Coral Reefs

Long term demographics of a coral-reef fish: growth, survival and abundance at several spatial scales

--Manuscript Draft--

Manuscript Number:	CORE-D-20-00295R2
Full Title:	Long term demographics of a coral-reef fish: growth, survival and abundance at several spatial scales
Article Type:	Report
Funding Information:	
Abstract:	In marine organisms, pelagic larval dispersal often results in genetic panmixis among widely-separated populations, however local conditions may produce populations of marine organisms that differ in key life history traits. Here, we assess spatial differences in growth, body condition, survivorship and movement over a decade for lemon damselfish Pomacentrus moluccensis . Newly- recruited fish were tagged on the southern (One Tree Island, 23 0 S), and northern Great Barrier Reef (Lizard Island, 15 0 S), 1200km apart, and monitored for over a decade to provide direct data on growth and survivorship. New recruit physiological condition (lipid content) had a weak positive influence on early survival, but not on long-term persistence or growth, and the larval supply signal was lost after 2 years, suggesting post-settlement processes were key in long-term population persistence. Fish exhibited extreme site fidelity, with older/larger fish moving most (all less than 7 metres). At Lizard Island, under 5% of individuals remained after 3 years, none after 4 years, while at One Tree Island 5% of individuals survived over 5 years, with 1% remaining after a decade, suggesting Lizard Island populations may require more frequent replenishment to persist. Among-site (within location) variation in mortality was high, and not related to density, suggesting local conditions such as wave exposure and predators were important. Surprisingly, mean growth at the two locations, which differ by around 2 o C on average in sea temperature, was practically identical, levelling off after 3 years, but with high variation among nearby sites within each location, which would affect size-based fecundity and time of first reproduction at these smaller spatial scales. Neither early post-settlement growth nor mortality were density-dependent, and early growth was not related to overall longevity. These small reef fishes are highly sedentary and some demographic parameters, but not others, differ at a range of scales, with post-settlement populations likely driven largely by mortality patterns at the larger spatial scale. Latitudinal and smaller-spatial scale differences in performance (growth, survival) of this species, leading to offsets in expected time to maturity an fecundity, are contrasted by evidence of stability of adult populations over two decades at One Tree Island, which suggests that resilience to environmental change/climate change and other externalities differ considerably across this species' distribution.
Corresponding Author:	David Booth University of Technology, Sydney NSW, Australia
Corresponding Author Secondary Information:	
Corresponding Author's Institution:	University of Technology, Sydney
Corresponding Author's Secondary Institution:	
First Author:	David J Booth
First Author Secondary Information:	
Order of Authors:	David J Booth
	Giglia A. Beretta

Order of Authors Secondary Information:	
Author Comments:	
Response to Reviewers:	

UTS

University of Technology, Sydney

David J. Booth
Professor of Marine Ecology,
School of Life Sciences
Univ. of Technology, Sydney
PO Box 123, Broadway NSW 2007
AUSTRALIA
email: David.Booth@uts.edu.au
Ph: +61 2 9514 4053

April 10 2021

To: Prof. Morgan Pratchett
Editor Coral Reefs

Re: Revised versions of CORE-D-20-00295 for your consideration for Coral Reefs

Dear Morgan,

We are very happy to have our ms accepted for publication in Coral Reefs. We have now revied our ms, in particular fixing spelling and grammar errors and also Site labels on Fig 1. Many thanks for your constrictive comments throughout to process, as well as the two Reviewers.

All the best

David Booth

Dave

Long term demographics of a coral-reef fish: growth, survival and abundance at several spatial scales

David J. Booth[1] and Giglia A. Beretta[1]

[1] School of the Life Sciences, University of Technology Sydney, PO Box 123 Broadway NSW 2007 AUSTRALIA

David.Booth@uts.edu.au

Abstract. In marine organisms, pelagic larval dispersal often results in genetic panmixis among widely-separated populations, however local conditions may produce populations of marine organisms that differ in key life history traits. Here, we assess spatial differences in growth, body condition, survivorship and movement over a decade for lemon damselfish *Pomacentrus moluccensis*. Newly- recruited fish were tagged on the southern (One Tree Island, 23^0S), and northern Great Barrier Reef (Lizard Island, 15^0S), 1200km apart, and monitored for over a decade to provide direct data on growth and survivorship.

New recruit physiological condition (lipid content) had a weak positive influence on early survival, but not on long-term persistence or growth, and the larval supply signal was lost after 2 years, suggesting post-settlement processes were key in long-term population persistence. Fish exhibited extreme site fidelity, with older/larger fish moving most (all less than 7 metres). At Lizard Island, under 5% of individuals remained after 3 years, none after 4 years, while at One Tree Island 5% of individuals survived over 5 years, with 1% remaining after a decade, suggesting Lizard Island populations may require more frequent replenishment to persist. Among-site (within location) variation in mortality was high, and not related to density, suggesting local conditions such as wave exposure and predators were important. Surprisingly, mean growth at the two locations, which differ by around 2^{o}C on average in sea temperature, was practically identical, levelling off after 3 years, but with high variation among nearby sites within each location, which would affect size-based fecundity and time of first reproduction at these smaller spatial scales. Neither early post-settlement growth nor mortality were density-dependent, and early growth was not related to overall longevity.

These small reef fishes are highly sedentary and some demographic parameters, but not others, differ at a range of scales, with post-settlement populations likely driven largely by mortality patterns at the larger spatial scale. Latitudinal and smaller-spatial scale differences in performance (growth, survival) of this species, leading to offsets in expected time to maturity an fecundity, are contrasted by evidence of stability of adult populations over two decades at One Tree Island, which suggests that resilience to environmental change/climate change and other externalities differ considerably across this species' distribution.

Keywords: coral-reef fish, growth, latitudinal demography, physiological condition, *Pomacentrus moluccensis*, survival and longevity.

Introduction

Spatial and temporal variation in species' demography is of fundamental interest in population ecology, and bears on fitness (Galliard et al. 2000). However, few studies have reported key demographic traits (e.g., survival and growth) across the entire lifespan of fish living over a decade. One valuable approach is to conduct small-scale experimental manipulations of organisms *in situ* that definitively linking demography to mechanisms at specific ages over very short time intervals (e.g., Booth and Hixon 1999), but rarely can these be integrated across the whole lifespan. For marine fishes, these demographic variables can be expected to vary greatly as the fish move among habitats ontogenetically, and because habitat quality and risks differ spatially (Dahlgren and Eggleston 2000), but may even differ for fish growing in the same location. While larval supply through pelagic dispersal has been predicted as a key process regulating reef fish populations (e.g., Armsworth 2002), after fish settle onto reef habitat from offshore waters, post settlement processes can decouple links between larval dynamics and adult dynamics (Jones 1990; Hixon et al. 2012). Once settlement has established initial population densities at a site, spatial and temporal variation in persistence is driven by key demographic parameters of growth and survival, and to varying extents, movement (e.g., Kritzer and Sale 2006).

Post-settlement, key demographic variables can vary considerably. Patterns of growth can indicate fecundity (fecundity is size-related in reef fishes: Duarte and Alcaraz 1989) and predation risk (Tupper and Boutilier 1997). They can also be scaled up when combined with survivorship to estimate biomass distribution of a species on a reef (important for trophic understanding and functional groups (e.g, Mora et al. 2011). However, causes for variation in spatial and temporal patterns of growth and survival are manifold. For reef fishes, a myriad of factors, such as food availability, predator densities, and ambient temperature will determine survivorship (Tupper and Boutilier 1997, Taylor et al. (2019). Phenotypic traits can vary with latitude, with larger size and greater longevity characteristic of fish at higher latitudes (Munch and Salinas 2009). The physiological state of the settling larva has been shown to exert an ongoing influence on how it responds to predators and food, and consequently on post-settlement survival and growth. Physiological state, or condition, can critically affect a reef fish’s chances of early survival ((Booth and Hixon 1999), (Hoey and McCormick 2004), (Booth and Beretta 2004), and this effect can vary across latitudes (e.g., Booth 2002). However, whether such early recruit condition effects persist across the entire life span is unclear. Taylor et al (2019) demonstrated that for a coral- reef surgeonfish (*Naso* sp.), both spatial and individual differences in demographics (growth, mortality, longevity) were attributable partly to sea temperature (SST), but there were also intrinsic diffs among individuals, with suggestions that these features of populations may facilitate ecological resilience.

Doherty and Fowler (1994a,b) examined spatial and temporal variation in survival and longevity of the lemon damselfish (*Pomacentrus moluccensis*) across reefs in the Capricorn-Bunker group in the southern Great Barrier Reef. Using a large one-off otolith collection across 7 reefs, they reconstructed the cohort strengths across a number of years and showed that a strong recruit year class was preserved in older age classes. They concluded that over 90% of the variation in year class strength over 9 years could be explained by supply of larvae at settlement. Recruits were censused as individuals that were present in April of the year in question, thus they were the products of larval supply (i.e., settlement) and unknown post-settlement processes (e.g., variable mortality) for several months. Settlement of this species is typically highest January-February each year, so fish used in the study may have experienced 2-4 months on the reef prior to censusing, including high variable and likely large post-settlement mortality. Therefore, the fate of the high proportion of individuals that did not survive the early months remained unrecorded and the role of early mortality may have been underestimated. Also, episodic otolith collections of older fish may not allow a comparison of success within a cohort and can be biased towards individuals that persist longer (Booth 2014).

The direct approach, that is following the fate of a cohort of individuals, is less prone to issues of unknown mortality, but is difficult because it requires sustained field sampling over the longevity of the species, and either tagging or an assumption that all fish in the original cohort are either available for counting or have died. Fish tagging is most effective if the tag itself does not interfere and can persist for years, and if the fish has high site fidelity. Here, we present data from a cohort of the lemon damselfish *Pomacentrus moluccensis*, individually tagged with Visual Implant Elastomer (VIE, Northwest Marine Technology Inc.) in 2000 and re-censused until all tagged fish had disappeared in 2011 at sites at both the southern and northern Great Barrier Reef. We asked

(1) How did cohort survivorship/longevity vary at smaller and larger spatial and temporal scales?

(2) How did growth vary at smaller and larger spatial and temporal scales? Is individual growth performance preserved across life history (e.g., are some fish consistently fast growers through life?)?

(3) How far did tagged fish move over the course of the study? and

(4) Did patterns of growth and survival over the entire lifespan relate to larval supply (physiological condition, density) or sea temperature?

(5) How do the above indicate resilience of this species across latitudes and time?

Methods

Sites

One Tree Island is located in the southern Great Barrier Reef (23 º 30' S, 152 º 06' E). Seven long-term monitoring sites inside and outside One Tree lagoon were used. Four sites were within First Lagoon, plus Notch (NW outer reef) and two sites in Third lagoon. At Lizard Island [location (14º 40' S, 145º 28' E)] 6 sites were surveyed across the main lagoon and northern coastline (Figure 1, Supp Table 1). Temperature loggers were deployed at most sites in both locations (HOBO Pendant Temperature loggers) from 2000, reading at one hr intervals)

Fish tagging and censuses

In early 2000, at each site, density of new settler, juvenile and adult lemon damselfish *Pomacentrus moluccensis* were determined within 6, 15m long transects. All new settlers were captured at each site, their positions noted along a permanent transect, and tagged with VIE (numbers tagged shown in Supplementary Table 1). Given these small fish may have been prone to tagging mortality if tagged multiple times (as needed for individual identification) each cohort was tagged with one tag only (one colour), such that fish within a cohort and location could not be distinguished initially. Change in density of these tagged settlers at each site was monitored weekly from January 2000-March 2000 and again in April at One Tree Island, and in November at Lizard Island. At that time, each remaining fish was provided with a further VIE coloured tag to assist in individual recognition, and its position along the transect (to the nearest 0.5m) recorded. Josephsen et al. (2008) demonstrated that fish retain VIE tags for at least 3 years in field conditions and we never noted tags missing from fish that had multiple tags (unpub. data), suggesting tag loss was rare. Subsequently, surveys were taken 1-2 times per year, mostly in summer months. For each survey, densities were again determined, and a thorough search to the reef base and crest, within and adjacent to all transects was undertaken for tagged individuals. When found, behaviour and position on the transect of tagged fish were observed, to ensure fish were resident at that position and not transient, then fish were captured using clove oil and transferred underwater into Ziploc© bags. In bags, tags of fish were closely examined *in situ* and fish were measured (Total Length: TL in mm) then fish were carefully released. Note field length measurements were accurate to ± 1mm TL, unpublished data)

Body condition

Groups of 10 new recruits were collected immediately adjacent to transects when each cohort of recruits was initially tagged at each sample site, und the assumption that their physiological condition was similar to nearby tagged recruits. These fish were frozen and transported to University of Technology, Sydney, where gravimetric total lipid analysis was undertaken. Total neutral storage lipids of sampled fish were measured by freeze-drying the sample and performing a methanol-chloroform extraction (Mann & Gallagher, 1985; Booth & Hixon, 1999) then expressing total lipids as a percentage of dry body mass. Total lipids was considered a useful index of overall physiological condition (McCormick and Molony 1994, Booth and Hixon 1999, Booth and Alquezar 2004, Booth and Beretta 2004)

Analyses

Movement (metres) for individuals was calculated as linear distance between position of original release and subsequent recapture, and compared among sizes by 1 Factor ANOVA (log transformed). Growth for each tagged individual was recorded for both One Tree and Lizard

Islands as change in length over years, and plotted as individual growth trajectory, but also by site. Growth differences between locations were tested using ANOVA to compare mean lengths after one year (i.e., comparing first year's growth). Survivorship was plotted as percentage of fish remaining at yearly intervals and was compared between locations (Log-Rank test of survival curves, IBM SPSS Version 25, 2017). Relationships between growth, survivorship, fish density and water temperature (temperature logger-derived average annual temperature) were explored via linear regression analyses (Supplementary data), focussing on growth and survival in the first year post settlement when most losses occur (e.g., Sale and Ferrell 1988). Sample sizes are shown in Supplementary Table 1.

Results

Movement

Extensive searches for tagged fish throughout the study sites (along entire transect and well above (reef crest) and below reef) reinforced that this species has strong site fidelity over decadal time scales. Fish less than 55m TL were rarely found more than one metre from their original tagging location. For larger fish, most were found within 1-2 metres of the original tagging location, but some individuals ventured further, with one 67mm TL fish found 7 metres away from the tagging point (ANOVA F= 40.35, P<.0001, Tukey's test Figure 2).

Growth and maturity

Mean growth was similar for fish tagged at Lizard Island and at One Tree Island (Figure 3a) was not significantly different over the first year (ANOVA F=.01, p>.05) and over the first 4 years (ANOVA F=.03, p>.05). Overall, tagged recruits were approximately 15mm Total Length (14.7 mm ± 0.8 SE) and overall mean length after one year was 35mm TL. However, tagged fish growth among sites within locations differed considerably, particularly at One Tree Island (Figure 3b). Within a site, individuals differed in their growth trajectories, with no consistent individual differences in growth (Linear regression: growth in Year 1 vs Year 2 growth, $R^2 = 0.096$, p>.05; also see Figure 3c). No relationship was detected between annual water temperature, individual survivorship or local fish density (*P. moluccensis* only, since these fish live in social groups: Brunton and Boot 2003), and growth to Year 2 among sites (Figure S1 Linear regressions, p's>.05).

Fecundity is size-related in *P. moluccensis* with maturity at around 48 mm TL at both Lizard Island and One Tree Island (Mapstone 1988; T. Brolund unpub. PhD thesis). Based on growth trajectories recorded in this study, fish would therefore be 1.5-2.5 years of age (depending on site) at maturity at One Tree Island, and 1.5 to 2 years at first maturity at Lizard Island (Fig. 3b).

Survivorship and body condition

There was a dramatic difference in survivorship between Lizard and One Tree Island (higher survival at One Tree: Log-Rank (Mantel-Cox) test, p<.0001): Early (first year) survival was low at both locations, from 9-30% at One Tree Island and from 3 to 13% a Lizard Island. No Lizard Island fish lived over 4 years, while at One Tree Island, some individuals survived up to 11 years old (under 1% of initial tags, or 5% of April survivors, Figures 4a,b). Survival was not density-dependent, with no relationship between recruit density within a transect and % surviving to the following April or over the following year (Fig S1, Linear Regression, p>.05). At One Tree Island, individual fish that lived over 3 years had higher early growth (Fig 3c inset) but the overall relationship between survival and growth was not significant (see Supplementary Data Figure 1, Linear regressions all non-significant (p's>.05)). There was also no relationship between annual water temperature, individual growth or local fish density (*P. moluccensis* only, since these fish live in social groups), and survivorship to Year 2 among sites (Supp Figure 1, Linear regressions all non-significant (p's>.05).

Condition of recruit cohorts was similar between Lizard Island and One Tree, but differed considerably among sites (One Tree: mean=10.9% lipid dw/dw, range 7.2-14.5; Lizard Island: 10.5, range 7.6-13.2, Figure 5). There was a weak but non-significant positive relationship between recruit body lipid and subsequent survival to Year 1 among sites at each location (r^2=0.11 for One Tree, for Lizard), and for Year 3 (One Tree r^2=0.16, Lizard : r^2=0.31, p's >.05, Figure 5).

Population fluctuations

Adult densities across 22 year (One Tree Island) and 5 years (Lizard Island are plotted in Figure 6. One Tree Island sites differed in adult densities, but all showed a high degree of density stability over decades. At Lizard Island, the survey period was only 5 years, but most sites had consistent adult densities over that period.

Discussion

Intra-specific life-history trait variation among latitudes can indicate differences in population persistence, and be related to key environmental factors. Here, a long-term field tagging study has demonstrated that for a common coral-reef damselfish, growth and survivorship differed across a range of spatial scales, yet adult populations showed remarkable stability over decades.

Surprisingly, average growth at the northern GBR (Lizard) vs southern GBR (One Tree) locations, despite being separated by over 1000 km (8 degrees latitude) and with different annual water temperature regimes (over 2^0C), was almost identical. In contrast Taylor et al. (2019) found a threefold geographic variation of a coral-reef fish (*Naso* sp.) across 20 degrees of latitude north and south) in life span that was strongly linked to water temperature, but not to anthropogenic pressure or ocean productivity. Munch and Salinas (2009) noted that in general, relative to individuals from low latitudes, high-latitude individuals tend to have higher growth rates and attain larger body size, and made general prediction of a strong link between environmental temperature and longevity (e.g., warmer water temperatures at lower latitudes link to lower longevity for marine fishes). Rather it was smaller-scale differences in growth among sites within locations that were significant. For instance, mean body length of 10-year-old fish ranged from 57 mm TL to 70 mm TL across sites at One Tree Island. This represents a range of from 4.5 to 9.5 grams wet weight (unpub. data.). Given fecundity is related to body weight, especially in females (Mapstone 1988), fecundity among nearby sites may have varied by approximately 100% (Mapstone 1988) and sites with slower-growing fish may have reproduction delayed by one year, given reproduction is seasonal. Faster growing, larger individuals appeared not to have strong survival advantages, but given earlier maturity, may have lifetime fecundity benefits.

Survival was significantly reduced at the northern vs southern Great Barrier Reef location (Lizard Island vs One Tree Island) which follows the intraspecific trend of lower longevity of fishes in more tropical locations (Munch and Salinas 2009; Taylor et al. 2019) related to sea temperature. Using large otolith collections, Beukers (1996) found maximum ages of *P. moluccensis* to be six years at Lizard Island, while Doherty and Fowler estimated maximum age at 14-16 years at One Tree Island, and one cohort had over 20% of fish over 10 years. In contrast, only 1% of tagged fish in our study persisted beyond 10 yeas at One Tree Island. This may be due to inter-cohort variability, with the percent of cohort over 11 years varying from 1 to 20% in their study) but was partly explained by initial ages of fish. Doherty and Fowler followed persistence of fish from April onwards, so considerable mortality may have already occurred since actual settlement (i.e., were possibly 4 months post-settlement). Mortality of new recruits from near settlement to April in our study varied from 30 to 80%. As with growth, survival was very variable among sites within locations, with early survival low at all sites (see Sale and Ferrell 1988). Some compensation in terms of replenishment may occur; for example, the site with the lowest survivorship also had the consistently highest settlement of larvae (unpub. data). Beukers and Jones (1998) demonstrated density-dependent mortality of new recruits of *Pomacentrus moluccensis* over 1 year at Lizard Island, Great Barrier Reef, which was directly correlated with the density of piscivores, and inversely correlated with the percent cover of structurally complex corals, so these factors may have a role in survivorship differences seen in this study..

Fish were remarkably site-specific over decadal time scales, with fish remaining within metres of their settlement site for over a decade (c.f. Lewis 1997). In addition, this species also has strong homing ability (Booth 2016) so it exhibits extreme site philopatry. Jones et al. (1999) found some offshore larval philopatry in closely-related small benthic damselfishes at Lizard Island, which may preserve smaller-scale variation in new recruit condition documented here.

In reef fishes, demographic trade-offs between growth and survival have bene predicted, e.g., Taylor et al. (2019) demonstrated differences in individuals of the surgeonfish *Naso* sp. in life history traits pertaining to growth and survival. Such variation in traits is also evident in coral reef fishes exposed to marked environmental variation across relatively small spatial scales (10 s of kilometres; e.g., Gust et al., 2002; Brandl, et al., 2018).

Physiological condition at settlement was not strongly related to long-term persistence. This contrasts with findings of Booth and Beretta (2004) who manipulated condition of very new *P. moluccensis* settlers had strong short-term effects on survival, via enhanced predation. It appears that processes happening over years post-settlement are decoupling links between early condition and longer-term persistence. The “larval supply signal” (e.g., Jones 1990) in both fish abundance and condition appears weak, suggesting post-settlement processes are paramount (see also Jones 1986).

Field cohort tagging and censusing, as adopted here, allows an accurate understanding of individual fish growth, persistence and movement, but is field-intensive and only follows one or a few cohorts, while otolith hindcasting methods, in contrast, have the advantage of requiring comparatively little field time, and examining a range of age-cohorts simultaneously. Both methods have merit, in that a one-off otolith collection allows a snapshot of persistence of many age cohorts, while tagging allows tracking of detailed survival and growth patterns in individual cohorts (e.g., Meekan 1992, Elsdon et al. 2008; Booth 2014). The data presented here are from one of the longest tagging series for coral reef fishes worldwide. One issue with growth as estimated here is that longer-lived individuals will be increasingly dominating the population growth curve over time. If these individuals grow faster in general, they will bias later growth, however while Figure 3c suggests older fish had grown faster early in life, they had not grown faster overall (Supp. Figure 1).

Despite the documented demographic variation among sites, and disturbances such as global coral bleaching episodes (e.g., in 1998 and 2002), our long-term monitoring at One Tree Island indicates the densities of adult *P. moluccensis* were surprisingly stable over decades, and even Lizard island adult densities appeared generally stable over 5 years (Figure 6), This suggesting that the species shows resilient to change over decadal periods despite large recruitment variation (e,g. Booth et al. 2000) with its longevity contributing to strong “storage effects (*sensu* Warner and Chesson (1985).

Lifetime reproductive output is likely to be lower at Lizard Island overall compared to One Tree Island, given much shorter longevity there, but among sites within locations, onset of maturity would have varied by up to one year, likely considerably affecting lifetime fecundity and site-specific population demography and reproductive output at these small spatial scales (*sensu* Lee et al. 2011). In fact, at some sites around Lizard Island, size at mean longevity was below that required for maturity.

While local, regional and biogeographical persistence of populations of this species may be driven in part by variable larval supply (e.g., Doherty and Fowler 1994a), this study has indicated that high variability in post-settlement demography of this very common coral-reef fish, especially variable mortality, may be a key to persistence of local populations, and likely generate the development of significant variability among populations in overall biomass and productivity. Long-term adult abundances appear to be largely decupled from settlement processes, which can fluctuate by orders of magnitude (e.g. Booth et al. 2000), and growth independence from sea temperature may afford this species a degree of resilience from future environmental challenges.

Acknowledgements. We would like to acknowledge the staff at Lizard Island Research Station, and One Tree Island Research Station for their support, and Will Figueira, Marcus Gregson, Ralph Alquezar for field assistance. The study was one under Great Barrier Reef Marine Park Authority Permit G11/34452.1 and UTS Animal Care and Ethics 2008-016A.

Conflict of Interest: The corresponding author states that there is no conflict of interest.

References

Armsworth PR (2002) Recruitment Limitation, Population Regulation, and Larval Connectivity in Reef Fish Metapopulations. Ecology 83:1092-1104.

Beukers J (1996) The relative roles of recruitment and post-recruitment processes in the regulation of a coral reef damselfish population. PhD thesis. James Cook University, Australia, 128pp

Beukers J, Jones G (1998) Habitat complexity modifies the impact of piscivores on a coral reef fish population. Oecologia 11:, 50–59

Booth DJ, Beretta GA (2004) Influence of recruit condition on food competition and predation risk in a coral reef fish. Oecologia 140: 289-294

Booth DJ, Kingsford MJ, Doherty PJ, Beretta GA (2000) Recruitment of Damselfishes in One Tree Island Lagoon: Persistent Interannual Spatial Patterns. Marine Ecology Progress Series, 202: 219-230

Booth DJ (2002) Larval supply, condition and persistence of the coral reef fish, *Pomacentrus moluccensis* pp.463 – 468 In: Kasim Moosa, M.K., Soemodihardjo, S., Nontji, A., Soegiarto, A., Romimohtarto, Sukarno and Suharsono. (Editors) *Proceedings of the Ninth International Coral*

Reef Symposium, Bali, Indonesia, October 23-27 2000. Published by the Ministry of Environment, the Indonesian Institute of Sciences and the International Society for Reef Studies.

Booth DJ (2014) Do otolith increments allow correct inferences about age and growth of coral reef fishes? Coral Reefs. 33: 255–258

Booth DJ (2016) Ability to home in small site-attached coral reef fishes. Journal of Fish Biology, *89*(2), 1501-1506.

Booth D, Alquezar R (2002) Food supplementation increases larval growth, condition and survival of *Acanthochromis polyacanthus*. Journal of Fish Biology 60:1126–1133

Booth DJ, Hixon MA (1999) "Food ration and condition affect early survival of the coral reef damselfish, Stegastes partitus." Oecologia 121(3): 364-368

Brandl SJ, Goatley CHR, Bellwood DR, Tornabene L (2018) The hidden half: ecology and evolution of cryptobenthic fishes on coral reefs. Biol Reviews 93: 1846-1873

Brolund T (2008) Growth patterns along environmental gradients of tropical pomacentrid fishes. Unpub. PhD thesis University of Technology, Sydney. 69pp

Brunton, B. J., & Booth, D. J. (2003). Density- and size-dependent mortality of a settling coral-reef damselfish (*Pomacentrus moluccensis* Bleeker). Oecologia, *137*(3), 377-384

Dahlglen C, Eggleston DB (2000) Ecological processes underlying ontogenetic habitat shifts in a coral reef fish. Ecology 81:2227-2240

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

Doherty PJ, Fowler A (1994b) Demographic consequences of variable recruitment to coral reef fish populations: a congeneric comparison of two damselfishes. Bulletin of Marine Science 54: 297-313

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

Elsdon TS, Wells BK, Campana SE, Gillanders BM, Jones CM, Limburg KE, Secor DH, Thorrold SR, Walther BD (2008) Otolith chemistry to describe movements and life-history parameters of fishes – hypotheses, assumptions, limitations and inferences. Oceanography and Marine Biology Annual Review. 46:297-330

Gaillard J-M, Festa-Bianchet M, Yoccoz NG, Loison A, Toigo Annu C (2000) Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics 31:367–93

Gust N, Choat J, Ackerman J (2002) Demographic plasticity in tropical reef fishes. Marine Biology 140: 1039–1051

Hixon A., Anderson TW, Buch KL, Johnson DW, McLeod R, Stallings C (2012) Density dependence and population regulation in marine fish: a large-scale, long-term field manipulation. Ecological Monographs 82: 467–489

Hoey AS, McCormick MI (2004) Selective predation for low body condition at the larval-juvenile transition of a coral reef fish. Oecologia 139: 23-29

Jones P. (1986) Food availability affects growth in a coral-reef fish. Oecologia 70: 136-139

Jone GP (1990) The importance of recruitment to the dynamics of a coral reef fish population. Ecology 71:1691-1698

Jones GP, Milicich MJ, Emslie MJ, Lunow C (1999) Self-recruitment in a coral reef fish population. Nature 4902:802-804

Josephson DC, Robinson JM, Widell BC, Kraft, C.E. 2008. Long-term retention and visibility of Visible Implant Elastomer tags in brook Trout. North American Journal of Fisheries Management 28:1758–1761

Kritzer JP, Sale, PF (2006) The metapopulation ecology of coral reef fishes In: Sale JPKF, editor. Marine Metapopulations. Chapter 2. Burlington: Academic Press; pp. 31–67

Lee AM, Engen S, Sæther BE (2011) The influence of persistent individual differences and age at maturity on effective population size. Proceedings of Biological Science. 278:3303-12

Lewis AR (1997) Recruitment and post-recruit immigration affect the local population size of coral reef fishes Coral Reefs 16: 139-149

Mann R, Gallagher SM (1985) Physiological and biochemical energetics of larvae of *Teredo navalis* and *Bankia gouldi*. Journal of Experimental Marine Biology and Ecology 85: 211–228

Mapstone BD (1988) The determination of patterns in the abundance of *Pomacentrus moluccensis* Bleeker on the southern Great Barrier Reef. Unpublished PhD Thesis, University of Sydney, pp. 240

Meekan MG (1992) Limitations to the back-calculation of recruitment patterns from otoliths. Proceedings of the Seventh International Coral Reef Symposium, Guam, 1*:* 624-628

McCormlck M1, Molony BW (1995) Influence of water temperature during the larval stage, on size, age and body condition of a tropical reef fish at settlement Marine Ecology Progress Series 118:59-68

Mora C, Aburto-Oropeza O, Bocos A, Ayotte PM, Banks S, Bauman AG, . Zapata FA, plus 55 authors (2011) Global human footprint on the linkage between biodiversity and ecosystem functioning in reef fishes. PLOS Biology, 9: e10006.

Munch SB, Salinas S (2009) Latitudinal variation in lifespan within species is explained by the metabolic theory of ecology. Proceedings of the National Academy of Sciences of the United States of America. 106:13860-4

Sale PF, Ferrell DJ (1988) Early survival of juvenile coral reef fishes. Coral Reefs. 7: 117-124

Taylor BM, Choat JH, DeMartini EE, et al. (2019) Demographic plasticity facilitates ecological and economic resilience in a commercially important reef fish. Journal of Animal Ecology 2019;88:1888–1900

Tupper M, Boutilier RG (1997) Effects of habitat on settlement, growth, predation risk and survival of a temperate reef fish. Marine Ecology Progress Series. 151:225-236

Warner RR, Chesson PL (1985) Coexistence mediated by recruitment fluctuations: a field guide to the storage effect. American Naturalist. 125:769-787

Figure Legends

Figure 1: Map of Queensland Australia indicating Great Barrier Reef and study locations. One Tree Island and Lizard Island maps showing sites (Coded as per Table S1)

Figure 2: Maximum distance from release location of tagged *Pomacentrus moluccensis* (metres, Mean ± SE) at One Tree Island 2000-2011. (ANOVA and Tukey's post-hoc tests on movement: 35mm=40mm=50mm=55mm<60mm=65mm)

Figure 3: Growth of tagged *Pomacentrus moluccensis* 2000-2011:

a. Growth of fish (mean TL ± SE) at One Tree Island (solid line, top panel) and Lizard Island (broken line, bottom panel, SE's shown, n's see Table S1
b. Growth (mean ± SE) among sites: Upper panel: One Tree island Lower panel: Lizard Island sites. Horizontal dotted line indicates size at maturity. Colours used to help distinguish sites.
c. Individual growth histories of tagged fish at One Tree Island. Heavier line is longest lived fish. Horizontal dotted line indicates size at maturity. Colours used to help distinguish individual fish. INSET: mean Year One growth (%) of fish under and over 3 years longevity (t-test, P<.05).

Figure 4: Survivorship of tagged *Pomacentrus moluccensis* 2000-2011, for n's tagged see Table S1:

a: ($\log_{10}$) survival (Mean ± SE, n= 6 sites) of fish at One Tree Island (solid line) and Lizard Island (broken line)

b: ($\log_{10}$) survival: One Tree island individual sites (solid lines, n=6) vs. Lizard Island sites (broken lines, n=6). Colours used to help distinguish sites

Figure 5: Condition (% lipid, dw/dw, mean ± SE, n=10) of newly-recruited cohorts of *Pomacentrus moluccensis* vs survival at (a) One Tree island (closed circles: 3 years, open circles: 1 year n=10 fish each) vs (b) Lizard Island (closed circles: 3 years, open circles: 1 year n=10 fish each).

Figure 6: Adult densities of *Pomacentrus moluccensis*, means for each site over 22 years in One Tree Island (Mean + SE, n=6 transects, Red arrows indicate major coral bleaching years), and Lizard Island (Mean + SE, n=10 transects)

Supplementary Table and Figure

Table S1 Locations, sites, GPS fixes and sample sizes of tagged fish in this study

Figure S1:

A. Growth (% TL) vs survivorship (%) from tagging in year 200 to recapture in 2001, ie first year) for *P. moluccensis* at One Tree Island (n= 7 sites, blue symbols) and Lizard Island, n-= 6 sites, red symbols)

B. Growth (% TL in first year post tagging) vs Fish density (# per 15m of reef) for *P. moluccensis* at One Tree Island ((Mean # per 15m of reef , n= 7 sites, blue symbols) and Lizard Island, Mean # per 10m of reef, n-= 6 sites, red symbols)

C. Survival (% over first year) vs Fish density (# per 15m of reef) for *P. moluccensis* at One Tree Island (n= 7 sites, blue symbols) and Lizard Island, n-= 6 sites, red symbols)

D. Growth (% TL in first year post tagging) vs. Sea Temperature (annual average, ^{o}C) (logger data) for *P. moluccensis* at One Tree Island (n= 7 sites, blue symbols) and Lizard Island, n-= 6 sites, red symbols)

E. Survival (% over first year) vs Sea Temperature (annual average, ^{o}C) (logger data) for *P. moluccensis* at One Tree Island (n= 7 sites, blue symbols) and Lizard Island, n-= 6 sites, red symbols)

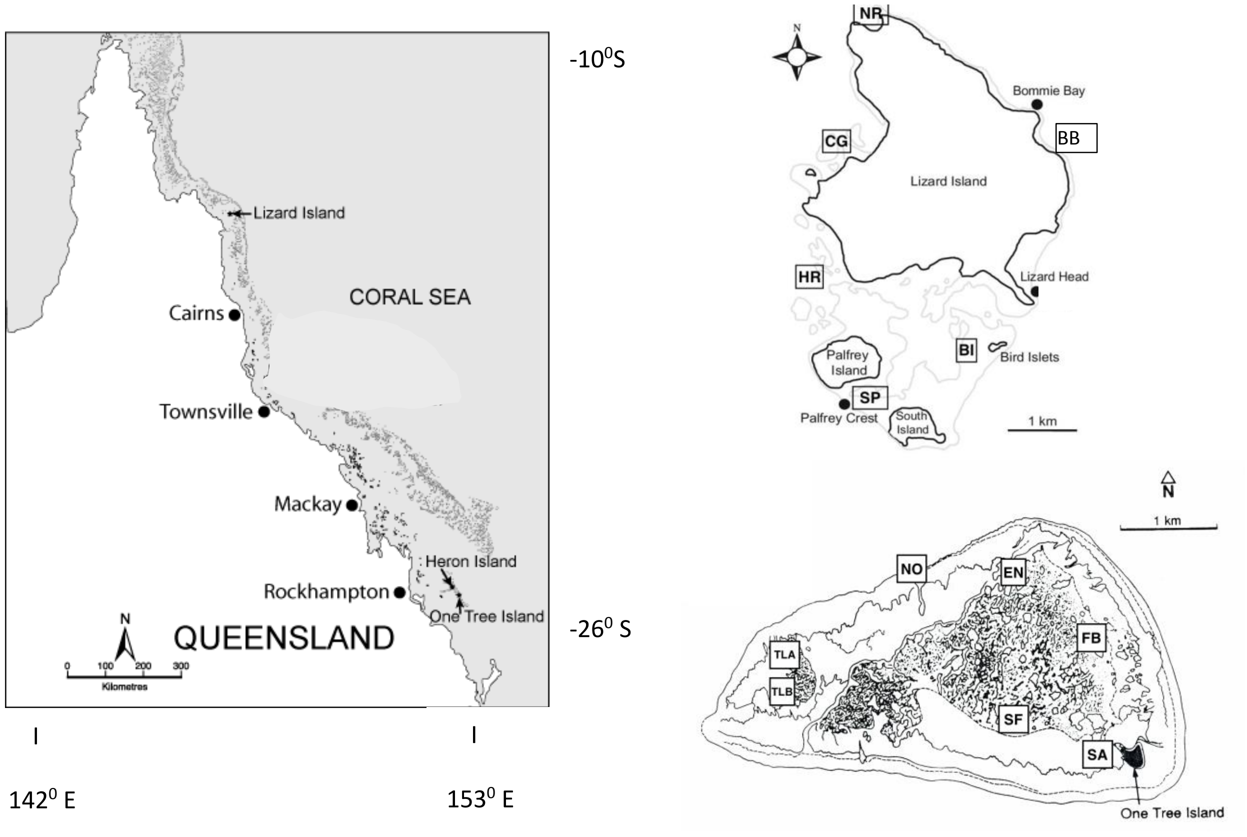

-10⁰S
-26⁰ S
142⁰ E
153⁰ E
Lizard Island
CORAL SEA
Cairns
Townsville
Mackay
Heron Island
Rockhampton
One Tree Island
QUEENSLAND
N
0
100
200
300
Kilometres
N
NR
Bommie Bay
BB
CG
Lizard Island
HR
Lizard Head
BI
Bird Islets
Palfrey Island
SP
Palfrey Crest
South Island
1 km
N
1 km
NO
EN
FB
TLA
TLB
SF
SA
One Tree Island

Figure 1

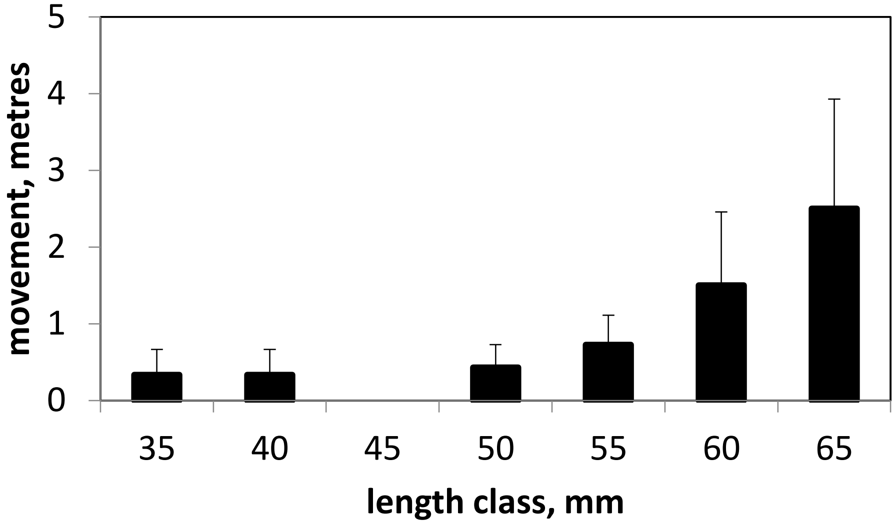


Figure 2

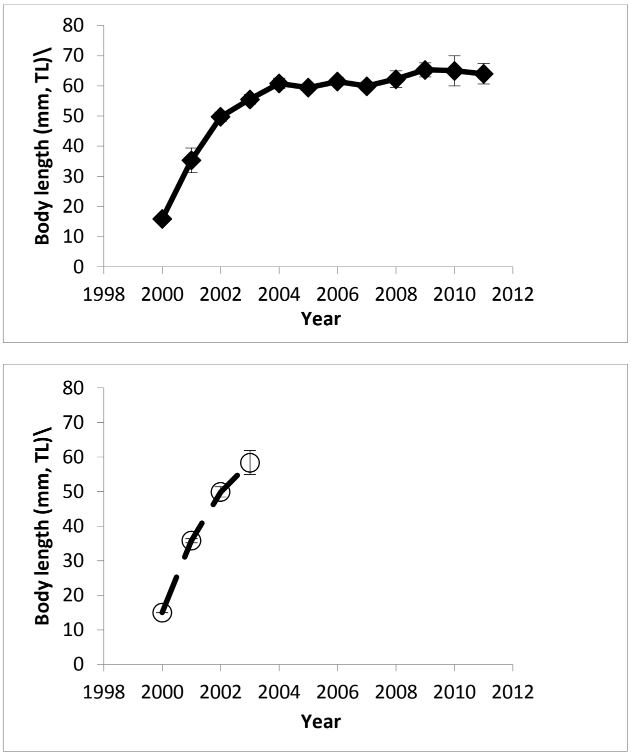

Body length (mm, TL)\
80
70
60
50
40
30
20
10
0
1998
2000
2002
2004
2006
2008
2010
2012
Year
Body length (mm, TL)\
80
70
60
50
40
30
20
10
0
1998
2000
2002
2004
2006
2008
2010
2012
Year

Figure 3a.

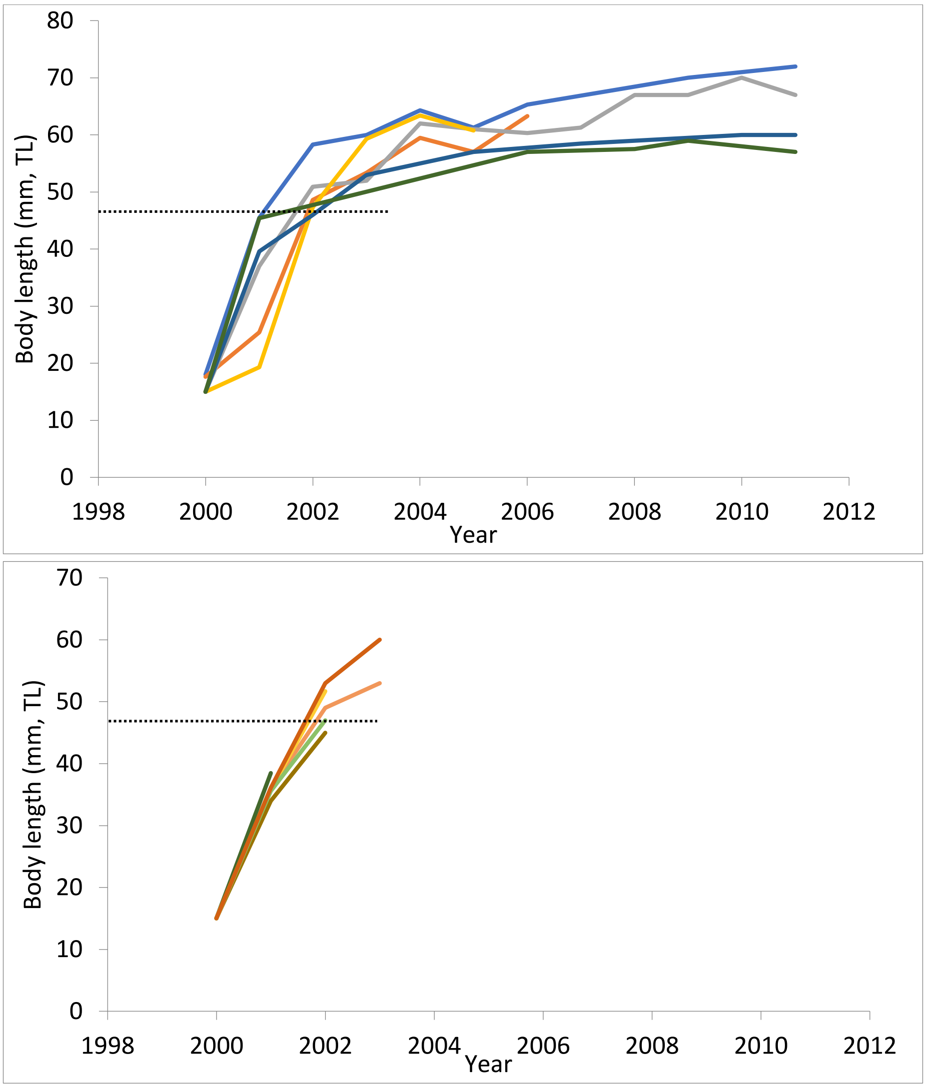

80
70
60
50
40
30
20
10
0
Body length (mm, TL)
1998
2000
2002
2004
2006
2008
2010
2012
Year
70
60
50
40
30
20
10
0
Body length (mm, TL)
1998
2000
2002
2004
2006
2008
2010
2012
Year

Figure 3b.

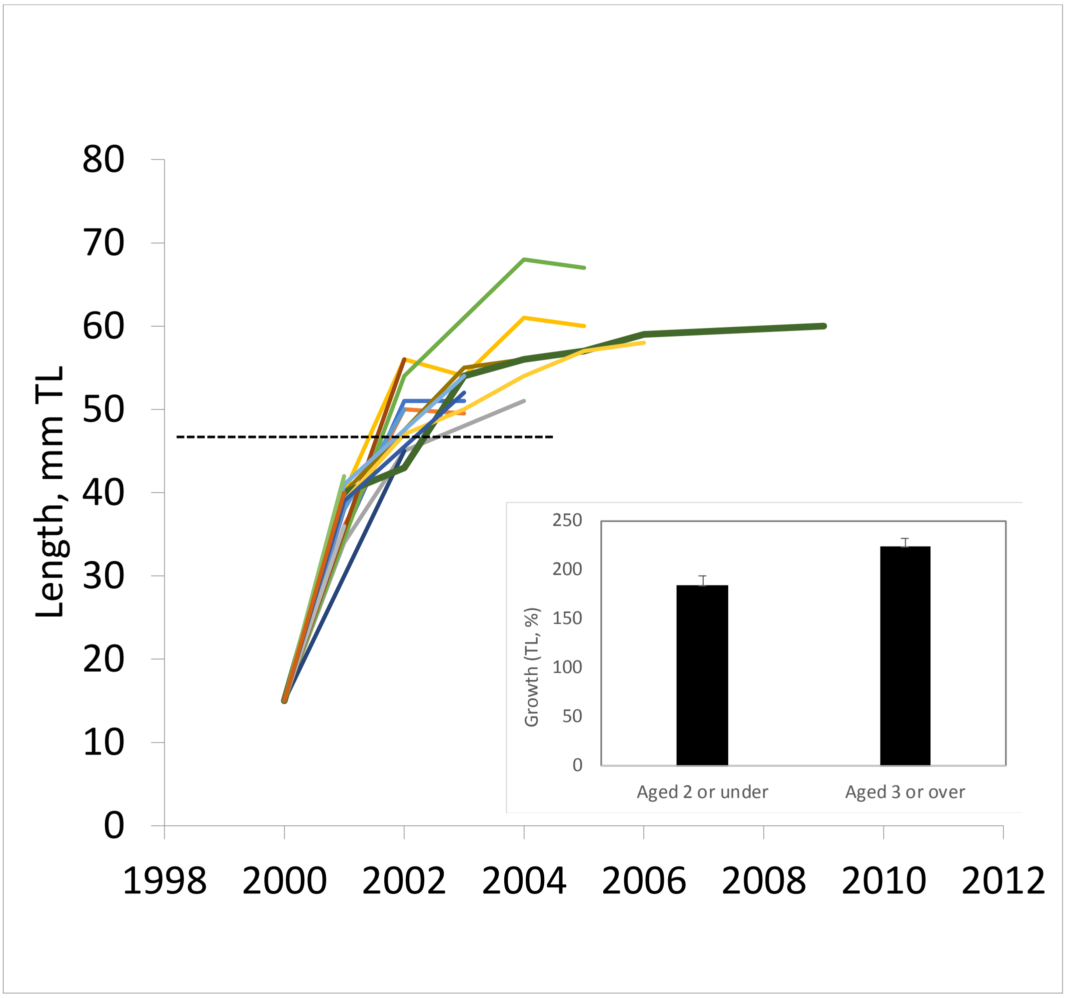

80
70
60
50
40
30
20
10
0
Length, mm TL
1998
2000
2002
2004
2006
2008
2010
2012
250
200
150
100
50
0
Growth (TL, %)
Aged 2 or under
Aged 3 or over

Figure 3c.

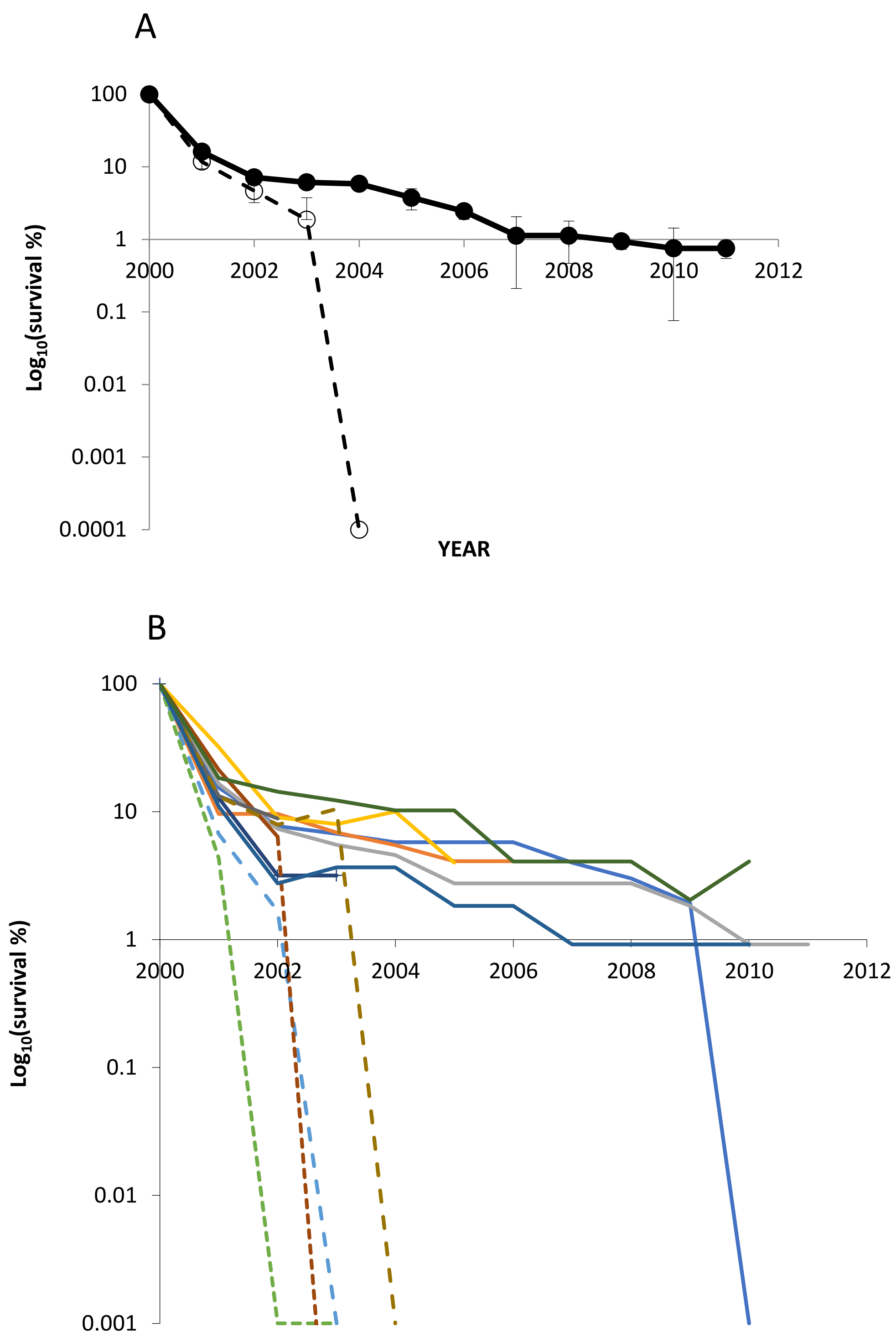

A
100
10
1
0.1
0.01
0.001
0.0001
2000
2002
2004
2006
2008
2010
2012
Log10(survival %)
YEAR
B
100
10
1
0.1
0.01
0.001
2000
2002
2004
2006
2008
2010
2012
Log10(survival %)

Figure 4

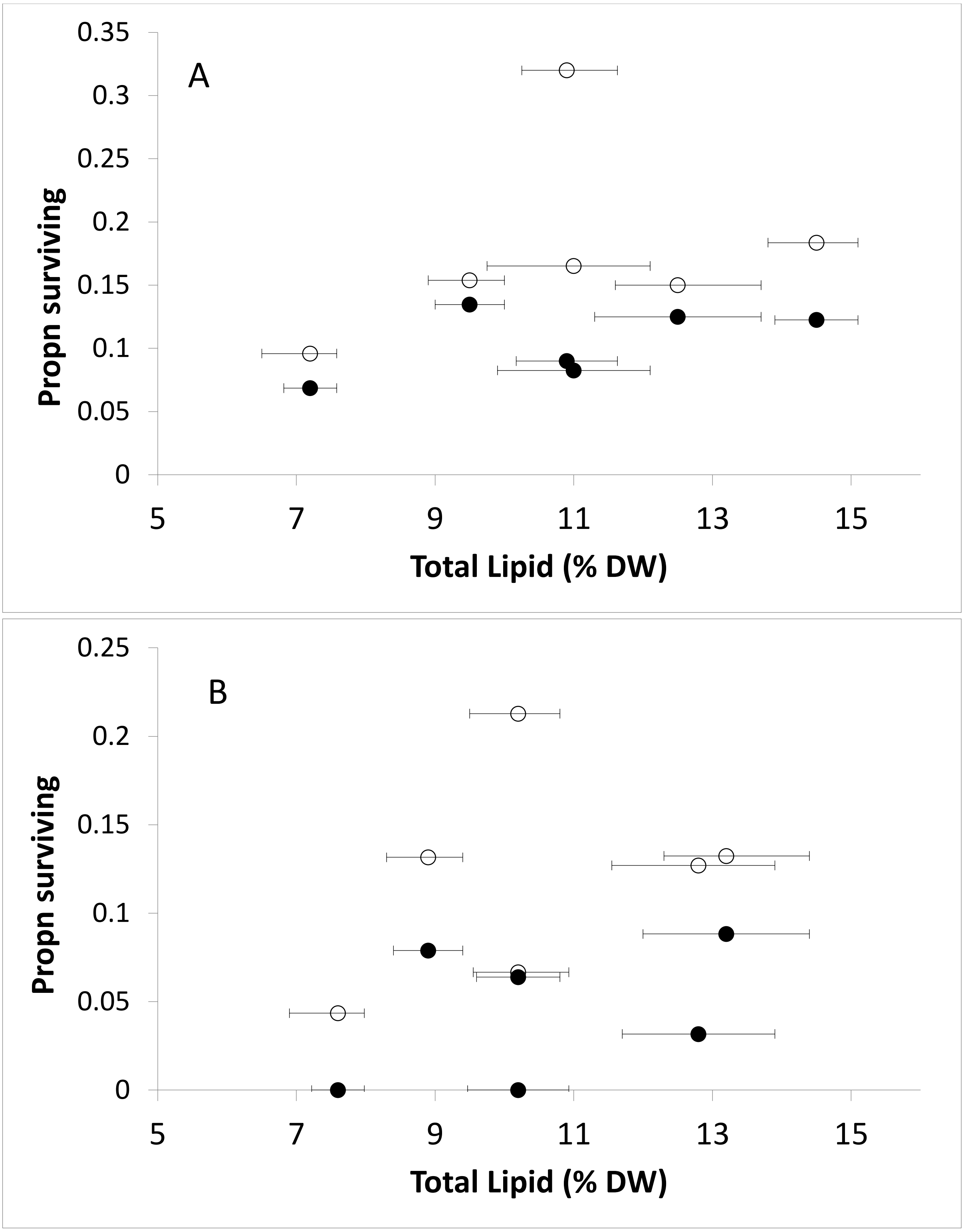
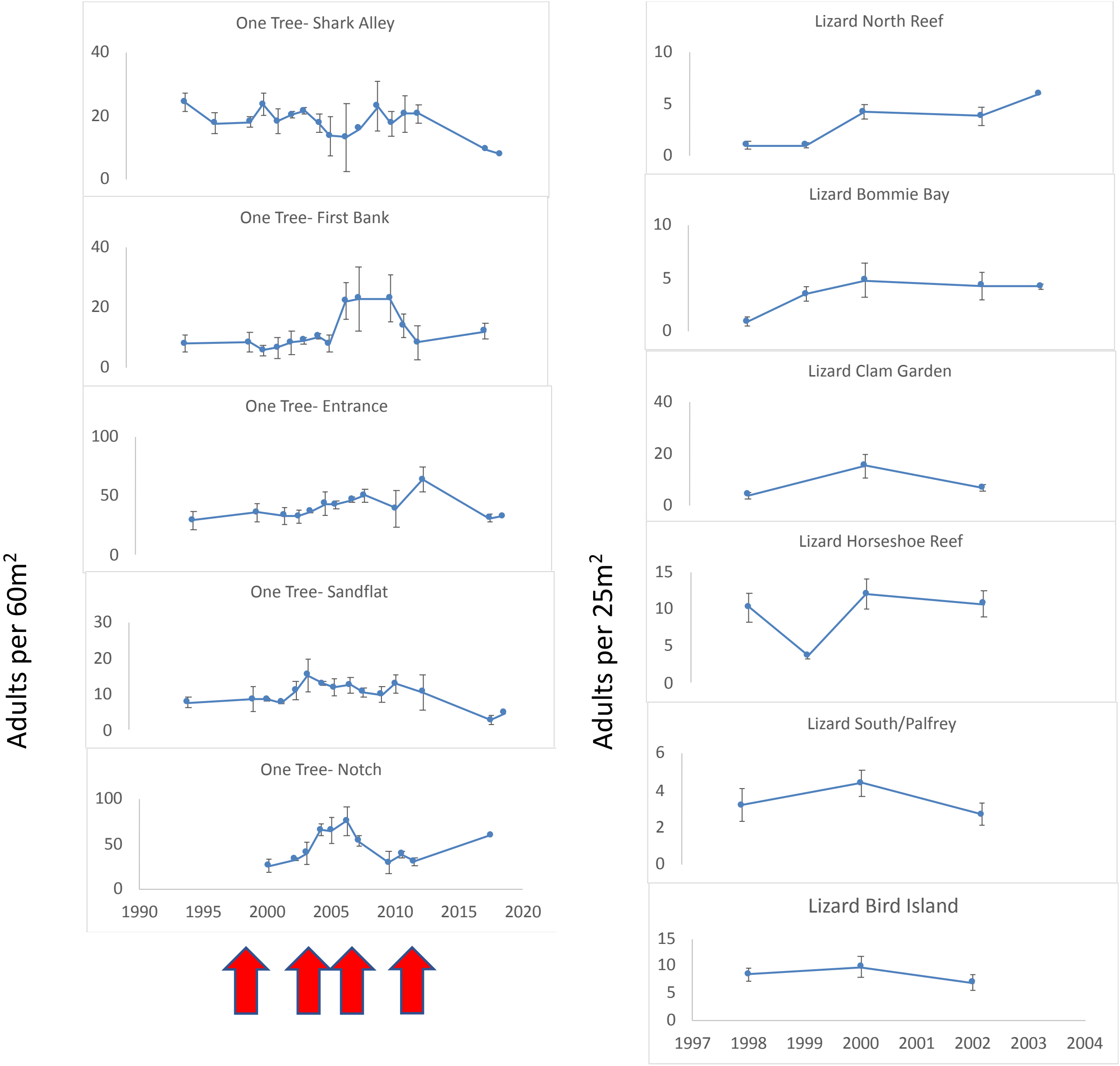

A
Propn surviving
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
5
7
9
11
13
15
Total Lipid (% DW)
B
Propn surviving
0.25
0.2
0.15
0.1
0.05
0
5
7
9
11
13
15
Total Lipid (% DW)

Figure 5

Figure 6


Adults per 60m^2
One Tree- Shark Alley
40
20
0
One Tree- First Bank
40
20
0
One Tree- Entrance
100
50
0
One Tree- Sandflat
30
20
10
0
One Tree- Notch
100
50
0
1990
1995
2000
2005
2010
2015
2020
Adults per 25m^2
Lizard North Reef
10
5
0
Lizard Bommie Bay
10
5
0
Lizard Clam Garden
40
20
0
Lizard Horseshoe Reef
15
10
5
0
Lizard South/Palfrey
6
4
2
0
Lizard Bird Island
15
10
5
0
1997
1998
1999
2000
2001
2002
2003
2004

Supplementary Material Figure 1

Supplementary Material Table 1

Running head: damselfish large-scale life-history variation

Long term demographics of a coral-reef fish: growth, survival and abundance at several spatial scales

David J. Booth[1] and Giglia A. Beretta[1]

[1] School of the Life Sciences, University of Technology Sydney, PO Box 123 Broadway NSW 2007 AUSTRALIA

David.Booth@uts.edu.au

Abstract. In marine organisms, pelagic larval dispersal often results in genetic panmixis among widely-separated populations, however local conditions may produce populations of marine organisms that differ in key life history traits. Here, we assess spatial differences in growth, body condition, survivorship and movement over a decade for lemon damselfish *Pomacentrus moluccensis*. Newly- recruited fish were tagged on the southern (One Tree Island, 23^0S), and northern Great Barrier Reef (Lizard Island, 15^0S), 1200km apart, and monitored for over a decade to provide direct data on growth and survivorship.

New recruit physiological condition (lipid content) had a weak positive influence on early survival, but not on long-term persistence or growth, and the larval supply signal was lost after 2 years, suggesting post-settlement processes were key in long-term population persistence. Fish exhibited extreme site fidelity, with older/larger fish moving most (all less than 7 metres). At Lizard Island, under 5% of individuals remained after 3 years, none after 4 years, while at One Tree Island 5% of individuals survived over 5 years, with 1% remaining after a decade, suggesting Lizard Island populations may require more frequent replenishment to persist. Among-site (within location) variation in mortality was high, and not related to density, suggesting local conditions such as wave exposure and predators were important. Surprisingly, mean growth at the two locations, which differ by around 2^{o}C on average in sea temperature, was practically identical, levelling off after 3 years, but with high variation among nearby sites within each location, which would affect size-based fecundity and time of first reproduction at these smaller spatial scales. Neither early post-settlement growth nor mortality were density-dependent, and early growth was not related to overall longevity.

These small reef fishes are highly sedentary and some demographic parameters, but not others, differ at a range of scales, with post-settlement populations likely driven largely by mortality patterns at the larger spatial scale. Latitudinal and smaller-spatial scale differences in performance (growth, survival) of this species, leading to offsets in expected time to maturity an fecundity, are contrasted by evidence of stability of adult populations over ~~2~~two decades~~5 years~~ at One Tree Island, which suggests that resilience to environmental change/climate change and other externalities differ considerably across this species' distribution.

Keywords: coral-reef fish, growth, latitudinal demography, physiological condition, *Pomacent~~tn~~rus moluccensis*, survival and longevity.

Introduction

Spatial and temporal variation in species' demography is of fundamental interest in population ecology, and bears on fitness (Galliard et al. 2000). However, few studies have reported key demographic traits (e.g., survival and growth) across the entire lifespan of fish living over a decade. One valuable approach is to conduct small-scale experimental manipulations of organisms *in situ* that definitively linking demography to mechanisms at specific ages over very short time intervals (e.g., Booth and Hixon 1999), but rarely can these be integrated across the whole lifespan. For marine fishes, these demographic variables can be expected to vary greatly as the fish move among habitats ontogenetically, and because habitat quality and risks differ spatially (Dahlgren and Eggleston 2000), ~~-~~but may even differ for fish growing in the same location. While larval supply through pelagic dispersal has been predicted as a key process regulating reef fish populations (e.g., Armsworth 2002), after fish settle onto reef habitat from offshore waters, post settlement processes can decouple links between larval dynamics and adult dynamics (Jones 1990; Hixon et al. 2012). Once settlement has established initial population densities at a site, spatial and temporal variation in persistence ~~are~~ is driven by key demographic parameters of growth and survival, and to varying extents, movement (e.g., Kritzer and Sale 2006).

Post-settlement, key demographic variables can vary considerably. Patterns of growth can indicate fecundity (fecundity is size-related in reef fishes: Duarte and Alcaraz 1989) and predation risk (Tupper and Boutilier 1997). They can also be scaled up when combined with survivorship to estimate biomass distribution of a species on a reef (important for trophic understanding and functional groups (e.g, Mora et al. 2011). However, causes for variation in spatial and temporal patterns of growth and survival are manifold. For reef fishes, a myriad of factors, such as food availability, predator densities, and ambient ~~temerpture~~temperature will determine survivorship (Tupper and Boutilier 1997, Taylor et al. (2019). Phenotypic traits can vary with latitude, with larger size and greater longevity characteristic of fish at higher latitudes (Munch and Salinas 2009). The physiological state of the settling larva has been shown to exert an ongoing influence on how it responds to predators and food, and consequently on post-settlement survival and growth. Physiological state, or condition, can critically affect a reef fish's chances of early survival ((Booth and Hixon 1999), (Hoey and McCormick 2004), (Booth and Beretta 2004), and this effect can vary across latitudes (e.g., Booth 2002). However, whether such early recruit condition effects persist across the entire life span is unclear. Taylor et al (2019) demonstrated that for a coral- reef surgeonfish (*Naso* sp.), both spatial and individual differences in demographics (growth, mortality, longevity) were attributable partly to sea temperature (SST), but there were also intrinsic diffs among individuals, with suggestions that these features of populations may facilitate ecological resilience.

Doherty and Fowler (1994a,b) examined spatial and temporal variation in survival and longevity of the lemon damselfish (*Pomacentrus moluccensis*) across reefs in the Capricorn-Bunker group in the southern Great Barrier Reef. Using a large one-off otolith collection across 7 reefs, they reconstructed the cohort strengths across a number of years and showed that a strong recruit year class was preserved in older age classes. They concluded that over 90% of the variation in year class strength over 9 years could be explained by supply of larvae at settlement. Recruits were censused as individuals that were present in April of the year in question, thus they were the products of larval supply (i.e., settlement) and unknown post-settlement processes (e.g., variable mortality) for several months. Settlement of this species is typically highest January-February each year, so fish used in the study may have experienced 2-4 months on the reef prior to censusing, including high variable and likely large post-settlement mortality. Therefore, the fate of the high proportion of individuals that did not survive the early months remained unrecorded and the role of early mortality may have been underestimated. Also, episodic otolith collections of older fish may not allow a comparison of success within a cohort and can be biased towards individuals that persist longer (Booth 2014).

The direct approach, that is following the fate of a cohort of individuals, is less prone to issues of unknown mortality, but is difficult because it requires sustained field sampling over the longevity of the species, and either tagging or an assumption that all fish in the original cohort are either available for counting or have died. Fish tagging is most effective if the tag itself does not interfere and can persist for years, and if the fish has high site fidelity. Here, we present data from a cohort of the lemon damselfish *Pomacentrus moluccensis*, individually tagged with Visual Implant Elastomer (VIE, Northwest Marine Technology Inc.) in 2000 and re-censused until all tagged fish had disappeared in 2011 at sites at both the southern and northern Great Barrier Reef. We asked

(1) How did cohort survivorship/longevity vary at smaller and larger spatial and temporal scales?
(2) How did growth vary at smaller and larger spatial and temporal scales? Is individual growth performance preserved across life history (e.g., are some fish consistently fast growers through life?)?
(3) How far did tagged fish move over the course of the study? and
(4) Did patterns of growth and survival over the entire lifespan relate to larval supply (physiological condition, density) or sea temperature?
(5) How do the above indicate resilience of this species across latitudes and time?

Methods

Sites

One Tree Island is located in the southern Great Barrier Reef (23 º 30' S, 152 º 06' E). Seven long-term monitoring sites inside and outside One Tree lagoon were used. Four sites were within First Lagoon, plus Notch (NW outer reef) and two sites in Third lagoon. At Lizard Island [location (14º 40' S, 145º 28' E)] 6 sites were surveyed across the main lagoon and northern coastline (Figure 1, Supp Table 1). Temperature loggers were deployed at most sites in both locations (HOBO Pendant Temperature loggers) from 2000, reading at one hr intervals)

Fish tagging and censuses

In early 2000, at each site, density of new settler, juvenile and adult lemon damselfish *Pomacentrus moluccensis* were determined within 6, 15m long transects. All new settlers were captured at each site, their positions noted along a permanent transect, and tagged with VIE (numbers tagged shown in Supplementary Table 1). Given these small fish may have been prone to tagging mortality if tagged multiple times (as needed for individual identification) each cohort was tagged with one tag only (one colour), such that fish within a cohort and location could not be distinguished initially. Change in density of these tagged settlers at each site was monitored weekly from January 2000-March 2000 and again in April at One Tree Island, and in November at Lizard Island. At that time, each remaining fish was provided with a further VIE coloured tag to assist in individual recognition, and its position along the transect (to the nearest 0.5m) recorded. Josephsen et al. (2008) demonstrated that fish retain VIE tags for at least 3 years in field conditions and we never noted tags missing from fish that had multiple tags (unpub. data), suggesting tag loss was rare. Subsequently, surveys were taken 1-2 times per year, mostly in summer months. For each survey, densities were again determined, and a thorough search to the reef base and crest~~-~~, within and adjacent to all transects was undertaken for tagged individuals. When found, behaviour and position on the transect of tagged fish were observed, to ensure fish were resident at that position and not transient, then fish were captured using clove oil and transferred underwater into Ziploc© bags. In bags, tags of fish were closely examined *in situ* and fish were measured (Total Length: TL in mm) then fish were carefully released. Note field length measurements were accurate to ± 1mm TL, unpublished data)

~~Condition determination~~Body condition

Groups of 10 new recruits were collected immediately adjacent to transects when each cohort of recruits was initially tagged at each sample site, und the assumption that their physiological condition was similar to nearby tagged recruits. These fish were frozen and transported to University of Technology, Sydney, where gravimetric total lipid analysis was undertaken. Total neutral storage lipids of sampled fish were measured by freeze-drying the sample and performing a methanol-chloroform extraction (Mann & Gallagher, 1985; Booth & Hixon, 1999) then expressing total lipids as a percentage of dry body mass. Total lipids was considered a useful index of overall physiological condition (McCormick and Molony 1994, Booth and Hixon 1999, Booth and Alquezar 2004, Booth and Beretta 2004)

Analyses

Movement (metres) for individuals was calculated as linear distance between position of original release and subsequent recapture, and compared among sizes by 1 Factor ANOVA (log transformed). Growth for each tagged individual was recorded for both One Tree and Lizard

Islands as change in length over years, and plotted as individual growth trajectory, but also by site. Growth differences between locations were tested using ANOVA to compare mean lengths after one year (i.e., comparing first year's growth). Survivorship was plotted as percentage of fish remaining at yearly intervals and was compared between locations (Log-Rank test of survival curves, IBM SPSS Version 25, 2017). Relationships between growth, survivorship, fish density and water temperature (temperature logger-derived average annual temperature) were explored via linear regression analyses (Supplementary data), focussing on growth and survival in the first year post settlement when most losses occur (e.g., Sale and Ferrell 1988). Sample sizes are shown in Supplementary Table 1.

Results

Movement

Extensive searches for tagged fish throughout the study sites (along entire transect and well above (reef crest) and below reef) reinforced that this species has strong site fidelity over decadal time scales. Fish less than 55m TL were rarely found more than one metre from their original tagging location. For larger fish, most were found within 1-2 metres of the original tagging location, but some individuals ventured further, with one 67mm TL fish found 7 metres away from the tagging point (ANOVA F= 40.35, P<.0001, Tukey's test Figure 2).~~,~~

Growth and maturity

Mean growth was similar for fish tagged at Lizard Island and at One Tree Island (Figure 3a) was not significantly different over the first year (ANOVA F=.01, p>.05) and over the first 4 years (ANOVA F=.03, p>.05). Overall, tagged recruits were approximately 15mm Total Length (14.7 mm ± 0.8 SE) and overall mean length after one year was 35mm TL. However, tagged fish growth among sites within locations differed considerably, particularly at One Tree Island (Figure 3b). Within a site, individuals differed in their growth trajectories, with no consistent individual differences in growth (Linear regression: growth in Year 1 vs Year 2 growth,~~:~~ R^2 = 0.096, p>.05; also see Figure 3c). No relationship was detected between annual water temperature, individual survivorship or local fish density (*P. moluccensis* only, since these fish live in social groups:~~.~~ Brunton and Boot 2003), and growth to Year 2 among sites (Figure S1 Linear regressions, p’s>.05).

Fecundity is size-related in *P. moluccensis* with maturity at around 48 mm TL at both Lizard Island and One Tree Island (Mapstone 1988; T. Brolund unpub. PhD thesis). Based on growth trajectories recorded in this study, fish would therefore be 1.5-2.5 years of age (depending on site) at maturity at One Tree Island, and 1.5 to 2 years at first maturity at Lizard Island (Fig. 3b).

Survivorship and body condition

There was a dramatic difference in survivorship between Lizard and One Tree Island (higher survival at One Tree: Log-Rank (Mantel-Cox) test, p<.0001): Early (first year) survival was low at both locations, from 9-30% at One Tree Island and from 3 to 13% a Lizard Island. No Lizard Island fish lived over 4 years, while at One Tree Island, some individuals survived up to 11 years old (under 1% of initial tags, or 5% of April survivors, Figures 4a,b). Survival was not density-dependent, with no relationship between recruit density within a transect and % surviving to the following April or over the following year (Fig S1, Linear Regression, $p>.05$). At One Tree Island, individual fish that lived over 3 years had higher early growth (Fig 3c inset) but the overall relationship between survival and growth was not significant (see ~~Supplmentary~~Supplementary Data Figure 1, Linear regressions all non-significant (p~~P~~’s>.05))). There was also no relationship between annual water temperature, individual growth or local fish density (*P. moluccensis* only, since these fish live in social groups), and survivorship to Year 2 among sites (Supp Figure 1, Linear regressions all non-significant (p~~P~~’s>.05~~).~~).

Condition of recruit cohorts was similar between Lizard Island and One Tree, but differed considerably among sites (One Tree: mean=10.9% lipid dw/dw, range 7.2-14.5; Lizard Island: 10.5, range 7.6-13.2, Figure 5). There was a weak but non-significant positive relationship between recruit body lipid and subsequent survival to Year 1 among sites at each location (r^2=0.11 for One Tree, for Lizard), and for Year 3 (One Tree r^2=0.16, Lizard : r^2=0.31, p’s >.05, Figure 5).

Population fluctuations

Adult densities across 22 year (One Tree Island) and 5 years (Lizard Island are plotted in Figure 6. One Tree Island sites differed in adult densities, but all showed a high degree of density stability over decades. At Lizard Island, the survey period was only 5 years, but most sites had consistent adult densities over that period.

Discussion

Intra-specific life-history trait variation among latitudes can indicate differences in population persistence, and be related to key environmental factors. Here, a long-term field tagging study has demonstrated that for a common coral-reef damselfish, growth and survivorship differed across a range of spatial scales, yet adult populations showed remarkable stability over decades.

Surprisingly, average growth at the northern GBR (Lizard) vs southern GBR (One Tree) locations, despite being separated by over 1000 km (8 degrees latitude) and with different annual water temperature regimes (over 2^0C), was almost identical. In contrast Taylor et al. (2019) found a threefold geographic variation of a coral-reef fish (*Naso* sp.) across 20 degrees of latitude north and south) in life span that was strongly linked to water temperature, but not to anthropogenic pressure or ocean productivity. Munch and Salinas (2009) noted that in general, relative to individuals from low latitudes, high-latitude individuals tend to have higher growth rates and attain larger body size, and made general prediction of a strong link between environmental temperature and longevity (e.g., warmer water temperatures at lower latitudes link to lower longevity for marine fishes). Rather it was smaller-scale differences in growth among sites within locations that were significant. For instance, mean body length of 10-year-old fish ranged from 57 mm TL to 70 mm TL across sites at One Tree Island. This represents a range of from 4.5 to 9.5 grams wet weight (unpub. data.). Given fecundity is related to body weight, especially in females (Mapstone 1988), fecundity among nearby sites may have varied by approximately 100% (Mapstone 1988~~,~~) and sites with slower-growing fish may have reproduction delayed by one year, given reproduction is seasonal. Faster growing, larger individuals appeared not to have strong survival advantages, but given earlier maturity, may have lifetime fecundity benefits.

Survival was significantly reduced at the northern vs southern Great Barrier Reef location (Lizard Island vs One Tree Island) which follows the intraspecific trend of lower longevity of fishes in more tropical locations (Munch and Salinas 2009; Taylor et al. 2019) related to sea temperature. Using large otolith collections, Beukers (1996) found maximum ages of *P. moluccensis* to be six years at Lizard Island, while Doherty and Fowler estimated maximum age at 14-16 years at One Tree Island, and one cohort had over 20% of fish over 10 years. In contrast, only 1% of tagged fish in our study persisted beyond 10 yeas at One Tree Island. This may be due to inter-cohort variability, with the percent of cohort over 11 years varying from 1 to 20% in their study) but was partly explained by initial ages of fish. Doherty and Fowler followed persistence of fish from April onwards, so considerable mortality may have already occurred since actual settlement (i.e., were possibly 4 months post-settlement). Mortality of new recruits from near settlement to April in our study varied from 30 to 80%. As with growth, survival was very variable among sites within locations, with early survival low at all sites (see Sale and Ferrell 1988). Some compensation in terms of replenishment may occur; for example, the site with the lowest survivorship also had the consistently highest settlement of larvae (unpub. data). Beukers and Jones (1998) demonstrated density-dependent mortality of new recruits of *Pomacentrus moluccensis* over 1 year at Lizard Island, Great Barrier Reef, which was directly correlated with the density of ~~piscivores~~piscivores, and inversely correlated with the percent cover of structurally complex corals, so these factors may have a role in survivorship differences seen in this study..

Formatted: Default Paragraph Font

Formatted: Default Paragraph Font

Fish were remarkably site-specific over decadal time scales, with fish remaining within metres of their settlement site for over a decade (c.f. Lewis 1997). In addition, this species also has strong homing ability (Booth 2016) so it exhibits extreme site philopatry. Jones et al. (1999) found some offshore larval philopatry in closely-related small benthic damselfishes at Lizard Island, which may preserve smaller-scale variation in new recruit condition documented here.

In reef fishes, demographic trade-offs between growth and survival have bene predicted, e.g., Taylor et al. (2019) demonstrated differences in individuals of the surgeonfish *Naso* sp. in life history trai~~n~~ts pertaining to growth and survival. Such variation in traits is also evident in coral reef fishes exposed to marked environmental variation across relatively small spatial scales (10 s of kilometres; e.g., Gust et al., 2002; Brandl, et al., 2018).

Physiological condition at settlement was not strongly related to long-term persistence. This contrasts with findings of Booth and Beretta (2004) who manipulated condition of very new *P. moluccensis* settlers had strong -short-term effects on survival, via enhanced predation. It appears that processes happening over years post-settlement are decoupling links between early condition and longer-term persistence. The “larval supply signal” (e.g., Jones 1990) in both fish abundance and condition appears weak, suggesting post-settlement processes are paramount (see also Jones 1986).

Field cohort tagging and censusing, as adopted here, allows an accurate understanding of individual fish growth, persistence and movement, but is field-intensive and only follows one or a few cohorts, while otolith hindcasting methods, in contrast, have the advantage of requiring comparatively little field time, and examining a range of age-cohorts simultaneously. Both methods have merit, in that a one-off otolith collection allows a snapshot of persistence of many age cohorts, while tagging allows tracking of detailed survival and growth patterns in individual cohorts (e.g., Meekan 1992, Elsdon et al. 2008; B~~b~~ooth 2014). The data presented here are from one of the longest tagging series for coral reef fishes worldwide. One issue with growth as estimated here is that longer-lived ~~fish~~ individuals will be increasingly dominating the population growth curve over time. If these individuals grow faster in general, they will bias later growth, however while Figure 3c suggests older fish had grown faster early in life, they had not grown faster overall (Supp. Figure 1).

Despite the documented demographic variation among sites, and disturbances such as global coral bleaching episodes (e.g., in 1998 and 2002), our long-term monitoring at One Tree Island indicates the densities of adult *P. moluccensis* were surprisingly stable over decades, and even Lizard island adult densities appeared generally stable over 5 years (Figure 6), This suggesting that the species shows resilient to change over decadal periods despite large recruitment variation (e,g. Booth et al. 2000) with its longevity contributing to strong "storage effects (*sensu* Warner and Chesson (1985).

Formatted: Font: Not Italic

Lifetime reproductive output is likely to be lower at Lizard Island overall compared to One Tree Island, given much shorter longevity there, but among sites within locations, onset of maturity would have varied by up to one year, likely considerably affecting lifetime fecundity and site-specific population demography and reproductive output at these small spatial scales (*sensu* Lee et al. 2011). In fact, at some sites around Lizard Island, size at mean longevity was below that required for maturity.

While local, regional and biogeographical persistence of populations of this species may be driven in part by variable larval supply (e.g., Doherty and Fowler 1994a), this study has indicated that high variability in post-settlement demography of this very common coral-reef fish, especially variable mortality, may be a key to persistence of local populations, and likely generate the development of significant variability among populations in overall biomass and productivity. Long-term adult abundances appear to be largely decupled from settlement processes, which can fluctuate by orders of magnitude (e.g. Booth et al. 2000), and growth independence from sea temperature may afford this species a degree of resilience from future environmental challenges.

Acknowledgements. We would like to acknowledge the staff at Lizard Island Research Station, and One Tree Island Research Station for their support, and Will Figueira, Marcus Gregson, Ralph Alquezar for field assistance. The study was one under Great Barrier Reef Marine Park Authority Permit G11/34452.1 and UTS Animal Care and Ethics 2008-016A.

Conflict of Interest: The corresponding author states that there is no conflict of interest.

References

Armsworth PR (2002) Recruitment Limitation, Population Regulation, and Larval Connectivity in Reef Fish Metapopulations. Ecology 83:1092-1104.

Beukers J (1996) The relative roles of recruitment and post-recruitment processes in the regulation of a coral reef damselfish population. PhD thesis. James Cook University, Australia, 128pp

Beukers J, Jones G (1998) Habitat complexity modifies the impact of piscivores on a coral reef fish population. Oecologia 11:, 50–59

Booth DJ, Beretta GA (2004) Influence of recruit condition on food competition and predation risk in a coral reef fish. Oecologia 140: 289-294

Booth DJ, Kingsford MJ, Doherty PJ, Beretta GA (2000) Recruitment of Damselfishes in One Tree Island Lagoon: Persistent Interannual Spatial Patterns. Marine Ecology Progress Series, 202: 219-230

Booth DJ (2002) Larval supply, condition and persistence of the coral reef fish, *Pomacentrus moluccensis* pp.463 – 468 In: Kasim Moosa, M.K., Soemodihardjo, S., Nontji, A., Soegiarto, A., Romimohtarto, Sukarno and Suharsono. (Editors) *Proceedings of the Ninth International Coral*

Reef Symposium, Bali, Indonesia, October 23-27 2000. Published by the Ministry of Environment, the Indonesian Institute of Sciences and the International Society for Reef Studies.

Booth DJ (2014) Do otolith increments allow correct inferences about age and growth of coral reef fishes? Coral Reefs. 33: 255–258

Booth DJ (2016) Ability to home in small site-attached coral reef fishes. Journal of Fish Biology, *89*(2), 1501-1506.

Booth D, Alquezar R (2002) Food supplementation increases larval growth, condition and survival of *Acanthochromis polyacanthus*. Journal of Fish Biology 60:1126–1133

Booth DJ, Hixon MA (1999) "Food ration and condition affect early survival of the coral reef damselfish, Stegastes partitus." Oecologia 121(3): 364-368

Brandl SJ, Goatley CHR, Bellwood DR, Tornabene L (2018) The hidden half: ecology and evolution of cryptobenthic fishes on coral reefs. Biol Reviews 93: 1846-1873

Brolund T (2008) , Growth patterns along environmental gradients of tropical pomacentrid fishes~~Spatial connectivity of Pacific insular species: Insights from modeling and tagging~~. Unpub. PhD thesis University of Technology, Sydney. 69pp

Formatted: Don't adjust space between Latin and Asian text, Don't adjust space between Asian text and numbers

Formatted: Font: 12 pt

Formatted: Font: English (United Kingdom)

Brunton, B. J., & Booth, D. J. (2003). Density- and size-dependent mortality of a settling coral-reef damselfish (*Pomacentrus moluccensis* Bleeker). Oecologia, *137*(3), 377-384

Dahlglen C, Eggleston DB (2000) Ecological processes underlying ontogenetic habitat shifts in a coral reef fish. Ecology 81:2227-2240

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

Doherty PJ, Fowler A (1994b) Demographic consequences of variable recruitment to coral reef fish populations: a congeneric comparison of two damselfishes. Bulletin of Marine Science 54: 297-313

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

Elsdon TS, Wells BK, Campana SE, Gillanders BM, Jones CM, Limburg KE, Secor DH, Thorrold SR, Walther BD (2008) Otolith chemistry to describe movements and life-history parameters of fishes – hypotheses, assumptions, limitations and inferences. Oceanography and Marine Biology Annual Review. 46:297-330

Gaillard J-M, Festa-Bianchet M, Yoccoz NG, Loison A, Toigo Annu C (2000) Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics 31:367–93

Gust N, Choat J, Ackerman J (2002) Demographic plasticity in tropical reef fishes. Marine Biology 140: 1039–1051

Hixon A., Anderson TW, Buch KL, Johnson DW, McLeod R, Stallings C (2012) Density dependence and population regulation in marine fish: a large-scale, long-term field manipulation. Ecological Monographs 82: 467–489

Hoey AS, McCormick MI (2004) Selective predation for low body condition at the larval-juvenile transition of a coral reef fish. Oecologia 139: 23-29

Jones P. (1986) Food availability affects growth in a coral-reef fish. Oecologia 70: 136-139

Jone GP (1990) The importance of recruitment to the dynamics of a coral reef fish population. Ecology 71:1691-1698

Jones GP, Milicich MJ, Emslie MJ, Lunow C (1999) Self-recruitment in a coral reef fish population. Nature 4902:802-804

Josephson DC, Robinson JM, Widell BC, Kraft, C.E. 2008. Long-term retention and visibility of Visible Implant Elastomer tags in brook Trout. North American Journal of Fisheries Management 28:1758–1761

Kritzer JP, Sale, PF (2006) The metapopulation ecology of coral reef fishes In: Sale JPKF, editor. Marine Metapopulations. Chapter 2. Burlington: Academic Press; pp. 31–67

Lee AM, Engen S, Sæther BE (2011) The influence of persistent individual differences and age at maturity on effective population size. Proceedings of Biological Science. 278:3303-12

Lewis AR (1997) Recruitment and post-recruit immigration affect the local population size of coral reef fishes Coral Reefs 16: 139-149

Mann R, Gallagher SM (1985) Physiological and biochemical energetics of larvae of *Teredo navalis* and *Bankia gouldi*. Journal of Experimental Marine Biology and Ecology 85: 211–228

Mapstone BD (1988) The determination of patterns in the abundance of *Pomacentrus moluccensis* Bleeker on the southern Great Barrier Reef. Unpublished PhD Thesis, University of Sydney, pp. 240

Meekan MG (1992) Limitations to the back-calculation of recruitment patterns from otoliths. Proceedings of the Seventh International Coral Reef Symposium, Guam, 1*:* 624-628

McCormlck M1, Molony BW (1995) Influence of water temperature during the larval stage, on size, age and body condition of a tropical reef fish at settlement Marine Ecology Progress Series 118:59-68

Mora C, Aburto-Oropeza O, Bocos A, Ayotte PM, Banks S, Bauman AG, .~~. .~~ Zapata FA, plus 55 authors (2011) Global human footprint on the linkage between biodiversity and ecosystem functioning in reef fishes. PLOS Biology, 9: e10006.

Munch SB, Salinas S (2009) Latitudinal variation in lifespan within species is explained by the metabolic theory of ecology. Proceedings of the National Academy of Sciences of the United States of America. 106:13860-4

Sale PF, Ferrell DJ (1988) Early survival of juvenile coral reef fishes. Coral Reefs. 7: 117-124

Taylor BM, Choat JH, DeMartini EE, et al. (2019) Demographic plasticity facilitates ecological and economic resilience in a commercially important reef fish. Journal of Animal Ecology 2019;88:1888–1900

Tupper M, Boutilier RG (1997) Effects of habitat on settlement, growth, predation risk and survival of a temperate reef fish. Marine Ecology Progress Series. 151:225-236

Formatted: Font color: Text 1

Warner RR, Chesson PL (1985) Coexistence mediated by recruitment fluctuations: a field guide to the storage effect. American Naturalist. 125:769-787

Figure Legends

Formatted: Left

Figure 1: Map of Queensland Australia indicating Great Barrier Reef and study locations. One Tree Island and Lizard Island maps showing sites (Coded as per Table S1)

Figure 2: Maximum distance from release location of tagged *Pomacentrus moluccensis* (metres, Mean ± SE) at One Tree Island 2000-2011. (ANOVA and Tukey's post-hoc tests on movement: 35mm=40mm=50mm=55mm<60mm=65mm)

Figure 3: Growth of tagged *Pomacentrus moluccensis* 2000-2011:

a. Growth of fish (mean TL ± SE) at One Tree Island (solid line, top panel) and Lizard Island (broken line, bottom panel, ~~)~~ SE's shown, n's see Table S1
b. Growth (mean ± SE) among sites: Upper panel: One Tree island Lower panel: Lizard Island sites. Horizontal dotted line indicates size at maturity. Colours used to help distinguish sites.
c. Individual growth histories of tagged fish at One Tree Island. Heavier line is longest lived fish. Horizontal dotted line indicates size at maturity. Colours used to help distinguish individual fish. INSET: mean Year One growth (%) of fish under and over 3 years longevity (t-test, $P<.05$).

Figure 4: Survivorship of tagged *Pomacentrus moluccensis* 2000-2011, for n's tagged see Table S1:

a: ($\log_{10}$) survival (Mean ± SE, n= 6 sites) of fish at One Tree Island (solid line) and Lizard Island (broken line)

b: ($\log_{10}$) survival: One Tree island individual sites (solid lines, n=6) vs. Lizard Island sites (broken lines, n=6). Colours used to help distinguish sites

Figure 5: Condition (% lipid, dw/dw, mean ± SE, n=10) of newly-recruited cohorts of *Pomacentrus moluccensis* vs survival at (a) One Tree island (closed circles: 3 years, open circles: 1 year n=10 fish each) vs (b) Lizard Island (closed circles: 3 years, open circles: 1 year n=10 fish each).

Figure 6: Adult densities of *Pomacentrus moluccensis*, means for each site over 22 years in One Tree Island (Mean + SE, n=6 transects, Red arrows indicate major coral bleaching years), and Lizard Island (Mean + SE, n=10 transects)

Supplementary Table and Figure

Table S1 Locations, sites, GPS fixes and sample sizes of tagged fish in this study

Figure S1:

A. Growth (% TL) vs survivorship (%) from tagging in year 200 to recapture in 2001, ie first year) for *P. moluccensis* at One Tree Island (n= 7 sites, blue symbols) and Lizard Island, n-= 6 sites, red symbols)

B. Growth (% TL in first year post tagging) vs Fish density (# per 15m of reef) for *P. moluccensis* at One Tree Island ((Mean # per 15m of reef , n= 7 sites, blue symbols) and Lizard Island, Mean # per 10m of reef, n-= 6 sites, red symbols)

C. Survival (% over first year) vs Fish density (# per 15m of reef) for *P. moluccensis* at One Tree Island (n= 7 sites, blue symbols) and Lizard Island, n-= 6 sites, red symbols)

D. Growth (% TL in first year post tagging) vs. Sea Temperature (annual average, ^{o}C) (logger data) for *P. moluccensis* at One Tree Island (n= 7 sites, blue symbols) and Lizard Island, n-= 6 sites, red symbols)

E. Survival (% over first year) vs Sea Temperature (annual average, ^{o}C) (logger data) for *P. moluccensis* at One Tree Island (n= 7 sites, blue symbols) and Lizard Island, n-= 6 sites, red symbols)