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Rapid growth and short life spans characterise pipefish populations in vulnerable seagrass beds. --Manuscript Draft--

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Corresponding Author:	David Booth University of Technology Sydney Sydney, NSW AUSTRALIA
Corresponding Author Secondary Information:	
Corresponding Author's Institution:	University of Technology Sydney
Corresponding Author's Secondary Institution:	
First Author:	Kerryn Parkinson
First Author Secondary Information:	
Order of Authors:	Kerryn Parkinson David Booth
Order of Authors Secondary Information:	
Abstract:	<p>The life history traits of two species of pipefish (F. Syngnathidae) from seagrass meadows in New South Wales, Australia were examined to understand whether they enhance resilience to habitat degradation. The spotted pipefish <i>Stigmatopora argus</i> (Richardson) and wide-bodied pipefish <i>Stigmatopora nigra</i> Kaup exhibit some of the shortest lifespans known for vertebrates (longevity up to 150 days) and rapid maturity (male <i>S. argus</i> 35 days after hatching (DAH) and male <i>S. nigra</i> at 16 to 19 DAH), key characteristics of opportunistic species. Growth rates of both species were extremely rapid (up to 2 mm.d⁻¹), with seasonal and sex differences in growth rate. We argue that short life spans and high growth rates may be advantageous for these species, which inhabit one of the most threatened ecosystems on earth.</p>

Ethics questionnaire for JFB

This questionnaire relates to the Editorial published in JFB **68**, 1-2, which you have been asked to read. Please note that submitted manuscripts will only be considered if the experimental methods employed are ethically justified. PLEASE SUBMIT THE COMPLETED QUESTIONNAIRE WITH YOUR MANUSCRIPT ONLINE THROUGH EDITORIAL MANAGER.

Corresponding author's name: David Booth

Question 1: If the fishes have been collected as part of faunal surveys, have the fishes, where feasible, been killed rapidly or returned to the wild after being held in aquaria?

Yes X

No

Question 2: What method was used if they were killed?

Ice water slurry

Question 3: If you have undertaken experimental work, has the care and use of experimental animals complied with local and or national animal welfare laws, guidelines and policies?

Yes X

No

If 'Yes', state these and provide suitable evidence (*e.g.* for the U.K. a Home Office PPL number is sufficient) that protocols have undergone an ethical review process by an institutional animal care and use (or similar) committee, a local ethics committee, or by appropriately qualified scientific and lay colleagues.

Animal Ethics approval UTS ACEC 2008-13. NSW Fisheries Scientific Research Permit F94/696(A)

Please read the exceptions below (Questions 4 to 7). If any of these exceptions apply to your study, complete the appropriate section. Otherwise leave blank.

If 'No', because these laws do not exist in your country, please state this.

Please read the exceptions below (Questions 4 to 7). If any of these exceptions apply to your study, complete the appropriate section. Otherwise leave blank.

Question 4: Did you use experimental conditions that severely distressed the animals?

Yes

No X

If 'Yes', state the conditions and how they can be justified.

Question 5: Did you use humane endpoints that minimized adverse effects?

Yes **X**

No

Question 6: Have you performed surgical procedures?

Yes

No **X (none on living fish)**

If 'Yes', have you suitably described these in your manuscript?

Question 7: If the procedures caused more than slight pain or distress, did you use appropriate sedation, analgesia and anaesthesia, with appropriate post-operative care?

Yes

No

If 'Yes', outline these.

N/A, no apparent pain or distress

If 'No', did any of your procedures involve sentient, un-anaesthetized animals paralysed by chemical agents such as muscle relaxants?

Yes

No

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Yes

No

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Rapid growth and short life spans characterise pipefish populations in vulnerable seagrass beds.

K.L. PARKINSON and D.J. BOOTH¹

University of Technology, Sydney, School of Life Sciences,

PO BOX 123, BROADWAY, NSW 2007, Australia

¹: Author to whom correspondence should be addressed.

Tel.: +61 2 9514 4053; fax: +61 2 9514 4079

email: David.Booth@uts.edu.au

Running headline: Extremely short life span and fast growth in pipefishes

Abstract

The life history traits of two species of pipefish (F. Syngnathidae) from seagrass meadows in New South Wales, Australia were examined to understand whether they enhance resilience to habitat degradation. The spotted pipefish *Stigmatopora argus* (Richardson) and wide-bodied pipefish *Stigmatopora nigra* Kaup exhibit some of the shortest life spans known for vertebrates (longevity up to 150 days) and rapid maturity (male *S. argus* 35 days after hatching (DAH) and male *S. nigra* at 16 to 19 DAH) -key characteristics of opportunistic species. Growth rates of both species were extremely rapid (up to 2 mm.d⁻¹), with seasonal and sex differences in growth rate. We argue that short life spans and high growth rates may be advantageous for these species, which inhabit one of the most threatened marine ecosystems on earth.

Keywords: short life span; pipefish; rapid growth; seagrass

INTRODUCTION

Resilience of a population to habitat disturbance is determined greatly by the life history strategies of that species. King and McFarlane (2003) suggest that fish species group into three different life history strategies: (1) small, rapidly maturing, short-lived fishes (opportunistic strategists); (2) larger, high fecundity fishes with longer life spans (periodic strategists); and (3) fishes of intermediate size that often exhibit parental investment and produce fewer, larger offspring (equilibrium strategists). In general, fish with an opportunistic life history strategy are considered to have a greater resilience to population disturbance (Winemiller, 2005). This is primarily due to their continual and rapid population turnover that allows repopulation and efficient recolonization over relatively small spatial scales while occupying habitats not only with a high degree of variability, but also, potentially, with large resources of energy.

Seagrass meadows are highly productive ecosystems that are experiencing worldwide decline due to direct and indirect human disturbance (Duarte, 2002). Massive reductions in seagrass meadows are being documented due to increased sediment and nutrient loading, localized changes in water quality, and from increasing effects of climate change (e.g., increased sea surface temperature, sea level changes and intensity of storms) (Orth *et al.*, 2006). In addition to stabilising sediment, altering water flow, nutrient recycling and acting as a carbon sink (Orth *et al.*, 2006) seagrass meadows are vitally important as critical nursery habitat for many commercial and recreational fish species (Pollard, 1984; Bell and Westoby, 1986). For instance, of 102 species of fish found to be inhabiting seagrass beds in Botany Bay NSW, about 20% were of fishery importance (Middleton *et al.*, 1984). On the east coast of Australia substantial loss of seagrass meadows (*Posidonia australis*) has been observed, particularly in Botany Bay, NSW (Larkum and West, 1990; Butler and Jernakoff, 1999; Creese *et al.*, 2009) and has prompted authorities to declare the *Posidonia australis* seagrass meadows of Botany Bay as 'endangered populations' in 2010 (West, 2010). The ability of fish species to cope with a rapidly degrading habitat is poorly understood, especially for smaller more cryptic species, which are strongly associated with seagrass meadows and may be greatly affected by its loss.

Fishes from the family Syngnathidae are numerically dominant in the seagrass meadows in south eastern Australia (Pollard, 1984) and are considered to be permanent residents (Hoese, 1978). Syngnathids are a diverse family of fishes that include seahorses, pipehorses, pipefishes and

seadragons, and are found in all types of structurally complex habitats such as corals, sponges and seagrass (Kuitert, 2000). Life histories of pipefishes in seagrass meadows are poorly known despite their abundance and vulnerability to changes in seagrass cover and composition (Foster and Vincent, 2004; Shokri *et al.*, 2009).

Studies assessing the life history traits of pipefishes in seagrass meadows have researched diet (Howard and Koehn, 1985; Steffe *et al.*, 1989; Payne *et al.*, 1998; Kendrick, 2002), distribution and utilisation of seagrass habitat (Bell and Westoby, 1986; Duque-Portugal, 1989; Steffe *et al.*, 1989; Ferrell *et al.*, 1993; Kendrick, 2002; Kendrick and Hyndes, 2003; Macreadie *et al.*, 2010) and briefly touched on reproductive ecology (Duque-Portugal, 1989; Edgar and Shaw, 1995). However, longevity, age at maturity and growth are poorly understood life history traits in these taxa, yet are key demographic parameters. The aim of this study was to assess the age at maturity, longevity and growth of two co-occurring species of seagrass-dwelling pipefish, *Stigmatopora argus* and *Stigmatopora nigra*. We then ask how these life history traits might support the long-term persistence of these species in a rapidly diminishing habitat.

MATERIALS AND METHODS

Species and field collection

The spotted pipefish, *S. argus* and the wide-bodied pipefish *S. nigra*, are almost exclusively found in seagrass beds along coastal south eastern Australia, although for *S. nigra* this distribution extends to southern Queensland and New Zealand (Hoese, 1978; Connolly, 1994).

Between January 2001 and December 2002, pipefishes were sampled monthly at two sites within the Botany Bay/Georges River catchment area, Sydney, Australia (33°57.39'S, 151°11.81'E) see Figure 1. At both sites, pipefish were collected in seagrass (*Zostera capricorni*) at depths of 0.5-1.5m using a 10m x 2m seine net. All specimens were identified to species, sexed and total length (TL) was measured. In particular the brooding status of males was noted (i.e. the presence or absence of an occupied brood pouch), to establish a minimum total length (MT_L) for mature males. This measure allows the reproductive status of the pipefish population to be assessed without the need for dissection of reproductive structures (Duque-Portugal, 1989; Steffe *et al.*, 1989). Specimens that did not exhibit a brood pouch (empty or full) and were equal to or greater

than the MT_L were considered to be females, those smaller than the MT_L were considered to be juveniles. It is possible therefore, that we may have overestimated the number of females in the population.

Growth and longevity determination

Otoliths (earstones) of pipefish were used to estimate growth and longevity. A subsample of pipefish collected each month was anesthetized in ice water *in situ*, prior to preservation in 70% alcohol for otolith extraction in the laboratory. Otoliths were removed from all specimens, and sagittal otoliths prepared for viewing with an environmental scanning electron microscope (ESEM) by grinding to the primordium using 3 μ m lapping film; wet polishing using a PMT 08A-10 multiflex 20.32cm (8") diameter polishing cloth (www.flatlap.co.uk) and 0.02–0.06 μ m colloidal silica (www.struers.com) on a Kent 3-automatic polishing unit (www.kemet.com.au), then etched with 5% solution of ethylene diamine tetra-acetic acid (EDTA). Digital images were recorded of each otolith, and then the number of growth increments was counted along the longest, most visible axis of the otolith three times, with the mean taken as the age of the fish. If counts differed by more than 5%, otoliths were re-examined and if subsequent counts again varied by over 5% otoliths were rejected (*sensu*(Campana, 1982)). We previously verified that these increments were daily for both *S. argus* and *S. nigra* (Parkinson *et al.*, 2012).

Statistical analyses

Age/length data were fitted to the von Bertalanffy growth curve using Excel Solver (Version 5.1.2600) to determine the longevity of the species. Growth rates were compared for males and females separately using a General Linear Model (GLM) with growth rate as the dependent, and season (1-Winter: June-September; 2-Spring: October-November; 3-Summer: December-February; 4-Autumn: March-May) as the independent variable (SPSS Version 21). For *S. argus* males, low numbers in spring and autumn precluded these seasons from analysis. We inspected the homogeneity of variances and transformed the growth rate using (\log_{10}) to assume normality.

Minimum male total length for the analysis of maturity was estimated as described above and did not require statistical analysis.

RESULTS

A total of 1629 *S. nigra* and 362 *S. argus* were collected and measured, from both sites in the Botany Bay catchment area (pooled data, see Table 1). Growth increments were visible on 304 sagittal otoliths prepared for aging, with increments on an additional 82 otoliths unclear and therefore unsuitable for analysis. Overall, data for both species were fitted to von Bertalanffy growth curves, which indicated maximum length (L_T) to be approximately 165mm for both *S. argus* and *S. nigra* (Figure 2). The growth rates (G^R) for *S. argus* from birth to brooding size were rapid, with males reaching minimum total length (MT_L) of 75mm at approximately 35 days (based on age/length), approaching a growth rate of $1.6 \pm 0.4 \text{ mm} \cdot \text{d}^{-1}$. Female *S. argus* grew at $2.1 \pm 0.2 \text{ mm} \cdot \text{d}^{-1}$ and reached 75mm in approximately 27-29 days. As *S. argus* matured, however, the growth rates slowed to around $1 \text{ mm} \cdot \text{d}^{-1}$. Male *S. nigra* reached MT_L of 54mm in only 16-19 days growing at $2.3\text{-}2.8 \text{ mm} \cdot \text{d}^{-1}$. In comparison, female *S. nigra* reached brooding size in 25-30 days, at a rate of $1.4\text{-}1.8 \text{ mm} \cdot \text{d}^{-1}$. Again a similar pattern of reduced growth (to approx. $0.6 \text{ mm} \cdot \text{day}^{-1}$) was found for mature male and female *S. nigra*.

Growth curves for each species/sex among seasons are indicated in Figure 2. *S. nigra* females grew similarly across all seasons, while male growth in spring was slower than in the 3 other seasons (LSD test, p 's $<.001$). For *S. argus* females, spring growth was higher than the other seasons ($F= 8.73$, $p<.0001$), while males grew faster in the summer than winter ($F=5.36$, $p=0.03$, note sample sizes precluded spring and autumn inclusion).

Age to maturity (taken from MT_L) was less in summer fishes (*S. nigra* Summer: 16-17 days; Winter: 23 days, *S. argus* Summer: 26 days; Winter: 33 days), but not significantly different for either species ($p=0.330$). Males of both species were observed with brood pouches all year round, suggesting that brooding is continuous and not seasonal. *S. argus* females lived up to 124 days with little seasonal variability (see Table 1) while males lived up to 100 days in winter and 150 days in summer (Spring and Autumn were precluded due to low numbers). For *S. nigra*, maximum longevity showed a very similar pattern: females lived approximately 120 days, (Table 1) while males lived approximately 105 days in winter and 150 days in summer, they surprisingly showed least longevity in Spring (86 days) than in Autumn (110 days).

DISCUSSION

General life history theory predicts that the resilience of a species to habitat disturbance is greatly determined by its life history traits (Winemiller and Rose, 1992; Winemiller, 2005). Traits that can support the long-term persistence of populations in unpredictable environments are the key determinants to that species future. As seagrass meadows worldwide are suffering declines from the direct and indirect pressures of humans (Duarte, 2002), the fish species that inhabit these habitats are also under increasing pressure for survival. Knowledge of the life history traits of syngnathids, one of the most numerically dominant families in seagrass meadows, can assist in the management of these species in the face of such anthropogenic disturbance.

The syngnathid populations of *S. argus* and *S. nigra* that inhabit the seagrass meadows in Botany Bay NSW exhibited extremely high growth rates in this study, that are some of the highest known for vertebrates (Hernaman *et al.*, 2000; Depczynski and Bellwood, 2005) while estimated longevity (less than 150 days for both species), are around the shortest known for marine vertebrates (Depczynski and Bellwood, 2005). From more detailed examination of the populations, we found males of both *S. nigra* and *S. argus* matured extremely quickly (16-19 days and 25-30 days respectively) and more quickly in summer compared to winter. Males of both species lived longer in summer than winter by up to 50 days but growth rates of both species were significantly higher in winter than summer. Interestingly, female *S. argus* and *S. nigra* showed little seasonal variation in longevity between seasons. Overall, our results suggest that short-lived “summer” vs. “winter” pipefishes can have very different life history traits.

These growth rates are considerably higher than for the northern hemisphere seagrass syngnathids *Syngnathus fuscus* and *Syngnathus floridae* (1.2mm day^{-1} (Campbell and Able, 1998) and $1.0\pm 0.1\text{mm day}^{-1}$ (Ripley and Foran, 2008) respectively). Such high growth rates coupled with rapid maturity and reduced longevity of these fishes creates populations that combine characteristics of both the opportunistic strategist (i.e., smaller adult size, early maturity, low fecundity) and the equilibrium strategist (i.e., larger offspring, greater investment in parental care). While these attributes may increase their resilience in a habitat of increasing environmental disturbance (Curtis and Vincent, 2006), the ability to reproduce while growing rapidly requires enormous energy reserves, particularly for males to brood and provide nutrients to the developing zygotes (Berglund *et al.*, 1986; Steffe *et al.*, 1989) that are born fully formed, essentially “miniature adults” (Payne *et al.*, 1998). Such energy use must come at a cost, and it is

perhaps that such high rates of growth and early maturation in these smaller fishes may compensate for reduced longevity (Depczynski and Bellwood, 2005; Curtis and Vincent, 2006).). Interestingly the growth rate of *S. nigra* was much higher than that of its conspecific *S. argus* ($2.3\text{-}2.8\text{mm d}^{-1}$ v $1.6\pm 0.4\text{mm. d}^{-1}$). While this difference could be due to low sample sizes for *S. argus*, it is possible that the structural complexity of the seagrass habitat may have favoured the smaller *S. nigra* species for prey availability and cryptic protection. While Kendrick and Hyndes (2003) argue that choice of habitat is dictated by the maintenance of camouflage, the increased growth rate of *S. nigra* suggests that this is not the only mechanism. Energy intake (prey consumed) must be considered over the maintenance of mimicry. It is possible that the smaller *S. nigra* is more manoeuvrable in these seagrass habitats and as a consequence exploits the structural complexity for growth advantage. Genetic difference between these species may also be possible for the variation in growth and would be ideal for a future study on these species.

The age of maturity of both species was relatively young with both *S. nigra* and *S. argus* able to reach minimum total length (ML_T) in as little as 16 and 35 days, respectively. This is considered to be the shortest known maturity time for small syngnathids (Strawn, 1958; Hora and Joyeux, 2009) or any marine vertebrate in natural conditions (Kon and Yoshino, 2002; Depczynski and Bellwood, 2005). Previous estimates from other seagrass Syngnathid species such as the pipefish *Syngnathoides biaculeatus*, has suggested maturation between 3-10 months (Takahashi *et al.*, 2003; Barrows *et al.*, 2009) or within the year for *Syngnathus fuscus* and *Syngnathus floridae* (Campbell and Able, 1998; Ripley and Foran, 2008) respectively. The benefit of such rapid maturation is best understood in the context of their variable environment. Early maturation allows for multiple overlapping generations per year, often with individuals potentially experiencing a lifecycle encapsulating just a single season, and when taken into consideration with published accounts of fecundity (*sensu* (Browne *et al.* (2008))) this equates to *S. argus* and *S. nigra* potentially producing between 2 to 5 broods throughout their lifecycle. While wholesale disappearance of seagrass beds would be catastrophic for these pipefishes, their life history structure shown here indicates a high intrinsic rate of population increase and therefore high capacity to recolonise recovered seagrass beds.

Longevity estimates for *S. argus* and *S. nigra* have previously been inferred from length frequency analysis (Duque-Portugal, 1989; Kendrick, 2002) and not otoliths, as in this study. The recent

validation of daily increments on otoliths for these species (Parkinson *et al.*, 2012) has enabled accurate analysis of the otolith microstructure resulting in evidence of much shorter longevity times than previously documented. Shorter than other seagrass syngnathids which are considered to live between 1.5-4years (Takahashi 2003 , Barrow et al 2009, Campbell and Able 1998, Ripley and Foran 2006) based solely on length frequency data. While length frequency analysis is traditionally a powerful demographic indicator, for *S.argus* and *S. nigra*, the reduced longevity, rapid growth, continuous breeding of these fishes may well have made it impossible to distinguish generations based on this method. The accuracy that otoliths provide to estimates of longevity clearly enhances our knowledge of the demography of the species and could be used to increase our knowledge base of this family as a whole.

Determining the importance of demographic patterns in structuring populations within increasingly disturbed habitats will be critical in understanding the impact of climate change on seagrass meadows and its inhabitants. While syngnathids appear to have many life history traits which enhance their resilience in a rapidly degrading habitat, spatial and temporal limitations must be taken into consideration. For example, the close association syngnathids have with structured habitats and subsequent loss of such habitat is seen as a primary factor in the population decline of many common species (Pogonoski *et al.*, 2002). Their low reproductive potential, restricted dispersal and in some species, monogamous mating systems, all combine to limit their viability and increase their susceptibility to exploitation (Pogonoski *et al.*, 2002). In New South Wales, *S.argus* and *S.nigra* are not considered to be exploited for the Traditional Chinese Medicine trade or aquarium markets (Vincent, 1996). They are, however, found almost exclusively in seagrass habitats (Kuitert, 1995) and as such fall into the category of being susceptible through habitat loss. So while these pipefishes exhibit life history traits that appear to enhance their resilience to habitat degradation, the maintenance of such habitat is essential.

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Table I: Estimated maximum length L_T (from Von Bertalanffy estimates, see text) and longevity of 2 species of seagrass pipefish *S. argus* and *S. nigra*. Sample sizes are indicated

Species/ Sex	Season	Maximum length, mm TL (L_T)	Maximum Longevity, days	# of specimens examined by otoliths	Total # of specimens collected and measured
<i>S. argus</i> , female	Winter	155	124	26	88
	Spring	165	122	9	27
	Summer	155	121	30	64
	Autumn	137	117	23	27
<i>S. argus</i> , male	Winter	120	100	14	76
	Spring	-	-	-	26
	Summer	140	150	11	47
	Autumn	-	-	-	7
<i>S. nigra</i> , female	Winter	108	114	25	386
	Spring	165	122	29	84
	Summer	110	124	64	147
	Autumn	137	117	44	126
<i>S. nigra</i> , male	Winter	84	105	23	424
	Spring	90	86	16	124
	Summer	144	152	42	219
	Autumn	131	110	20	119

Figure 1. Study sites within Botany Bay, New South Wales, Australia. Site 1 is parallel to Foreshore Road (33°57.39'S, 151°11.81'E); Site 2 is adjacent to the St Georges Sailing Club (34°00.34'S, 151°07.76'E).

Figure 2: Length at age (days after hatch, curves Von Bertalanffy fitted) for a) *S.argus* females; b) *S.argus* males; c) *S.nigra* females and d) *S.nigra* males.

Figure 1

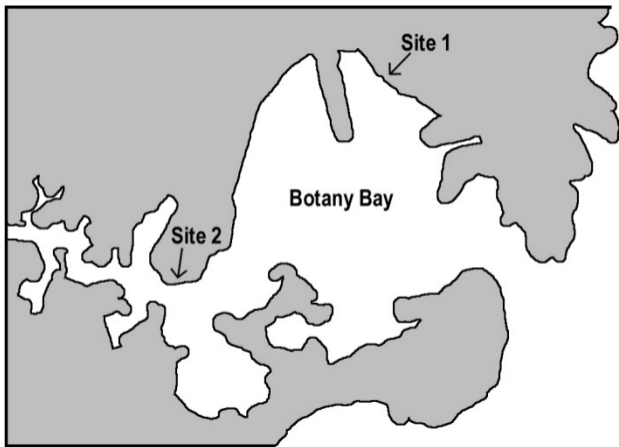


Figure 2

