967-72. Journal of the Fisheries Research Board Canada 31:21-34.

Gunderson DR. 1997. Trade-off between reproductive effort and adult survival in oviparous and viviparous fishes. Journal of Fisheries and Aquatic Sciences 54:990-998.

Günther A. 1860. Catalogue of the acanthopterygian fishes in the collection of the British Museum. 2. Squamipinnes, Cirrhitidae, Triglidae, Trachinidae, Sciaenidae, Polynemidae, Sphyraenidae, Trichiuridae, Scombridae, Carangidae, Xiphiidae. British Mus., London. i-xxi + 1-548. p.

Hajisamae S, Chou LM. 2003. Do shallow water habitats of an impacted coastal strait serve as nursery grounds for fish? Estuarine Coastal and Shelf Science 56:281-290.

Hajisamae S, Chou LM, Ibrahim S. 2003. Feeding habits and trophic organization of the fish community in shallow waters of an impacted tropical habitat. Estuarine, Coastal and Shelf Science 58:89-98.

Haldorson L, Love MS. 1991. Maturity and fecundity in the rockfishes, Sebastes spp., a review. Marine Fisheries Review 53(2):25-31.

Hallacher LE, Roberts DA. 1985. Differential utilization of space and food by the inshore rockfishes (Scorpaenidae: Sebastes) of Carmel Bay, California. Environmental Biology of Fishes 12(2):91-110.

Harden Jones FR. 1968. Fish migrations. Arnold E, editor. London. 325 p.

Hare JA, Whitfield PE. 2003. An integrated assessment of the introduction of lionfish (*Pterois volitans/miles* complex) to the western Atlantic Ocean. NOAA Technical Memorandum NOS NCCOS 2:iiv, 1-21.

Harley CDG, Hughes AR, Hultgren KM, Miner G, Sorte CJB, Thomber CS, Rodriguez LF, Tomanek L, Williams SL. 2006. The impact of climate change in coastal marine systems. Ecology letters 9:228-241.

Harmelin-Vivien ML, Bouchon C. 1976. Feeding behavior of some carnivorous fishes (Serranidae and Scorpaenidae) from Tuléar (Madagascar) Marine Biology 37(4):329-340.

Harmelin-Vivien ML, Kaim-Malka RA, Ledoyer M, Jacob-Abraham SS. 1989. Food partitioning among scorpaenid fishes in Mediterranean seagrass beds. . Journal of Fish Biology 34:715-734.

Helfman GS, Collette BB, Facey DE. 1997. The diversity of fishes. London, England: Blackwell Science.

Hernaman V, Munday PL. 2005a. Life-history characteristics of coral reef gobies. I. Growth and life-span. Marine ecology progress series 200:207-221.

Hernaman V, Munday PL. 2005b. Life-history characteristics of coral reef gobies. II. Mortality rate, mating system and timing of maturation. Marine ecology progress series 200:223-237.

Herre AWCT, Myers GS. 1937. A Contribution to the Ichthyology of the Malay Peninsula: Straits Settlements. 8 pl, 75 pp.

Hewitt DA, Hoenig JM. 2005. Comparison of two approaches for estimating natural mortality based on longevity. Fisheries Bulletin 103:433-437.

Hickford MJH, Schiel DR. 2003. Comparative dispersal of larvae from demersal versus pelagic spawning fishes. Marine Ecology Progress Series 252:255-271.

Hightower JE, Grossman GD. 1985. Comparison of Constant Effort Harvest Policies for Fish Stocks with Variable Recruitment. Canadian Journal of Fisheries and Aquatic Sciences 42:982-988.

Hildrew AG, Raffaelli DG, Edmonds-Brown R. 2007. Body size: the structure and function of aquatic ecosystems: Cambridge University Press. 343 p.

Hilton MJ, Manning SS. 1995. Conversion of coastal habitats in Singapore: Indications of unsustainable development. Environmental Conservation 22:307-322.

Hislop JRG. 1984. A comparison of the reproductive tactics and strategies of cod, haddock, whiting and Norway pout in the Northern Sea. In: Ports GW, Wooton RJ, editors. Fish reproduction: strategies and tactics. Oxford: Academic Press. p 311-330.

Hislop JRG. 1988. The influence of maternal length and age on the size and weight of the eggs and the relative fecundity of the haddock, *Melanogrammus aeglefinus*, in British water. Fish Biology 32:923-930.

HjaltiÍJákupsstovu S, Haug T. 1988. Growth, sexual maturation, and spawning season of Atlantic halibut, *Hippoglossus hippoglossus*, in Faroese waters. Fisheries Research 6(3):201-215.

Hoenig JM. 1983. Empirical use of longevity data to estimate mortality rates. Fisheries Bulletin 82:898-903.

Hoese DF, Bray DJ, Paxton JR, Allen GR. 2006. Fishes. Beasley OL, Wells A, editors. Australia: ABRS & CSIRO Publishing. Part 1, pp. xxiv 1-670; Part 672, pp. xxi 671-1472; Part 1473, pp. xxi 1473-2178 p.

Huh S-H, Kitting CL. 1985. Trophic relationships among concentrated populations of small fishes in seagrass meadows. Journal of Experimental Marine Biology and Ecology 92(1):29-43.

Hume F, Hindell MA, Pemberton D, Gales R. 2004. Spatial and temporal variation in the diet of a high trophic level predator, the Australian fur seal (*Arctocephalus pusillus doriferus*). Marine Biology 144(3):407-415.

Hunter JR, Macewicz BJ. 1987. Measurement of Spawning Frequency in Multiple Spawning Fishes. California: Southwest Fisheries Science Center. p 79-84.

Hurlbert SH. 1978. The measurement of niche overlap and some relatives. Ecology 59:67-77.

Hussain L, Alam MA, Islam S, Bapary MAJ. 2003. Estimation of fecundity and gonado somatic index (GSI) to detect the peak-spawning season of Dhela (*Osteobrama cotio cotio*). Pakistan Journal of Biological Sciences 6(3):231-233.

Hutchins JB. 2001 Checklist of the fishes of Western Australia. Records of the Western Australian Museum 63:9-50.

Hyslop EJ. 1980. Stomach contents analysis - a review of methods and their application. Journal of Fish Biology 17:411-429.

Isbister GK. 2001. Venomous fish stings in tropical northern Australia. The American Journal of Emergency Medicine 19(7):561.

Islam MS, Tanaka M. 2005. Nutritional condition, sarvation status and growth of early juvenile Japanses sea bass (*Lateolabrax japonicas*) related to prey distribution and feeding in the nursery ground. . Journal of Experimental Marine Biology and Ecology 323:172-183.

Jaafar Z, Hajisamae S, Chou LM, Yatiman Y. 2004. Community structure of coastal fishes in relation to heavily impacted human modified habitats. Hydrobiologia 511:113-123.

Johannes RE. 1978. Reproductive strategies of coastal marine fishes in the tropics. Environmental Biology of Fishes 3(1):65-84.

Johnson JW. 1999. Annotated checklist of the fishes of Moreton Bay, Queensland, Australia. Memoirs of the Queensland Museum 43(2):709-762.

Johnson JW. 2004. Two new species and two new records of Aploactinid fishes (Pisces: Scorpaeniformes) from Australia. Records of the Australian Museum 56:179-188.

Johnston IA, Battram J. 1993. Feeding energetics and metabolism in demersal fish species from Antarctic, temperate and tropical environments. Marine Biology 117:7-14.

Jones GP. 1980. Growth and reproduction in the protogynous hermaphrodite Pseudolabrus celidotus (Pisces: Labridae) in New Zealand. Copeia 1980:660-675.

Jones GP, McCormick MI, Srinivasan M, Eagle JV. 2004. Coral decline threatens fish biodiversity in marine reserves. Proceedings of the National Academy of Sciences of the United States of America 101(21):8251-8253.

Joseph EB. 1972. The status of the sciaenid stocks of the middle Atlantic coast. Chesapeake Science 13:87-100.

Kailola PJ. 1987. The fishes of Papua New Guinea: a revised and annotated checklist. Vol. II Scorpaenidae to Callionymidae. . Papua New Guinea: Dept. of Fisheries and Marine Resources.

Kamler E. 1992. Early life history of fish. An energetics approach. London: Chapman and Hall. 267 p.

Karoli J. 1881. Termesz. Fuzetek. Budapest. p 158.

Kelly CJ, Connolly PL, Bracken JJ. 1999. Age estimation, growth, maturity, and distribution of the bluemouth rockfish *Helicolenus d. dactylopterus* (Delaroche 1809) from the Rockall Trough. ICES Journal of Marine Science 56:61-74.

Key M, MacCall AD, Bishop T, Leos B. 2005. Stock assessment of the gopher rockfish (*Sebastes carnatus*) California: California Department of Fish & Game.

Khan MS, Ambak MA, Ang KJ, Mohsin ABK. 1990. Reproductive biology of a tropical catfish, *Mystics nemurus* Cuvier & Valenciennes, in Chenderoh reservoir, Malaysia. Aquaculture Research 21(2):173-180.

Kimura S, Matsuura K. 2003. Fishes of Bitung, northern tip of Sulawesi, Indonesia. . 1-244 p.

King M. 1995. Fisheries biology, assessment and management. London: Blackwell Science.

Kirkwood TBL. 1981. Repair and its evolution: survival versus reproduction. In: Townsend CR, Calow P, editors. Physiological Ecology: An evolutionary approach to resource use. Oxford: Blackwell. p 165-189

Koh T, Lin J. 2006. The land reclamation case: Thoughts and reflections. Singapore Year Book of International Law and Contributors 10:1-7.

Kohler A. 1981. Fluktuationen der Fischfauna im Elbe-Ästuar als Indikator für ein gestörtes Ökosystem. Helgoland Marine Research 34:263-285.

Kohler CC, Ney JJ. 1982. A comparison of methods for quantitative analysis of feeding selection of fishes. Environmental Biology of Fishes 7:363-368.

Kottelat M, Lim KKP. 1995. Freshwater fishes of Sarawak and Brunei Darussalam: a preliminary annotated check-list. The Sarawak Museum Journal 48(69):227-256.

Kottelat M, Whitten AJ, Kartikasari SN, Wirjoatmodjo S. 1993. Freshwater fishes of Western Indonesia and Sulawesi. Hong Kong: Periplus Editions. i-xxxviii + 1-259, Pls. 251-284.

Koya Y, Munoz M. 2007. Comparitive study on ovarian structures in scorpaenids: possible evolutional process of reproductive mode. Ichthyological Research 54:221-230.

Kozlowski J. 1992. Optimal allocation of resources to growth and reproduction: Implications for age and size at maturity. Trends in Ecology & Evolution 7(1):15-19.

Kozlowski J. 1996. Optimal allocation of resources explains interspecific life-history patterns in animals with indeterminate growth. Proceedings of the Royal Society of London B 263:559-566.

Kozlowski J, Teriokhin AT. 1999. Allocation of energy between growth and reproduction: The Pontryagin Maximum Principle solution for the case of age- and season-dependent mortality. Evolutionary Ecology Research 1:423-441.

Krebs CJ. 1999. Ecological Methodology. Menlo Park, California: Benjamin/Cummings.

Kuiter RH, Tonozuka T. 2001. Pictorial guide to Indonesian reef fishes. Part 1. Eels-Snappers, Muraenidae - Lutjanidae. . Australia. 302 p.

Kumari LK, Bhattathiri PMA, Matondkar SGP, John J. 2002. Primary productivity in Mandovi-Zuari estuaries in Goa. Journal of the MArine Biological Association of India 44(1&2):1-13.

Kuwamura T, Yogo Y, Nakashima Y. 1994. Population dynamics of goby *Paragobiodon echinoecephalatus* and host coral *Stylophora pistillata*. Marine ecology progress series 100:17-23.

Kwik JTB, Chen ZP, Sin TM, Ng KLP. 2010. Diel variations and diversity of fish communities along the unreclaimed shallow coastal habitat of Changi Point Beach, Singapore. Raffles Bulletin of Zoology 58(1):125 - 135.

La Mesa M, La Mesa G, Micalizzi M. 2005. Age and growth of madeira scorpionfish, *Scorpaena maderensis* Valenciennes, 1833, in the central Mediterranean. Fisheries Research 74(1-3):265-272.

La Mesa M, Scarcella G, Grati F, Fabi G. 2010. Age and growth of the black scorpionfish, *Scorpaena porcus* (Pisces: Scorpaenidae) from artificial structures and natural reefs in the Adriatic Sea. Scientia Marina 74(4):677-685.

Labropoulou M, Eleftheriou A. 1997. The foraging ecology of two pairs of congeneric demersal fish species: Importance of morphological characteristics in prey selection. . Journal of Fish Biology 50:324-340.

Labropoulou M, Machias A. 1998. Effect of habitat selection on the dietary patterns of two triglid species. Marine ecology progress series 173:275-288.

Labropoulou M, Machias A, Tsimenides N. 1999. Habitat selection and diet of juvenile red porgy, *Pagrus pagrus* (Linnaeus, 1758). Fisheries Bulletin 97:495-507.

Labropoulou M, Machias A, Tsimenides N, Eleftheriou A. 1997. Feeding habits and ontogenetic diet shift of the striped red mullet, *Mullus surmuletus* Linnaeus, 1758. Fisheries Research 31(3):257-267.

Lam K, Tsui T, Nakano K, Randall DJ, Adalberto L. Val VMFDA-V, David JR. 2005. Physiological Adaptations of Fishes to Tropical Intertidal Environments. Fish Physiology: Academic Press. p 501-581.

Lam TJ. 1974. Siganids: Their biology and mariculture potential. Aquaculture 3:325-354.

Larson RJ. 1991. Seasonal cycles of reserves in relation to reproduction in Sebastes. Environmental Biology of Fishes 30:57-70.

Leaman BM. 1991. Reproductive styles and life history variables relative to exploitation and management of Sebastes stocks. Environmental Biology of Fishes 30:253-271.

Lee JYL, Teoh LC, Leo SPM. 2004. Stonefish envenomations of the hand - A local marine hazard: A series of 8 cases and review of the literature. Annals Academy of Medicine Singapore 33(4):515-520.

Lee KY. 2000. From Third World to First, The Singapore Story: 1965-2000. Australia: Harper Collins.

Lester NP, Shuter BJ, Abrams PA. 2004. Interpreting the Von Bertalanffy model of somatic growth in fishes: the cost of reproduction. Proceedings of the Royal Society of London B 271:1625-1631.

Lim KKP, Low JKY, editors. 1998. A guide to common marine fishes of Singapore. Singapore: Singapore Science Centre. 163 p.

Lin SJ, Hwang DF, Shao KT, Jeng SS. 2000. Toxicity of Taiwanese gobies. Fisheries Science 66:547-552.

Linnaeus C. 1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata. Holmiae. Systema Naturae 10(1-2):1-824.

Linnaeus C. 1766. Sive regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Laurentii Salvii, Holmiae. Systema naturae 1(1):1-532.

Lobel PS. 1978. Diel, Lunar, and Seasonal Periodicity in the Reproductive Behavior of the Pomacanthid Fish, *Centropyge potteri*, and Some Other Reef Fishes in Hawaii. Pacific Science 32(2):193-207.

Locket MM, Suthers IM. 1998. Ontogenetic diet shifts and feeding activity in the temperate reef fish *Cheilodactylus fuscus*. Proceedings of the Linnean Society of New South Wales 120:105-116.

Love MS, Carr MH, Haldorson LJ. 1990a. The ecology of substrate-associated juveniles of the genus Sebastes. Environmental Biology of Fishes 30:225-243.

Love MS, Morris P, McCrae M, Collins R. 1990b. Life history aspects of 19 rockfish species (Scorpaenidae: Sebastes) from the south California Bight. National Marine Fisheries Service.

Low JKY, Leng CB, Chou LM (1997) Pomacentrid population dynamics on Singapore coral reefs. Environmental Monitoring and Assessment 44:33-43.

Lowe-McConnell RH. 1979. Ecological aspects of seasonality in fishes of tropical waters. Symposia of the Zoological Society of London 44:219-241.

MacArthur RH, Wilson EO. 1967. The theory of island biogeography. Princeton, NJ: Princeton University Press. 203 p.

Macpherson E. 1981. Resource Partitioning in a Mediterranean Demersal Fish Community. Marine Ecology Progress Series 4:183-193.

Magnifico G. 2007. New insights into fish growth parameter estimation by means of length-based methods. Rome: University of Rome "Tor Vergata". 202 p.

Malecha PW, Hanselman D, Heiferz J. 2007. Growth and Mortality of Rockfishes (Scorpaenidae) From Alaska Waters. Alaska: U.S. DEPARTMENT OF COMMERCE. 61 p.

Maljkovic A, Van Leeuwen TE, Cove SN. 2008. Predation on the invasive red lionfish, *Pterois volitans* (Pisces: Scorpaenidae), by native groupers in the Bahamas. Coral Reefs 27:501.

Mallin MA. 1991. Zooplankton abundance and community structure in a mesohaline North Carolina estuary. Estuaries 14:481-488.

Manly BE, McDonald LL, Thomas DL. 1993. Resource selection by animals. London: Chapman & Hall. 177 p.

Martens V. 1876. Preuss. Exped. Ost. Asien. 1:389.

Massutí E, Morales-Nin B, Moranta J. 2000. Age and growth of blue-mouth, *Helicolenus dactylopterus* (Osteichthyes: Scorpaenidae), in the western Mediterranean. Fisheries Research 46(1-3):165-176.

Masuda H, Amaoka K, Araga C, Uyeno T, Yoshino T. 1984. The fishes of the Japanese Archipelago.: Tokai Univ. Press. i-xxii + 1-437, Atlas: Pls. 431-370 p.

McArthur RH, Pianka ER. 1966. On optimal use of patchy environment. The American Naturalist 100(916):603-610.

McGurk MD. 1986. Natural mortality of marine pelagic fish eggs and larvae: role of spatial patchiness. Marine ecology progress series 34:227-242.

McLusky DS, Elliot M. 2004. The estuarine ecosystem: ecology, threats and management: Oxford University Press. 214 p.

Meekan MG, Ackerman JL, Wellington GM. 2001. Demography and age structures of coral reef damselfishes in the tropical eastern Pacific Ocean. Marine ecology progress series 212:223-232.

Megina C, Carballo JL, Cervera JL, Garcia-Gomez JC. 2002. The diet of *Platydoris argo* (Gastropoda: Nudibranchia) and the dietary specialization of sponge eating dorids. Journal of Molluscan Studies 68(2):173-179.

Meister HS, Wyanski DM, Loefer JK, Ross SW, Quattrini AM, Sulak KJ. 2005. Further evidence for the invasion and establishment of *Pterois volitans* (Teleostei: Scorpaenidae) along the Atlantic Coast of the United States. Southeastern Naturalist 4(2):193-206.

Mesa GL, Mesa ML, Tomassetti P. 2007. Feeding habits of the Madeira rockfish *Scorpaena maderensis* from central Mediterranean Sea. Marine Biology 150:1313-1320.

Mesa ML, Mesa GL, Micalizzi M. 2005. Age and growth of madeira scorpionfish, *Scorpaena maderensis* Valenciennes, 1833, in the central Mediterranean. Fisheries Research 74(1-3):265-272.

Miller D, Poucher S, Coiro L. 2002. Determination of lethal dissolved oxygen levels for selected marine and estuarine fishes, crustaceans, and a bivalve. Marine Biology 140(2):287-296.

Miller JM, Crowder JB, Moser LM. 1985. Migration and utilization of estuarine nurseries by juvenile fishes: an evolutionary perspective Contributions to Marine Science 27:338-352.

Miller PJ. 1984. Tokology of Gobies. In: Potts GW, Wootton RJ, editors. Fish Reproduction. London: Acadenic Press. p 119-153.

Mittelbach GG, Chesson PL. 1992. Predation risk: indirect effects on fish populations. In: Kerfoot WC, Sih A, editors. Predation: direct and indirect impacts on aquatic communities. Hanover: University of England Press. p 315-332.

Mohsin ABK, Ambak MA. 1996. Marine fishes & Fisheries of Malaysia and neighbouring countries: Universiti Pertanian Malaysia Press. 744 p.

Moller P, Rosenberg R. 1982. Production and abundance of the amphipod *Corophium volutator* on the west coast of Sweden. Netherlands Journal of Sea Research 140:127-140.

Monkolprasit S, Sontirat S, S. V, T. S. 1997. Checklist of Fishes in Thailand. Office of Environmental Policy and Planning. Bangkok, Thailand. 353 p.

Moreno T, Castro JJ. 1995. Community structure of the juvenile of coastal pelagic fish species in the Canary Islands waters. Scientia marina 59:405-413.

Morris JA, Akins JL. 2009. Feeding ecology of invasive lionfish (*Pterois volitans*) in the Bahamian archipelago. Environmental Biology of Fishes 86:389-398.

Morris JA, Akins JL, Barse A, Cerino D, Freshwater DW, Green SJ, Munoz RC, Paris C, Whitfield PE. Biology and Ecology of the Invasive Lionfishes, Pterois miles and Pterois volitans; 2008; Gosier, Goudeloupe, French West Indies. p 1-6.

Morris JA, Whitfield PE. 2009. Biology, Ecology, Control and Management of the Invasive Indo-Pacific Lionfish: An Updated Integrated Assessment. 57 p.

Morrison MA, Francis MP, Hartill BW, Parkinson DM. 2002. Dirunal and tidal variation in the abundance of the fish fauna of a temperate tidal mudflat. Estuarine, Coastal and Shelf Science 54(5):793-807.

Moser GH, Boehlert GW. 1991. Ecology of pelagic larvae and juveniles of the genus Sebastes. Environmental Biology of Fishes 30:203-224.

Motomura H. 2004. Revision of the scorpionfish genus Neosebastes (Scorpaeniformes: Neosebastidae), with descriptions of five new species. Indo-Pacific Fishes 37:1-76.

Motomura H, Iwatsuki Y. 1997. A preliminary report of Scorpaenid, Synanceiid, Tetrarogid and Aploactinid fishes in Miyazaki waters, southern Japan. Bulletin of the faculty of agriculture, Miyasaki University 44(1.2):127-138.

Motomura H, Kuriiwa K, Katayama E, Senou H, Ogihara G, Meguro M, Matsunuma M, Takata Y. 2010. Annotated checklist of marine and estuarine fishes of Yaku-shima Island, Kagoshima, southern Japan. . Fishes of Yaku-shima Island National Museum of Nature and Science. Tokyo. p 65-247.

Motomura H, Last PR, Gomon MF. 2006. A new species of the scorpionfish genus Maxillicosta from the southeast coast of Australia, with a redescription of *M. whitleyi* (Scorpaeniformes : Neosebastidae). Copeia(3):445-459.

Motomura H, Last PR, White WT. 2005. First records of a scorpionfish, *Maxillicosta raoulensis* (Scorpaeniformes, neosebastidae), from the tasman sea, with fresh colour notes for the species. Biogeography 7:85-90.

Motomura H, Sakurai Y, Senou H, Ho HC. 2009. Morphological comparisons of the Indo-Pacific scorpionfish, *Parascorpaena aurita* with a closely related species,*P. picta*, with first records of *P. aurata* from East Asia (Scorpaeniformes: Scorpaenidae). Zootaxa 2191:41-57.

Motomura H, Yoshino T, Takamura N. 2004. Review of the scorpionfish genus Scorpaenopsis (Scorpaeniformes:Scorpaenidae) in Japanese waters with three new records and an assessment of standard Japanese names. Japanese Journal of Ichthyology 51(2):89-115.

Motta PJ. 1982. Functional Morphology of the Head of the Inertial Suction Feeding Butterflyfish, *Chaetodon miliaris* (Perciformes, Chaetodontidae). Journal of Morphology 174:283-312.

Moyer JT, Zaiser MJ. 1981. Social organization and spawning behavior of the pteroine fish *Dendrochirus zebra* at Miyake-jima, Japan. Japanese Journal of Ichthyology 28(1):52-69.

Mummert JR, Drenner RW. 1986. Effect of fish size on the filtering efficiency and selective particle ingestion of a filter-feeding clupeid. Transactions of the American Fisheries Society 115:522-528.

Munday PL. 2000. Interactions between habitat use and patterns of abundance in coral-dwelling fishes. Environmental Biology of Fishes 58:355-369.

Munday PL. 2004. Habitat loss, resource specialisation and extinction on coral reefs. Global Change Biology 10:1642-1647.

Munday PL, Jones GP. 1998. The ecological implications of small body size among coral-reef fishes. Oceanography and Marine Biology: an Annual Review 36:373-411.

Munday PL, Jones GP, Caley MJ. 1997. Habitat specialisation and the distribution and abundance of coral-dwelling gobies. Marine ecology progress series 152:227-239.

Munday PL, Kuwamura T, Kroon FJ. 2010. Bi-directional sex change in marine fishes. Reproduction and sexuality in marine fishes: patterns and processes. Berkeley: University of California Press. p 241-271.

Munoz M, Saabat M, Vila S, Casadevall M. 2005. Annual reproductive cycle and fecundity of *Scorpaena notata* (Teleostei : Scorpaenidae). Scientia Marina 69(4):555-562.

Munro JL, Gaut VC, Thompson R, Reeson PH. 1973. The spawning season of Cariibean reef fishes. Journal of Fish Biology 5:69-84.

Murie DJ. 1995. Comparative feeding ecology of two sympatric rockfish congeners, *Sebastes caurinus* (copper rockfish) and *S. maliger* (quillback rockfish). Marine Biology 124:341-353.

Murua H, Saborido-Rey F. 2003. Female reproductive strategies of marine fish species of the North Atlantic. Journal of Northwestern Atlantic Fisheries Science 33:23-31.

Nicolas D, Le Loc'h F, Désaunay Y, Hamon D, Blanchet A, Le Pape O. 2007. Relationships between benthic macrofauna and habitat suitability for juvenile common sole (*Solea solea*, L.) in the Vilaine estuary (Bay of Biscay, France) nursery ground. Estuarine, Coastal and Shelf Science 73(3-4):639-650.

Ngo SYA, Ong SHJ, Ponampalam R. 2009. Stonefish envenomation presenting to a Singapore hospital. Singapore Medical Journal 50(5):506.

Nature Society Singapore. 2003. Singapore waters: Unveiling our seas. Singapore: New Era Press.

Odum EP. 1959. Fundamentals of Ecology. Philadelphia: W. B. Saunders Co.

Olden JD, Hogan ZS, Vander Zanden MJ. 2007. Small fish, big fish, red fish, blue fish: size-biased extinction risk of the world’s freshwater and marine fishes. Global Ecology and Biogeography 16:694-701.

Olson MH. 1996. Ontogenetic niche shifts in largemouth bass: variability and consequences for first year growth. Ecology 77:179-190.

Ordines F, Quetglas A, Massutí E, Moranta J. 2009. Habitat preferences and life history of the red scorpion fish, *Scorpaena notata*, in the Mediterranean. Estuarine, Coastal and Shelf Science 85(4):537-546.

Pallas PS. 1769. Spicilegia Zoologica quibus novae imprimis et obscurae animalium species iconibus, descriptionibus atque commentariis illustrantur. In: Berolini GAL, editor. p 1-42, Pls. 41-46.

Palumbi SR, Sandifer PA, Alan JD, Beck MW. 2009. Managing for ocean biodiversity to sustain marine ecosystem services. Frontiers in Ecology and Environment 7:204-211.

Pasquaud S, Elie P, Jeantet C, Billy I, Martinez P, Girardin M. 2008. A preliminary investigation of the fish food web in the Gironde estuary, France, using dietary and stable isotope analyses. Estuarine, Coastal and Shelf Science 78(2):267-279.

Patterson AW, Whitfield AK. 2000. Do shallow water habitats function as refugia for juvenile fishes? Estuarine and Coastal Marine Science 51:359-364.

Patton WK. 1994. Distribution and ecology of animals associated with branching corals (Acropora spp.) from the Great Barrier Reef, Australia. Bulletin of Marine Science 55(1):193-211.

Paulin C, Stewart A, Roberts C, McMillan P. 1989. New Zealand fish: a complete guide. xiv+279 p.

Paulin CD. 1982. Scorpionfishes of New Zealand (Pisces: Scorpaenidae). New Zealand Journal of Zoology 9:437-450.

Pauly D. 1981. The relationship between gill surface area and growth performance in fish: a generalization of Von Bertalanffy's theory of growth. Meeresforschung 28:251-282.

Pauly D. 1982. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. Journal du Conseil international pour l'exploration de la Mer 39(3):175-192.

Pauly D. 1983. Some simple methods for the assessment of tropical fish stocks. . 52 p.

Pauly D. 1998. Tropical fishes: patterns and propensities. Journal of Fish Biology 53(Suppl A):1-17.

Pauly D, Christensen V, Froese R, Palomares ML. 2000. Fishing down aquatic food webs. American Scientist 88:46-51.

Pavlov DA, Emel'yanova NG. 2007. Features of reproductive biology in two tropical fish species from the family Scorpaenidae. Journal of Ichthyology 47(5):353-365.

Pepin P. 1991. Effect of Temperature and Size on Development, Mortality, and Survival Rates of the Pelagic Early Life History Stages of Marine Fish. Canadian Journal of Fisheries and Aquatic Sciences 48(3):503-518.

Perrin N, Sibly RM. 1993. Dynamic-models of energy allocation and investment. Annual Review of Ecology and Systematics 24:379-410.

Perrin N, Sibly RM, Nichols NK. 1993. Optimal growth strategies when mortality and production rates are size dependent. Evolutionary Ecology 7:576-592.

Pianka ER. 1974. Evolutionary ecology. New York: Harper and Row. 356 p.

Pianka ER. 2000. Evolutionary Ecology. Cummings B, editor. San Francisco: Addison Wesley Longman. 528 p.

Pihl L, Baden S, Kautsky N, Rönnbäck P, Söderqvist T, Max.Troell, Wennhage H. 2006. Shift in fish assemblage structure due to loss of seagrass *Zostera marina* habitats in Sweden. Estuarine, Coastal and Shelf Science 67(1-2):123-132.

Pihl L, Rosenberg R. 1982. Production, abundance and biomass of mobile epibenthic marine fauna in shallow waters, western Sweden. Journal of Experimental Marine Biology and Ecology 57:273-301.

Pinkas L, Olipham MS, Iversor ILK. 1971. Food habits of albacore, bluefin tuna and bonito in California waters. Fisheries Bulletin of California 152:1-105.

Platell ME, Potter IC. 2001. Partitioning of food resources amongst 18 abundant benthic carnivorous fish species in marine waters on the lower west coast of Australia. Journal of Experimental Marine Biology and Ecology 261(1):31-54.

Poss SG. 1999. Scorpaenidae. Scorpionfishes (also, lionfishes, rockfishes, stingfishes, stonefishes, and waspfishes). In: Carpenter KE, Niem VH, editors. FAO species identification guide for fishery purposes The living marine resources of the Western Central Pacific. Rome. p 2291- 2352.

Post JR, PArkinson EA. 2001. Energy allocation strategy in young fish: allometry and survival. Ecology 82(4):1040-1051.

Pradeem Ram AS, Nair S, Chandramohan D. 2003. Seasonal shift in net ecosystem production in a tropical estuary. Limnological Oceanography 48(4):1601-1607.

Prandle D. 2009. Estuaries: Dynamics, Mixing, Sedimentation and Morphology. London: Cambridge University Press. 248 p.

Prokofiev AM. 2008. Scorpionfishes of Families Apistidae, Tetrarogidae, and Aploactinidae of Nha Trang Bay (South China Sea, Central Vietnam). Journal of Ichthyology 48(4):301-312.

Qasim SZ. 1956. Time and duration of the spawning season in some marine teleosts in relation to their distribution. ICES Journal of Marine Science 21:144-155.

Qasim SZ. 1973. Productivity of backwaters and estuaries. In: Zeitzschel B, Gerlach SA, editors. The Biology of the Indian Ocean. New York: Springer.

Quasim SZ. 1955. Time and duration of spawning season of teleosts in relation to their distribution. Journal du Conseil international pour l'exploration de la mer 21:144-155.

Quoy JRC, Gaimard JP. 1824. Description des Poissons. Chapter IX. In: Freycinet, L. de, Voyage autour du Monde...exécuté sur les corvettes de L. M. "L'Uranie" et "La Physicienne," pendant les années 1817, 1818, 1819 et 1820. Paris. . [1-328 in 1824; 1329-1616 in 1825], Atlas pls. 1843-1865 p.

Ralph PJ, Tomasko D, Moore K, Seddon S, Macinnis-Ng CMO. 2006. Human impacts on seagrasses: Eutrophication, sedimentation, and contamination. Larkum AWD, Orth RJ, Duarte CM, editors. Netherlands: Springer.

Randall JE, Delbeek JC. 2009. Comments on the extremes in longevity in fishes, with special reference to the Gobiidae. Proceedings of the California Academy of Sciences Series 4 60(13):447-454.

Randall JE, Eschmeyer WN. 2001. Revision of the Indo-Pacific scorpionfish genus Scorpaenopsis, with descriptions of eight new species. Indo-Pacific Fishes 34:1-79.

Randall JE, Lim KKP. 2000. A checklist of the fishes of the South China Sea. Raffles Bulletin of Zoology 8:569-667.

Randall JE, Lobel PS, Chave EH. 1985. Annotated Checklist of the Fishes of Johnston Island. Pacific Science 39(1):24-80.

Read AF, Harvey PH. 1989. Life history differences among the eutherian radiations. Journal of Zoology of London 219:329-353.

Reinboth R. 1962. Morphologische und funktionelle Zweigeschlechtlichkeit bei marinen Teleostiern (Serranidae, Sparidae, Centracanthidae) 69 : 405 - 480. Zool Jb Physiol 69:405-480.

Reise K. 1991. Macrofauna in mud and sand of tropical and temperate tidal flats. In: Elliott M, Ducrotoy JP, editors. Estuaries and Coasts: Spatial and Temporal Intercomparisons. Fredensborg: Olsen and Olsen. p 211-216.

Reiss MJ. 1989. The allometry of growth and reproduction. Cambridge: Cambridge University Press. 182 p.

Reynolds JD, Dulvy NK, Goodwin NB, Hutchings JA. 2005. Biology of extinction risk in marine fishes. Proceedings of the Royal Society B: Biological Sciences 272:2337-2344.

Reznick D, Bryant MJ, Roff D, Ghalambor CK, Ghalambor DE. 2004. Effect of extrinsic mortality on the evolution of senescence in guppies. Nature 431:1095-1099.

Reznick D, Endler JA. 1982. The impact of predation on life history evolution in Trinidadian guppies (*Poeciliea reticulata*). Evolution 36:160-177.

Rezsu E, Specziár A. 2006. Ontogenetic diet profiles and size-dependent diet partitioning of ruffe *Gymnocephalus cennus*, perch *Perca fluviatilis* and pumpkinseed *Lepomis gibbosus* in Lake Balaton. Ecology of Freshwater Fishes 15:339-349.

Ribas D, Muñoz M, Casadevall M, Gil de Sola L. 2006. How does the northern Mediterranean population of *Helicolenus dactylopterus dactylopterus* resist fishing pressure? Fisheries Research 79(3):285-293.

Richards A. 1993. Live reef fish exports to south-east asia from the south pacific. South Pacific Commission.

Richards WJ, Lindeman KC. 1987. Recruitment dynamics of reef fishes: Planktonic processes, settlement and demersal ecologies and fishery analysis. Bulletin Of Marine Science 41(2):392-410.

Richardson DL, Harrison PL, Harriott VJ. 1997. Timing of spawning and fecundity of a tropical and subtropical anemonefish (Pomacentridae: Amphiprion) on a high latitude reef on the east coast of Australia. Marine Ecology Progress Series 156:175-181.

Richardson J. 1844. Ichthyology of the voyage of H. M. S. Erebus & Terror,... In: J. Richardson & J. E. Gray. The zoology of the voyage of H. H. S. "Erebus & Terror," under the command of Captain Sir J. C. Ross London.

Richardson J. 1848. The zoology of the voyage of H. M. S. Samarang; under the command of Captain Sir Edward Belcher, during the years 1843-1846. London. 1-28, Pls. 21-10 p.

Ricker WE. 1973. Linear regressions in fishery research. Journal of Fisheries Research Board of Canada 30:409-434.

Ricker WE. 1975. Computation and interpretation of biological statistics of fish populations. Bulletin of the Fisheries and Research Board of Canada 191.

Ricklefs RE, Finch CE. 1995. Ageing: a natural history. Oxford, UK: WH Freeman and Company.

Robertson DR. 1991. The role of adult biology in the timing of spawning of tropical reef fishes. The ecology of fishes on coral reefs: Academic Press.

Robertson DR. 1992. Patterns of lunar settlement and recruitment in Caribbean reef fishes at Panama. Marine Biology 114:527-537.

Robertson DR, Choat JH. Protogrynous hermaphroditism and social systems in labrid fish; 1974; Brisbane. Great Barrier Reef Committee.

Robertson DR, Schober UM, Brawn JD. 1993. Comparative variation in spawning output and juvenile recruitment of some Caribbean fishes. Marine Ecology Progress Series 94:105-113.

Rochet MJ. 2000. A comparative approach to life-history strategies and tactics among four orders of marine teleost fish. ICES Journal of Marine Science 57:228-239.

Rodgers EW, Drane S, Grober MS. 2005. Sex reversal in pairs of *Lythrypnus dalli*: Behavioural and Morphological changes. Biological Bulletin 208:120-126.

Roessig JM, Woodley CM, Cech JJ, Hansen LJ. 2004. Effects of global climate change on marine and estuarine fishes and fisheries. Reviews in Fish Biology and Fisheries 14:251-275.

Roff D, Heibo E, Vollestad LA. 2006. The importance of growth and mortality costs in the evolution of the optimal life history. Journal of Evolutionary Biology 19(6):1920-1930.

Roff DA. 1992. The evolution of life histories: Theory and analysis. New York: Chapman and Hall. 528 p.

Rogers CS. 1990. Responses of coral reefs and reef organisms to sedimentation. Marine ecology progress series 62:185-202.

Root RB. 1967. The niche exploitation pattern of the bluegray gnatcatcher. Ecological Monograms 37:395-414.

Rothlisberg PC, Church JA, Fandry CB. 1995. A mechanism for near-shore concentration and estuarine recruitment of postlarval *Peneus plebejus* Hess (Decapoda, Penaeidae). Estuarine, Coastal and Shelf Science 40:115-138.

Roughgarden JS, Gaines S, Possingham H. 1988. Recruitment dynamics in complex life cycles. Science 241:1460-1466.

Rual F. 1999. Marine life envenomations: example in New Caledonia. Medecine Tropicale: Revue Du Corps De Sante Colonial 59(3):287.

Ruiz-Carus R, Matheson JRE, Roberts JDE, Whitfield PE. 2006. The western Pacific red lionfish, *Pterois volitans* (Scorpaenidae), in Florida: Evidence for reproduction and parasitism in the first exotic marine fish established in state waters. Biological Conservation 128(3):384.

Rüppell WPES. 1835-1838. Neue Wirbelthiere zu der Fauna von Abyssinien gehörig. Fische des Rothen Meeres. Frankfurt-am-Main. 1-148, Pls. 141-133. p.

Russell FE. 1973. Venomous animal injuries. Current Problems in Pediatrics 3(9):3-47.

Sadovy Y. 1991. A preliminary assessment of the export trade in marine aquarium organisms in Puerto Rico. Mayaguez, Puerto Rico: Fisheries Research Laboratory. 44 p.

Sadovy Y. Marketing live seafood and Ornamental products. In: Paust BC, Rice AA, editors. Proceedings of the second international conference and exhibition; 1999; Seattle, Washington. p 308.

Sadovy Y, Liu M. 2008. Functional hermaphroditism in teleosts. Fish and Fisheries 9:1-43.

Sadovy Y, Shapiro DY. 1987. Criteria for the Diagnosis of Hermaphroditism in Fishes. Copeia 1:136-156.

Saila SB, Recksiek CW, Prager MH. 1988. Basic fishery science programs: a compendium of microcomputer programs and manual of operation. New York: Elsevier Science Publishing Co. 230 p.

Samoilys MA, Squire LC. 1994. Preliminary observations on the spawning behaviour of coral trout, *Plectropomus leopardus* (Pisces: Serranidae), on the Great Barrier Reef. Bulletin Of Marine Science 54(1):332-342.

Sargent RC, Gross MR. 1993. William's principle: an explanation of parental care in teleost fishes. In: Pitcher TJ, editor. Behavior of teleost fishes. London: Chapman and Hall. p 333-362.

Saunders PR, Rothman S, Medrano VA, Chin HP. 1963. Cardiovascular actions of the venom of the stonefish *Synanceja horrida*. Toxicon 1(3):157-157.

Schaeffer JRC, Carlson RW, Russell FE. 1971. Some chemical properties of the venom of the scorpionfish *Scorpaena guttata* : and , Toxicon, 1971, 9, 69. (Laboratory of Neurological Research, University of Southern California School of Medicine, Los Angeles, California, U.S.A.). Toxicon 9(1):93-93.

Schafer LN, Platell ME, Valesini FJ, Potter IC. 2002. Comparisons between the influence of habitat type, season and body size on the dietary compositions of fish species in nearshore marine waters. Journal of Experimental Marine Biology and Ecology 278(1):67-92.

Schaffer WM, Elson PF. 1975. The adaptive significance of variations in life history among local populations of Atlantic salmoon in North America. Ecology 56:577-590.

Scharf FS, Juanes F, Rountree RA. 2000. Predator size – prey size relationships of marine fish predators: Interspecific variation and effects of ontogeny and body size on trophic niche breadth. Marine ecology progress series 208:229-248.

Schelske CL, Odum EP. Mechanisms maintaining high productivity in Georgia estuaries; 1959. p 75-80.

Schlacher TA, Wooldridge TH. 1996. Patterns of selective predation by juvenile, benthivorous fish on estuarine macrofauna. Marine Biology 125(2):241-247.

Schlosser IJ. 1987. The role of predation in age- and size-related habitat use by stream fishes. Ecology 68(3):651-659.

Schmidtt RJ, Holbrook SJ. 1984. Gape limitation foraging tactics and prey size selectivity in two microcarnivorous species. Oecologia 63:6-12.

Schofield PJ. 2009. Geographic extent and chronology of the invasion of non-native lionfish (*Pterois volitans* [Linnaeus 1758] and *P. miles* [Bennett 1828]) in the Western North Atlantic and Caribbean Sea. Aquatic Invasions 4(3):1-23.

Schubert M, Munday PL, Caley MJ, Jones GP, Llewelyn LE. 2003. The toxicity of skin secretions from coral-dwelling gobies and their potential role as a predator deterrent. Environmental Biology of Fishes 67(4):359-367.

Secor DH, Dean JM, Laban EH. 1991. Otolith Removal and Preparation for Microstructural Examination: A Users Manual.

Selleslagh J, Amara R. 2008. Environmental factors structuring fish composition and assemblages in a small macrotidal estuary (eastern English Channel). Estuarine, Coastal and Shelf Science 79(3):507-517.

Senou H, Kodato H, Nomura T, Yunokawa K. 2006. Coastal fishes of Ie-jima Island, the Ryukyu Islands, Okinawa, Japan. Bulletin of the Kanagawa Prefecture Museum 35:67-92.

Sequeira V, Neves A, Vieira AR, Figueiredo I, Gordo LS. 2009. Age and growth of bluemouth, *Helicolenus dactylopterus*, from the Portuguese continental slope. Journal of Marine Science 66:1-8.

Shahidul Islam M, Tanaka M. 2004. Impacts of pollution on coastal and marine ecosystems including coastal and marine fisheries and approach for management: a review and synthesis. Marine Pollution Bulletin 48(7-8):624-649.

Shallenberger RJ, Madden WD. 1972. Luring Behaviour in the scorpionfish, *Iracundus signifer*. Behaviour 47:3-47.

Shapiro DY. 1981a. Behavioural changes of protogynous sex reversal in a coral reef fish in the laboratory. Animal Behaviour 29(4):1185-1198.

Shapiro DY. 1981b. Intragroup behavioural changes and the initiation of sex reversal in a coral reef fish in the laboratory Animal Behaviour 29(4):1199-1212.

Shapiro DY. 1981c. Sequence of Coloration Changes During Sex Reversal in the Tropical Marine Fish *Anthias Squamipinnis*. Bulletin of Marine Science 31(2):383-398.

Shapiro DY. 1981d. Size, maturation and the social control of sex reversal in the coral reef fish *Anthais squamipinnis*. Journal of Zoology 193(1):105-128.

Sheaves M. 2001. Are there really few piscivorous fishes in shallow estuarine habitats? Marine ecology progress series 222(279-290).

Sinoda M, Lim PY, Tan SM. 1977. Preliminary study of trash fish landed at Kangkar fish market in Singapore. Bulletin of the Japanese Society of Scientific Fisheries 44(6):595-600.

Skaret G, Nottestad L, Ferno A, Johannessen A, Axelsen BE. 2003. Spawning of herring: day or night, today or tomorrow? Aquatic Living Resources 16(3):299-306.

Sokal RR, Rohlf FJ. 1969. Biometry. San Francisco: Freeman. 776 p.

Solan M, Cardinale BJ, Downing AL, Engelhardt KAM, Ruesink JL, Srivastava DS. 2004. Extinction and ecosystem function in the marine benthos. Science 306:1177-1180.

Sorokin VP. 1961. The redfish; gametogenesis and migrations of the *Sebastes marinus* (L.) and *Sebastes menella* Travin. Rapp. P.-V. Rwun Cons Perm Int Explor Mer 150:245-250.

Sponaugle S, Grorud-Colvert K, Pinkard D. 2006. Temperature-mediated variation in early life history traits and recruitment success of the coral reef fish Thalassoma bifasciatum in the Florida Keys. Marine ecology progress series 308:1-15.

Starrett A. 1993. Adaptive resemblance: a unifying concept for mimicry and crypsis. Biological Journal of the Linnean Society 48(4):299-317.

Stearns SC. 1992. The evolution of life histories. Oxford: Oxford University Press.

Steele MA, Schroeter SC, Page HM. 2006. Sampling characterisitics and biases of enclosure traps for sampling fishes in estuaries. Estuaries and Coasts 29(4):630-638.

Steiner UK, Pferffer T. 2007. Optimizing time and resource allocation trade-offs for investment into morphological and behavioral defense. The American Naturalist 169(1):118-129.

Stergiou KI, and Karpouzi, V.S. 2002. Feeding habits and trophic levels of Mediterranean fish. Reviews of Fish biology and Fisheries 11:217-254.

Stergiou KI, Fourtouni H. 1991. Food habits, ontogenetic diet shift and selectivity in *Zeus faber* Linnaeus, 1758. Journal of Fish Biology 39:589-603.

Stewart BD, Beukers JS. 2000. Baited technique improves consensus of cryptic fish in complex habitats. Marine Ecology Progress Series 197:259-272.

Susilo ES, Harnadi L, Takemura A. 2009. Tropical monsoon environments and the reproductive cycle of the orange-spotted spinefoot *Siganus guttatus*. Marine Biology Research 5:179-185.

Suthers IM, Frank KT. 1991. Comparative persistence of marine fish larvae from pelagic versus demersal eggs off southwestern Nova Scotia, Canada. Marine Biology 108:175-184.

Svedang H. 2003. The inshore demersal fish community on the Swedish Skagerrak coast: Regulation by recruitment from offshore sources. ICES Journal of Marine Science 60(1):23-31.

Sverker E. 1983. Production, predation and food niche segregation in a marine shallow soft-bottom community. Marine Ecology Progress Series 10:147-157.

Takahashi H, Takano K, Takemura A. 1991. Reproductive cycles of *Sebastes taczanowskii*, compared with those of other rockfishes of the genus Sebastes. Environmental Biology of Fishes 30:23-29.

Takano K, Takemura A, Furihata M, Nakanishi T, Hara A. 1991. Annual reproductive and spawning cycles of female *Sebasticus marmoratus*. Environmental Biology of Fishes 30:39-48.

Tan HTW, Chou LM, Yeo DCJ, Ng PKL. 2010. Waste and Reclaimed Land. In: Lee R, editor. The national heritage of Singapore. 3rd ed. Singapore: Pearson Education South Asia Pte Ltd. p 77-94.

Taylor BE, Gabriel W. 1993. Optimal adult growth of Daphnia in a seasonal environment. Functional Ecology 7:513-521.

Taylor PB, Chen LC. 1969. The Predator-Prey Relationship between the Octopus (*Octopus bimaculatus*) and the California Scorpionfish (*Scorpaena guttata*). Pacific Science 13:311-316.

Temminck CJ, Schlegel H. 1843. Pisces. In: Siebold PFd, editor. Fauna Japonica, sive descriptio animalium quae in itinere per Japoniam suscepto annis 1823-30 collegit, notis observationibus et adumbrationibus illustravit p1-20.

Tham AK. 1953. A preliminary study of the physical, chemical and biological characteristics of Singapore Straits. Fishery Publications 1(4):60-64.

Tham AK. 1976. Some aspects of fisheries biology of Singapore Straits. Singapore: Nanyang University. College of Graduate Studies, Institute of Natural Sciences. 12-14 p.

Thunberg CP. 1793. Beskrifning på nya fisk-arter utaf abbor-slågtet ifrån Japan. Kongliga Vetenskaps Akademiens nya Handlingar. Stockholm. 198-200, Pl. 197 p.

Toms JD, Lesperance ML. 2003. Piecewise regression: a tool for identifying ecological thresholds. Ecology 84(2034-2041).

Van Rijn LC. Estuarine and coastal sedimentation problems; 2004 October 18-21; Yichang, China.

Vecchione M, Mickevich MF, Fauchald K, Collette BB, Williams AB, Munroe TA, Young RE. 2000. Importance of assessing taxonomic adequacy in determining fishing effects on marine biodiversity. Journal of Marine Science 57:677-681.

Virnstein RW, Mikkelsen PS, Cairns KD, Capone MA. 1983. Seagrass beds versus sand bottoms: The trophic importance of their associated benthic invertebrates. Florida Scientist 46(3):363-381.

Vlaming V. 1971. The effects of food deprivation and salinity changes on reproductive function in the estuarine gobiid fish, *Gillichthys mirabilis*. Biological Bulletin 141:458-471.

Wainwright PC. 1988. Morphology and ecology: functional basis of feeding constraints in Caribbean labrid fishes. Ecology 69:635-645.

Wainwright PC, Richard BA. 1995. Predicting patterns of prey use from morphology of fishes. Environmental Biology of Fishes 44:97-113.

Waldichuk M. 1974. Coastal marine pollution and fish. Ocean Management 2(1):1-60.

Wantiez L. 1993. Les poissons des fonds meubles du lagon Nord et de la Baie de Saint-Vincent de Nouvelle-Calédonie: Description des peuplements, structure et fonctionnement des communautés. France: Université d' Aix-Marseille II.

Ward TM, Staunton-Smith J, Hoyle S, Halliday IA. 2003. Spawning patterns of four species of predominantly temperate pelagic fishes in the sub-tropical waters of southern Queensland. Estuarine and Coastal Marine Science 56:1125-1140.

Ware DM. 1975. Relation between egg size, growth, and natural mortality of larval fish. Journal of Fisheries Research Board of Canada 32:2503-2512.

Warner RR, Hoffman SG. 1980. Local population size as a determinant of mating system and sexual composition in two tropical marine fishes (Thalassoma spp.). Evolution 34(3):508-518.

Warrell DA. 1993. Venomous bites and stings in Saudi Arabia. Saudi Medical Journal 14(3):196-202.

Washington BB, Moser HG, Laroche WA, Richards WA. 1984. Scorpaeniformes: Development. Moser HG, Richards WJ, Cohen DM, Fahay MP, Kendall Jr. AW, Richardson SL, editors. Lawrence: Allen Press Inc.

Watters DL, Kline DE, Coale KH, Cailliet GM. 2006. Radiometric age confirmation and growth of a deep-water marine fish species: The bank rockfish, *Sebastes rufus*. Fisheries Research 81(2-3):251-257.

Weber M. 1913. Die Fische der Siboga-Expedition. E. J. Brill, editor. Leiden. i-xii + 1-710, Pls. 711-712 p.

Weber M, De Beaufort LF. 1962. The fishes of Indo-Australian Archipelago. Leiden, Netherlands: E.J. Brill Ltd. 481 p.

Wei J, Koon SH, Louidesamy I. The Design and Construction of the Reclamation at Tuas, Singapore; 1995; Barton, Australia. p 201-206.

Wells RJD, Boswell KM, Cowan Jr JH, Patterson Iii WF. 2008. Size selectivity of sampling gears targeting red snapper in the northern Gulf of Mexico. Fisheries Research 89(3):294-299.

Wendelaar Bonga SE. 1997. Stress response in fish. Physiological Reviews 77(3):591-625.

West G. 1990. Methods of Assessing Ovarian Development in Fishes - a Review. Australian Journal of Marine and Freshwater Research 41(2):199-222.

White DB, Wyanski DM, Sedberry GR. 1998. Age, growth, and reproductive biology of the blackbelly rosefish from the Carolinas, U.S.A. Journal of Fish Biology 53:1274-1291.

Whitfield AK. 1980. A quantitative study of the trophic relationships within the fish community of the Mhlanga estuary, South Africa. Estuarine and Coastal Marine Science 10(4):417-435.

Whitfield AK. 1994. Fish species diversity in southern African estuarine systems: An evolutionary perspective. Environmental Biology of Fishes 40(1):37-48.

Wiener S. 1963. Stonefish stingings, venom and treatment. Bulletin Of The Post-Graduate Committee In Medicine, University Of Sydney 18(3)Suppl:106.

Williams AJ, Currey LM, Begg GA, Murchie CD, Ballagh AC. 2008. Population biology of coral trout species in eastern Torres Strait: Implications for fishery management. Continental Shelf Research 28(16):2129-2142.

Williams GC. 1957. Pleiotropy, natural selection and the evolution of senescence. Evolution 11:398-411.

Wilson DT, Meekan MG. 2002. Growth-related advantages for survival to the point of replenishment in the coral reef fish *Stegastes partitus* (Pomacentridae). Marine ecology progress series 231:247-260.

Winnemiller KO, Rose A. 1992. Patterns of life-history diversification in North American fishes: implications for population regulation. Canadian Joural of Fisheries and Aquatic Science 49:2196-2218.

Winterbottom R, Emery AR, Holm E. 1989. An annotated checklist of the fishes of the Chagos Archipelago, Central Indian Ocean. Royal Ontario Museum Life Science Contributions 145:1-226.

Winterbottom R, Southcott L. 2008. Short lifespan and high mortality in the western Pacific coral reef goby *Trimma nasa*. Marine ecology progress series 366:203-208.

Wootton RJ. 1984. Introduction to tactics and strategies in fish reproduction. In: Potts GW, Wootton R, J, editors. Fish reproduction: Strategies and tactics. New York: Academic Press. p 12.

Wootton RJ. 1990. Ecology of teleost fishes. . London, UK: Chapman and Hall.

Wourms JP. 1991. Reproduction and development of Sebastes in the context of the evolution of piscine viviparity. Environmental Biology of Fishes 30:111-126.

Yamashita Y, Tominaga O, Takani H, Yamada H. 2003. Comparison of growth, feeding and cortisol level in *Platichthys bicoloratus* juveniles between estuarine and nearshore nursery grounds. Journal of Fish Biology 63:617-630.

Yang TH, Somero GN. 1993. Effects of feeding and food deprivation on oxygen consumption, muscle protein concentration and activities of energy metabolism enzymes in muscle and brain of shallow-living (*Scorpaena guttata*) and deep-living (*Sebastolobus alascanus*) scorpaenid fishes. Journal of Experimental Biology 181:213-232.

Yeung WSB, Adal MN, Hui SWB, Chan STH. 1985. The ultrastructural and biosynthetic characteristics of steroidogenic cells in the gonad of *Monopterus albus* (Teleostei) during natural sex reversal Cell and Tissue Research 239(2):383-394.

Yoneda M, Miura H, Mitsuhashi M, Matsuyama M, Matsuura S. 2000. Sexual maturation, annual reproductive cycle, and spawning periodicity of the shore scorpionfish, *Scorpaenodes littoralis*. Environmental Biology of Fishes 58(3):307-319.

Yong KY, Lee SL, Karunaratne GP. Coastal reclamation in Singapore: A review. In: Chia LS, Chou LM, editors; 1991; Phillipines. International Center for Living Aquatic Resouce Management. p 59-67.

Zajonz U, Klausewitz W. 2002. Neomerinthe bathyperimensis sp nov from deep waters of the southern Red Sea. Journal of Fish Biology 61(6):1481-1488.

Zar JH. 1999. Biostatistical Analysis. Upper Saddle River, NJ.: Prentice Hall.

Zimmermann C, Kunzmann A. 2001. Baseline respiration and spontaneous activity of sluggish marine tropical fish of the family Scorpaenidae. Marine Ecology-Progress Series 219:229-239.

Appendix

Protocol for Histology

Fixing and storage
5% bouin's solution for minimum 48hrs
storage in 70% ethanol

Embedding for histology
70% ethanol – 1hr
70% ethanol – 1hr
80% ethanol – 1hr
95% ethanol – 1hr
100% ethanol – 20mins
Clove oil – 48hrs or 72hrs
Wax 1 – 1hr
Wax 2 – 1hr
Wax 3 – 1hr

Sectioning
Cut wax block to shape
Pyramid/Rhombus shape from top perspective
Sectioning thickness – 16 um for S. horrida, 12 um for T. uranoscopus

Staining
Sections into histoclear 1 – 20 dips
Sections into histoclear 2 – 20 dips
Sections into histoclear 3 – 20 dips

Dewaxing
Sections into abs alcohol 1 – 20 dips
Sections into abs alcohol 2 – 20 dips

Hydration

Sections into abs alcohol 3 – 20 dips
Sections into 95% alcohol – 20 dips
Sections into 90% alcohol – 20 dips
Sections into 70 % alcohol – 20 dips

Staining (H&E)

Sections into Haemotoxylin – 5mins
Sections into running tap water – 3 mins
Sections into Eosin – 2.5 mins

Dehydration
Sections into 70% alcohol – 20 dips
Sections into 90% alcohol – 20 dips
Sections into 95% alcohol – 20 dips
Sections into abs alcohol 3 – 20 dips

Clearing and mounting
Sections into abs alcohol 2 – 20 dips
Sections into abs alcohol 1 – 20 dips
Sections into histoclear 4 – 20 dips
Sections into histoclear 3 – 20 dips
Sections into histoclear 2 – 20 dips

Mounting
Sections mounted onto slide using dpx

Statistical tables for ANCOVAs

ANCOVA for *P. longispinis*

Tests of Between-Subjects Effects[b]

Dependent Variable:twy

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	106.628[a]	2	53.314	23352.974	.000
Intercept	91.063	1	91.063	39887.965	.000
slx	106.626	1	106.626	46705.020	.000
slope	.002	1	.002	.927	.336
Error	1.386	607	.002		
Total	181.881	610			
Corrected Total	108.013	609			

a. R Squared = .987 (Adjusted R Squared = .987)

b. species = P. longispinis

ANCOVA for *T. uranoscopus*

Tests of Between-Subjects Effects[b]

Dependent Variable:twy

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	47.434[a]	2	23.717	9826.296	.000
Intercept	36.153	1	36.153	14978.515	.000
slx	47.208	1	47.208	19559.058	.000
slope	.226	1	.226	93.534	.000
Error	.495	205	.002		
Total	129.438	208			
Corrected Total	47.929	207			

a. R Squared = .990 (Adjusted R Squared = .990)

b. species = T. uranoscopus

ANCOVA for *S. horrida*

Tests of Between-Subjects Effects[b]

Dependent Variable:twy

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	22.186[a]	2	11.093	3280.716	.000
Intercept	8.990	1	8.990	2658.829	.000
slx	22.113	1	22.113	6539.716	.000
slope	.073	1	.073	21.716	.000
Error	.463	137	.003		
Total	815.036	140			
Corrected Total	22.649	139			

a. R Squared = .980 (Adjusted R Squared = .979)

b. species = S. horrida

Statistical tables for nested ANOVAs

Nested ANOVA for GSI in *P. longispinis*

Univariate Tests of Significance for GSI (%) (GSI updated based on 2years) Over-parameterized model Type III decomposition

	SS	Degr. of - Freedom	MS	F	p
Intercept	13.30212	1	13.30212	463.1728	0.000000
year	0.01243	1	0.01243	0.4329	0.511712
month(year)	1.72765	22	0.07853	2.7344	0.000208
Error	3.87714	135	0.02872		

Nested ANOVA for GSI in *T. uranoscopus*

Univariate Tests of Significance for log+1 (GSI updated based on 2years) Over-parameterized model Type III decomposition

	SS	Degr. of - Freedom	MS	F	p
Intercept	29.61264	1	29.61264	573.1638	0.000000
Year	0.39536	1	0.39536	7.6524	0.007076
Month(Year)	2.19869	22	0.09994	1.9344	0.018044
Error	4.02989	78	0.05167		

Nested ANOVA for GSI in *S. horrida*

Univariate Tests of Significance for log+1 (GSI updated based on 2years) Over-parameterized model Type III decomposition

	SS	Degr. of - Freedom	MS	F	p
Intercept	7.905599	1	7.905599	130.2331	0.000000
Year	0.261174	1	0.261174	4.3025	0.045268
month(Year)	3.540032	22	0.160911	2.6508	0.004568
Error	2.185324	36	0.060703		

Nested ANOVA for abundance in *P. longispinis*

Univariate Tests of Significance for log+1 (size dist for 3 spp 1 aug 2011 test day) Over-parameterized model Type III decomposition

	SS	Degr. of - Freedom	MS	F	p
Intercept	37.57849	1	37.57849	247.0156	0.000000
Year	0.00019	1	0.00019	0.0012	0.972132
month(Year)	7.66170	22	0.34826	2.2892	0.002479
size class	7.98890	5	1.59778	10.5027	0.000000
Error	17.49495	115	0.15213		

Nested ANOVA for abundance in *T. uranoscopus*

Univariate Tests of Significance for log+1 (size dist for 3 spp 1 aug 2011 test day) Over-parameterized model Type III decomposition

	SS	**Degr. of - Freedom**	**MS**	**F**	**p**
Intercept	5.733797	1	5.733797	101.9906	0.000000
Year	0.109264	1	0.109264	1.9435	0.165525
month(Year)	2.689655	22	0.122257	2.1747	0.003611
size class	1.337372	6	0.222895	3.9648	0.001086
Error	7.758206	138	0.056219		

Nested ANOVA for abundance in *S. horrida*

Univariate Tests of Significance for log+1 (size dist for 3 spp 1 aug 2011 test day) Over-parameterized model Type III decomposition

	SS	**Degr. of - Freedom**	**MS**	**F**	**p**
Intercept	2.952266	1	2.952266	88.95651	0.000000
year	0.226787	1	0.226787	6.83347	0.010144
month(year)	0.590442	22	0.026838	0.80868	0.709527
size class	1.648335	5	0.329667	9.93340	0.000000
Error	3.816591	115	0.033188		