

Planktonic Larval Duration, age and growth of *Ostorhinchus doederleini* (Pisces: Apogonidae) on the southern Great Barrier Reef, Australia

M. J. Kingsford · M. D. Finn · M. D. O'Callaghan ·
J. Atema · G. Gerlach

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Abstract Cardinalfishes (Apogonidae) are abundant on corals reefs, but there are few data on demography to understand trophodynamics and population dynamics. *Ostorhinchus doederleini* is a small and abundant apogonid on the Great Barrier Reef (GBR) and throughout the western Pacific Ocean. We present key demographic parameters for the entire life history from the southern GBR. Daily deposition of increments in otoliths was validated. Fish had a Planktonic Larval Duration (PLD) of 16–26 days. PLD was established from fish collected immediately prior to settlement as no settlement mark was found. Fish grew at about 0.35 mm day^{-1} for the first 20 days after settlement. Fish reached a maximum standard length at about 200 days, and no fish lived longer than 368 days at four reefs separated by kilometers to tens of kilometers. There was no evidence for differences in size at age between sexes. Mortality was very high, and for fish greater than 60 days old, mortality rates ranged from 2.9 to $4.6 \% \text{ day}^{-1}$. Short lives and high mortality rates make

O. doederleini, and potentially other apogonids, vulnerable to recruitment failure. Here, we review data on the demographic characteristics of other reef fishes. Although some taxa live to over 50 years, the short lives of apogonids are most aligned with the Gobiidae and Blenniidae (i.e., typically <1.5 years). Descriptions of fish size, age, longevity, growth and mortality, from hatching to age maxima, are very rare for most taxa, even at the level of family.

Introduction

Nocturnal fishes are an important trophic group on both coral and temperate reefs (e.g., Marnane and Bellwood 2002; Annesse and Kingsford 2005). Fishes belonging to the Apogonidae, Holocentridae, Nemipteridae and Pempheridae are abundant on reefs, and species richness is high (Hobson and Chess 1978; Sale and Douglas 1984; Bellwood 1996; Greenfield 2003; Mabuchi et al. 2006; Thacker and Roje 2009; Gardiner and Jones 2010; Boaden and Kingsford 2012). These taxa feed at night on a range of invertebrates and fishes (Hiatt and Strasberg 1960; Marnane and Bellwood 2002; Annesse and Kingsford 2005; Barnett et al. 2006) and are the prey of many piscivorous taxa (e.g., Kingsford 1992).

Apogonids, and other nocturnal fishes, generally occupy caves and other habitats that provide shelter (e.g., coral Gardiner and Jones 2005) during the day and undergo feeding migrations at night. Movements range from spatial scales of meters to hundreds of meters. In general, these fishes feed in habitats that are different from those they occupy during the day (Gladfelter 1979; Marnane 2000; Annesse and Kingsford 2005; Boaden and Kingsford 2012). The trophic importance of these movements to reef ecosystems is potentially substantial in that their feeding

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Present Address:

M. J. Kingsford (✉) · M. D. Finn · M. D. O'Callaghan
School of Marine and Tropical Biology, ARC Centre
of Excellence for Coral Reef Studies, James Cook University,
Townsville, QLD 4811, Australia
e-mail: michael.kingsford@jcu.edu.au

J. Atema
Woods Hole Oceanographic Institution, Woods Hole, MA, USA

J. Atema
Boston University, Boston, MA, USA

G. Gerlach
Carl von Ossietzky University of Oldenburg, Carl von Ossietzky
Str. 9-11, 26111 Oldenburg, Germany

behavior and availability to predators are likely to be significant carbon pathways. Furthermore, feeding behavior often varies with size of fish. Many apogonids and other young nocturnal fishes (Annesse and Kingsford 2005) feed in different habitats than large juveniles and adults (Finn and Kingsford 1996).

Most apogonids have paternal mouth brooding and a larval phase (Brothers et al. 1983). An exception, the apogonid *Pterapogon kauderni* has paternal mouth brooding and direct development of juveniles with no larval phase (Vagelli and Volpedo 2004). Great attention has been given to filial cannibalism of eggs brooded in the buccal cavity of male *Ostorhinchus doederleini* (Okuda and Yanagisawa 1996) and other species (Okuda et al. 1997; 2003; Kume et al. 2000). Despite their novel reproductive biology, trophic importance and the recognition that there is high local population turnover (e.g., on patch reefs, Sale and Douglas 1984), there are few data on demography (but see Okuda et al. 1998). An exception is Longenecker and Langston (2006) who found that *Ostorhinchus rubrimacula* (Apogonidae) lived to a maximum of 274 days at a reef in Fiji. There are some estimates of Planktonic Larval Duration (PLD) for 14 species of apogonids in Japan (mean PLDs ranged from 14 to 31 days, Ishihara and Tachihara 2011), but the generality of these values is unknown.

A thorough understanding of population dynamics of any species requires information on growth and mortality at all stages of life history (Hilborn and Walters 1992). The potential for high volatility in population size would be greatest in species that have low age maxima as there would be little in the way of 'stored' year classes from seasons of high recruitment. Great variation in coral reef fish recruitment among seasons is common (Doherty and Williams 1988), but populations persist, often supported by a small number of large peaks in recruitment (Doherty and Fowler 1994; Kingsford 2009). Apogonids are abundant on tropical reefs, but predation on these fishes is known to be very high (e.g., Sale and Ferrell 1988). We have not found any other studies on the growth of apogonids prior to settlement, immediately after settlement and to their age maxima. We hypothesized that age maxima in *O. doederleini* would be low, and this would be consistent among reefs. If this were the case, it would greatly influence the outcomes of connectivity among reefs and the persistence of population genotypes. Recent evidence suggests that reef-based local populations of *O. doederleini* can be genetically distinct even when the reefs are only separated by kilometers to tens of kilometers. It has been proposed that despite the relatively poor swimming abilities of larval apogonids (Stobutzki and Bellwood 1997), they are capable of detecting olfactory cues from their natal reefs, and this combined with larval behavior facilitates reduced dispersal that can create genetically distinct populations (Gerlach et al.

2007), but a knowledge of fish demography is essential for a full understanding of connectivity.

The objective of the present study was to describe the growth and mortality of *O. doederleini* at four sites within the southern Great Barrier Reef. We examined otolith microstructures to (1) validate the aging technique and (2) determine the duration of the presettlement phase, i.e., Planktonic Larval Duration (PLD). We also describe (3) the early growth characteristics in presettlement and newly settled fish and (4) the potential differences in the growth rates and demographics of fish at multiple reefs. We also provide information on (5) mortality rates based upon length-at-age estimates of post-settlement fishes. Finally, we (6) review and compare the demographic characteristics of apogonids with other reef fishes.

Materials and methods

Study sites and fish sampling

Ostorhinchus doederleini were sampled at multiple sites on four reefs of the Capricorn–Bunker group, southern Great Barrier Reef: Heron Island, One Tree Island, Lamont and Fitzroy reefs (Fig. 1). Presettlement fish were only collected at One Tree Island. Channel nets were set to sample fish on the flood tides only at night in January 1994, February 1995 and February 2009 (Table 1). The net was square mouthed (0.75 × 0.75 m), and the mesh was 500 µm, organized as a box/pyramid with an efficiency of 1:12 (mouth area: open sifting surface; for full procedures, see Kingsford and Finn 1997). To preserve the calcium carbonate of otoliths, subsamples of collections from nets were preserved in ethanol. Samples were then rinsed in alcohol to reduce the seawater content; the final percentage of ethanol was 80 %. *O. doederleini* entering the lagoon to settle were easily identified by morphology and pigmentation (e.g., a black dot on the caudal peduncle).

Newly settled *O. doederleini* (10–18 mm SL) settle on sand and often away from continuous reef (Finn and Kingsford 1996). We constructed six peaked patch reefs on sand (diameter ~1.5 m by 0.5 m maximum height) 20–60 m from continuous reef. Patch reefs were monitored on a daily basis, and all newly settled fish were collected with fine-meshed hand nets, and a wide size range was preserved in 80 % ethanol for aging. Some fish that colonized patch reefs were larger than new settlers (18–27 mm SL), but were collected for a description of early post-settlement growth (Table 1).

Juvenile and adult *O. doederleini* were collected at four reefs during January and February of 2009 and 2010 and two large individuals in 2013 (Table 1). At each reef, we sampled at multiple sites separated by hundreds of meters

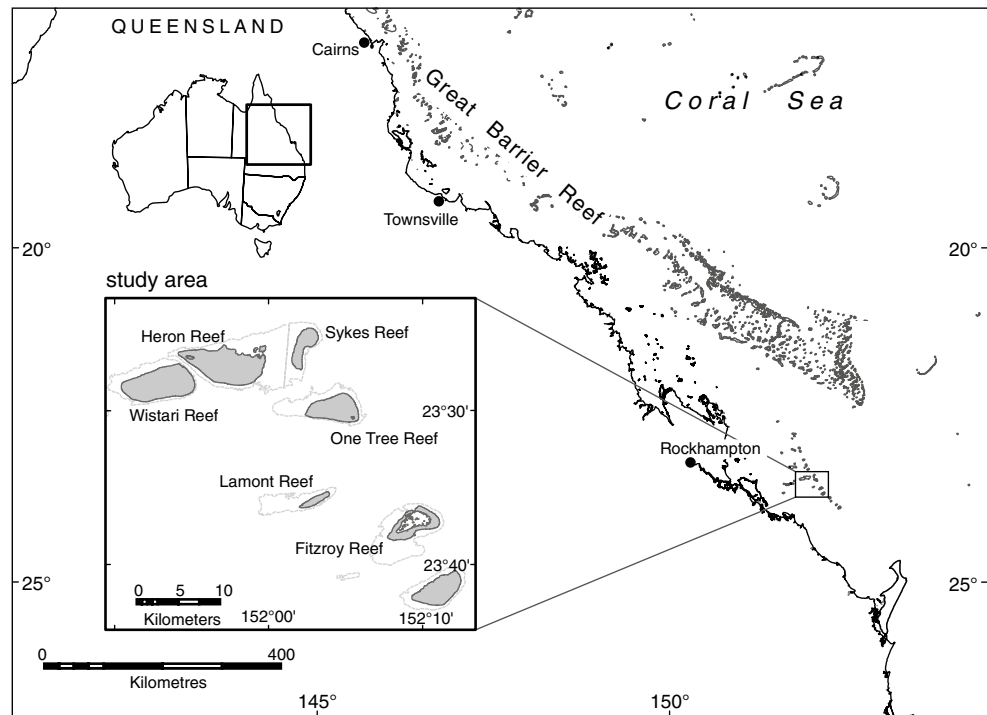


Fig. 1 Map showing the location of the four reefs in the Capricorn–Bunker group, southern Great Barrier Reef, Australia, where *O. doederleini* was collected

Table 1 Collection details for *O. doederleini* specimens, 1994–2013

Dates sampled	Methods used	Reefs	Life stage
January 1994	Channel nets; patch reefs	OTI	Presettlement and early post-settlement
February 1995	Channel nets; patch reefs	OTI	Presettlement and early post-settlement
February 2009	Channel nets, hand nets; clove oil	OTI, H, F, L	Juveniles and adults
January–February 2010	Hand nets; clove oil	OTI, H, F, L	Juveniles and adults
October 2010	Hand nets; clove oil	OTI	Juveniles and adults
January 2013	Hand nets; clove oil	L	Adults

OTI One Tree Island, H Heron reef, F Fitzroy reef, L Lamont reef

to tens of kilometers to obtain a representative sample, and fish were pooled for analyses. Juveniles and adults were collected from caves or branching coral (especially *Porites cylindrica* and branching *Acropora* spp.) and preserved in 80 % ethanol. A wide size range of fish was collected using a mix of 5:1 ethanol: clove oil. At Heron Island and Lamont reef, we sampled all fish from some large patch reefs, and this allowed us to estimate mortality rates (see below). Great care was taken to obtain all size classes of fish, especially large individuals that can be missed because they are the most secretive in the backs of caves. Because *O. doederleini* were potentially short lived (e.g., Longenecker and Langston 2006), we also sampled fish in October 2010 in case the time of sampling altered our estimates of age maxima; these samples did not allow estimates of mortality

as only large fish were selected. All fish collected in October 2010 were sexed macroscopically (i.e., the presence of oocytes in females or fine-grain spermatogenic tissue in males) to determine size and age versus sex relationships.

Otolith preparation

Increments in otoliths were used to obtain estimates of the age and growth of *O. doederleini*. All fish were weighed (± 0.01 g) and then measured [standard length (SL) ± 1 mm]. Sagittal otolith pairs were dissected, rinsed in water and dried overnight. One otolith from each pair was randomly selected, embedded to the edge of a glass microscope slide using Crystal Bond thermoplastic glue. The sulcal groove of the otolith was orientated

perpendicular to the surface of the slide and the outer edge of the primordium was flush with the inside edge of the slide. Slides were then held vertically and ground to the transverse mid-plane using a Gemmasta GF4 Faceting Machine with a 3,000 μm diamond encrusted steel disk. The glue was then reheated and otoliths were remounted with the newly ground surface placed face down in the center of the glass slide. Otoliths were ground until a thin section (20 μm thick) was obtained, which included the primordium.

Analysis of growth increments

The opaque zones visible in the internal structure of the otolith were counted along a radius from the primordium to the outer edge of the otolith from an image taken with a compound microscope (Leica DMLB using a Leica DC300 digital camera); a white incident light source was used. Alternating translucent and opaque increments were interpreted as daily rings; no annuli were observed, even in the largest fish. The counting of increments began from the first clear increment closest to the primordium. Sections were coded and examined in random order, and the opaque increments counted on two occasions by the same observer separated by at least 7 days. Counts of daily rings were compared between these two occasions in order to assess the confidence that could be placed in the interpretation of otolith structure. If increment counts differed by more than 10 % between counting occasions, then the otoliths were re-examined. If, following a third reading, agreement between the third and one of the two other counts was not reached (only closely matching counts were used in the analyses), then the otolith was not included in the analysis. To calculate the age, an average of the two closest age estimates was used. Rejection rate over the entire sample was 2.8 %, leaving a total sample of $n = 581$ for aging.

Validation of aging technique

To determine the periodicity of increment deposition in *O. doederleini* otoliths, a validation experiment (using tetracycline) was completed at One Tree Island Research Station in January 1994. Fish were treated with tetracycline, which is transported to the endolymph of the inner ear via the blood and deposited in the otoliths and other bony tissues as a mark (Odense and Logan 1974). The tetracycline mark can be viewed as a fluorescent line under ultraviolet light. The otoliths of 20 untreated fish were examined for autofluorescence.

Newly settled and other juvenile *O. doederleini* between 16.2 and 32.0 mm SL were collected from isolated patch reefs. Fish were collected with a small hand net and transferred to buckets filled with seawater for transport back to

the laboratory. They were immersed in tetracycline-treated seawater (0.25 g L^{-1}) for 18 h in the laboratory in order to mark their otoliths (higher concentrations killed small fish). Fish were transferred to 25 L buckets with one mm mesh windows in the lagoon after removal from the tetracycline solution. Treated fish, therefore, were exposed to the natural cycle of day and night and to normal levels of salinity and water temperature. Fish were fed on wild zooplankton and *Artemia nauplii* that were reared in the laboratory. Fish of a range of sizes were euthanized after five, 10 and 15 days; fish were then preserved in 98 % ethanol. Sagittal otoliths were removed, processed and viewed under transmitted and fluorescent light using a compound microscope. Under fluorescent light, an ocular marker was aligned with the fluorescent band if present. The otolith was then viewed under natural light and increments counted between the ocular marker and the otolith margin. Processed otoliths from a similar size range of untreated *O. doederleini* were also examined for the presence of autofluorescence. All otoliths were examined without knowledge of size or treatment.

Spacing of otolith increments

Most reef fish have a mark in otoliths that correspond with the time of settlement (Brothers et al. 1983). Settlement marks are an abrupt change in increment spacing, usually from wide to narrow (Victor 1986; Kingsford et al. 2011). Our initial observation of otoliths in recently settled fish failed to detect a settlement mark. We tested this more critically by measuring the spacing of increments in eight randomly selected juvenile *O. doederleini* to determine how the increment pattern changed with distance from the primordium. Transverse sections of the sagittal otolith were prepared. In the first group of fish increment, widths were measured from the primordium to the otolith margin ($n = 4$ fish), and in the second group of fish, widths were measured from the sulcal groove along the longest axis of the otolith to the ventral edge ($n = 4$ fish). Increment widths were measured using a calibrated video-analysis system (Leica IM50) linked to a compound microscope (Leica DMLB).

Age and growth

Growth was described using the von Bertalanffy growth function (VBGF), that provided the best fit to size-at-age data when compared with the estimates of the Schnute growth function (Schnute 1981). The von Bertalanffy expression for length at age t (L_t), as a function of time, was calculated using Eq. (1):

$$L_t = L_\infty[1 - e^{-K(t-t_0)}], \quad (1)$$

where L_t = length at age t (days), L_∞ = the mean asymptotic standard length, K = the rate at which the growth curve approaches L_∞ , and t_0 = the age at which the fish have a theoretical length of zero. The growth function was run by solver (Microsoft Excel) that minimizes the sum of squares by changing L_∞ , K and t_0 . Some of our demographic comparisons use 'Age max' = maximum age of an individual within a sample; and adapted from the convention of Choat and Robertson (2002), where maximum 5 % refers to the average age of fish from the 95th to 100th percentile and, maximum 10 % the average age from the 90th to the 100th percentile of the sample.

Mortality

The instantaneous rate of mortality (Z) was calculated using log-linear regression analyses of age-frequency data sets for *O. doederleini* populations from two reefs where all fish from new recruits to large adults were collected. This method assumes that recruitment is consistent over time at each reef (Haddon 2001). Year classes to the left of the age-frequency mode were excluded from the analysis because our sampling technique was biased against small fish. Mortality was only estimated where fish (over 45 mm SL) were collected representatively (i.e., Heron Island and Lamont reef). The slope of the regression line for each reef provided an estimate of

daily instantaneous mortality (Z), Eq. (2), when expressed as a percentage = loss of individuals per day:

$$Z = F + M, \quad (2)$$

where F is the fishing mortality and M is the natural mortality (Gust et al. 2002). Since there is not a fishery for *O. doederleini* on the GBR, F equals zero, and therefore, Z estimates natural mortality only. Daily survival rate estimates (S) were then calculated (i.e., percentage surviving per day, Ricker 1975) according to Eq. (3):

$$S = e^{-Z} \quad (3)$$

Data from each site were pooled for each reef. Similarities in mortality rates among replicate reefs allowed comparisons of mortality between reefs.

Results

Validation of aging

The otoliths of most *O. doederleini* (75 %) immersed in tetracycline showed a bright fluorescent band close to the otolith edge (Fig. 2b). Twenty untreated *O. doederleini* otoliths were checked for autofluorescence and showed no fluorescent band ($n = 20$). There was close agreement

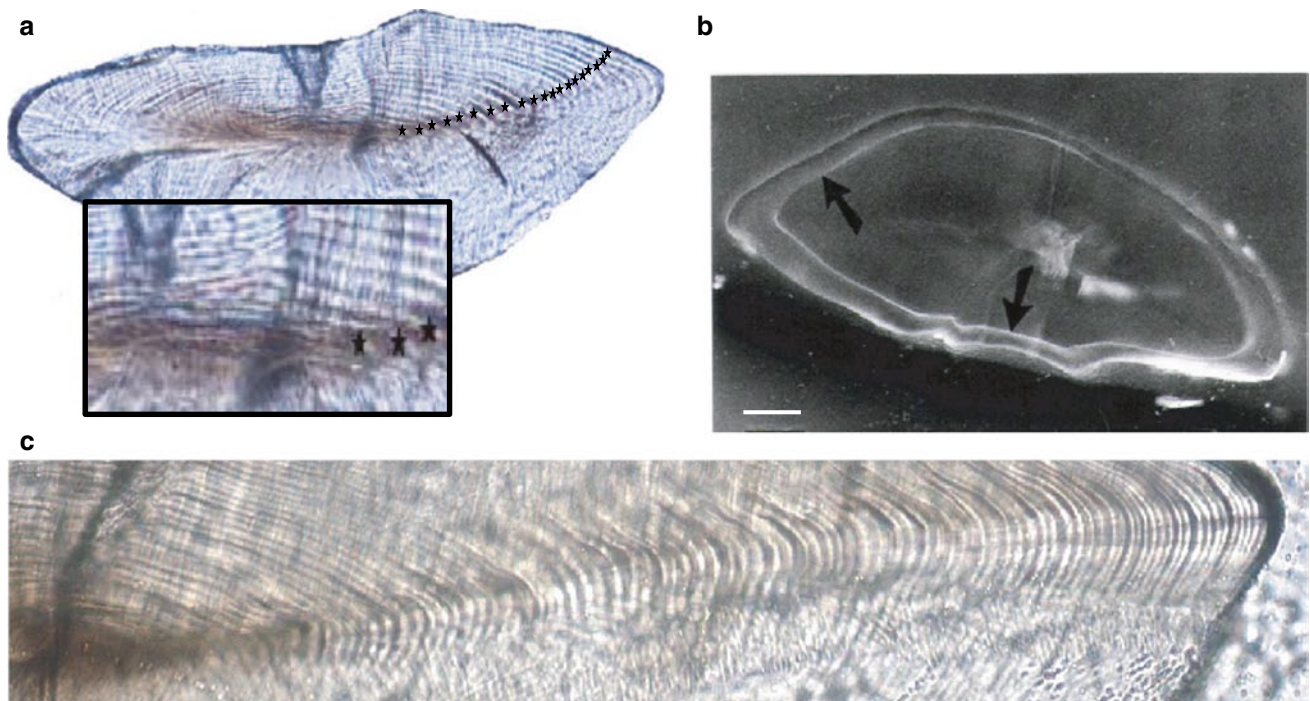


Fig. 2 **a** Sagittal otolith section of a 21-day-old *O. doederleini*. Width of otolith section is 1,500 µm. Initial measurement made at first visible increment (insert showing enlargement of 300 µm long); **b** Otolith of a fish euthanized 10 days after immersion in tetracy-

cline viewed under UV light, scale bar = 100 µm; **c** A section of an 90-day-old fish (from OTI; 34 mm SL) showing track used for aging, which extended from the primordium to the outer edge of the otolith along the longest axis (section is 2,100 µm long)

Table 2 Results of validation marking experiments for *O. doederleini*

No. of days	<i>n</i>	SL range (mm)	Mean of counts (SE)
5	42	17.0–25.2	4.95 (0.07)
10	16	17.4–34.0	10.06 (0.11)
15	11	16.2–25.0	14.82 (0.23)

No. of days = number of days since fish were immersed in tetracycline

Table 3 Age (days) and size (mm; SL) of presettlement and recently settled *O. doederleini* in two recruitment seasons

	1994	1995	<i>n</i>
Presettlement fish			
SL	10.7 (7.5–13.0) 4	10.6 (9.0–13.8) 30	34
Age	18 (15.7–19.7) 4	19.7 (16.0–26.0) 30	34
Recently settled fish			
SL	14.1 (9.8–18.0) 299	11.23 (8.6–18.0) 378	677
Age	28.2 (17.0–41.5) 113	22.5 (16.0–40.0) 119	232

Data shown are the mean (range) and total *n* is given by row. For recently settled fish, *n* varied for size and age, and more fish were collected for measurements of size and were not preserved in ethanol (Kingsford and Finn 1997)

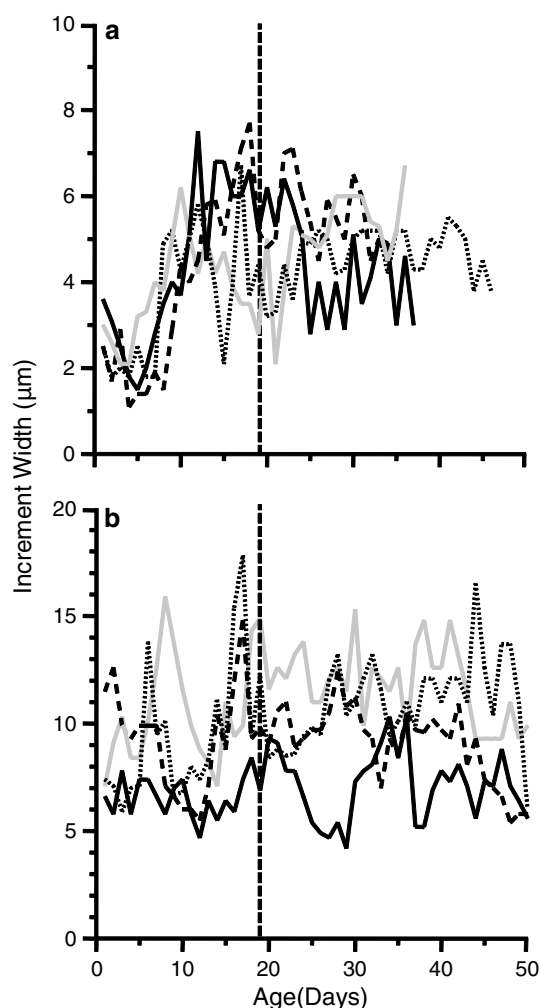


Fig. 3 Otolith increment widths plotted as a function of increment number for a subset of four post-settlement *O. doederleini*, **a** 1994 and 1995; **b** 2010 from One Tree Island, Great Barrier Reef, Australia. The dotted vertical line indicates the mean number of increments deposited by presettlement apogonids caught just prior to settlement measured from the primordium to the sulcal groove; from the primordium to the ventral edge of the otolith. Initial measurement made at first visible increment

between the number of increments laid down from the time of immersion in tetracycline and known number of days since treatment; this was true for fish sampled at 5, 10 and 15 days (Table 2).

Settlement marks were not found in settled *O. doederleini* regardless of the orientation of counts with respect to the otolith primordium (Fig. 3a, c). There were no rapid changes in increment width that could be attributed to settlement. The approximate age at settlement could be estimated from the average age that potential settlers entered the lagoon to settle (Fig. 4; Table 3). Although increment width varied across the otolith, they did not relate to settlement. Increments close to the primordium ranged from 2 to 4 μm in width and at approximately the 5–8 day mark increments rapidly became wider (5–7 μm); Fig. 3a. The rapid increase in increment widths at the 5–8 day mark was not related to settlement as the mean number of increments in *O. doederleini* caught just prior to the settlement was 19.5 (SE = 0.38, *n* = 34; Table 3). Similar patterns were found in separate profiles, but increments were generally wider (5–18 μm) across the 2010 profile (Fig. 3b).

Age and size of presettlement and recently settled *O. doederleini*

The age of presettlement *O. doederleini* caught in the channel nets ranged from 15.7 to 26.0 days (mean = 19.9; *n* = 34) and SL ranged from 7.5 to 13.8 mm (mean 10.7; *n* = 34); Table 3. The age of recently settled *O. doederleini* collected from experimental patch reefs ranged from 16 to 42 days (mean = 25.0; *n* = 232) and SL ranged from 8.6 to 18.0 mm (mean 12.7; *n* = 677); Table 3.

There was great overlap in the age and size of presettlement fish entering the lagoon and that of recently settled fish. Youngest fish on patch reefs were 16–17 days old and were as small as 8.6 mm SL. Older and larger fish were found on patch reefs, but many of them would have been associated with the reef for days as some recently settled fish move between patch reefs (Finn and Kingsford 1996). There was a strong linear relationship between age and standard length in presettlement fish over the first 20 days and recently settled fish, and growth was rapid at about 0.26 mm per day (Fig. 4).

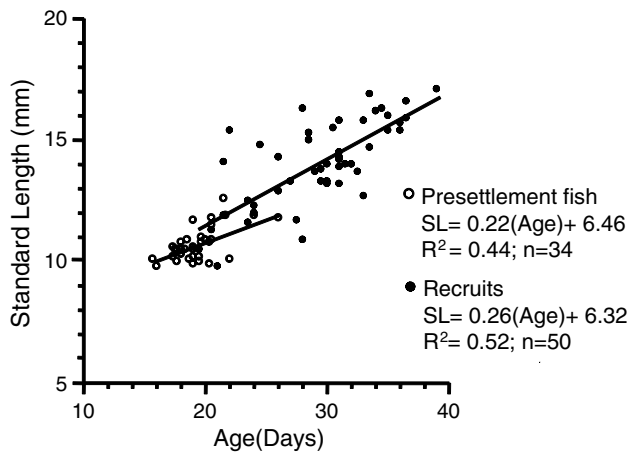


Fig. 4 Relationship between standard length and age (days) of pre-settlement versus newly settled recruits *O. doederleini* in 1994 and 1995 together with fitted regression lines and summary statistics

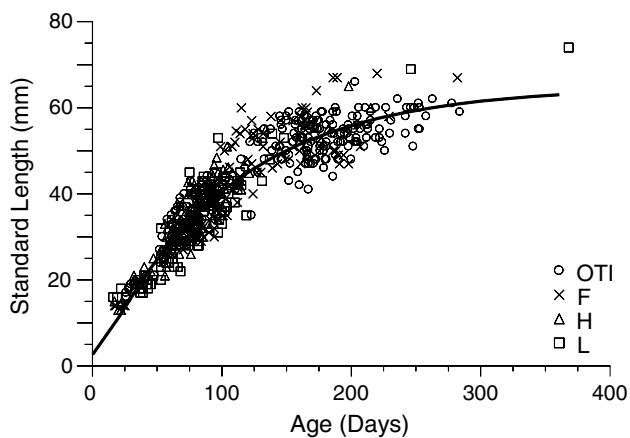


Fig. 5 von Bertalanffy growth curves for *O. doederleini* for the four reefs in the Capricorn–Bunker group, Great Barrier Reef, Australia

Variation in growth and sizes among reefs

The maximum age of *O. doederleini* among all reefs was 368 days, and at most reefs, few fish were older than 200 days (Fig. 5; Table 4). Time of sampling did not affect

estimates of age maxima. The oldest fish caught in January to February at One Tree Island was 284 days and 59 mm long (SL), while in October, it was 263 days and 62 mm long (SL). When the average age of the top 5 and 10 % of fish was considered at each reef, fish were 150 to 250 days old (Table 4). All von Bertalanffy relationships were well anchored with small fish around 15–20 mm SL. Best estimates of asymptotic length were obtained from One Tree Island, where fish grew little in length from 150 to 200 days old. Although there were no significant differences in the size of fish among reefs in the age range of 90–110 days (ANOVA, $F_{(3,60)} = 0.568$, $P = 0.63$), the maximum size of fish did vary. By reef, the average size for the top 5 % of fish and the maximum SL was (average, maximum): One Tree Island (61.0, 66 mm), Heron (57.0, 65 mm), Lamont (62.6, 74 mm) and Fitzroy (65.5, 68 mm). The largest fish caught at Heron Island, One Tree Island and Fitzroy reef were 65–70 mm SL (= ~80–85 total length). The two largest and oldest fish ever collected (days/SL, mm: 246/69, 368/74) were from Lamont reef, January 2013. The mean and range of lengths (SL) and ages differed little between males and females (Table 5).

Mortality

Instantaneous mortality rates calculated from catch-curves indicated that mortality rates were high for Lamont and Fitzroy reefs (2.9–4.6 % day⁻¹, Fig. 6). Further, mortality rates were highest at Lamont where large fish were rare. Survival (S) rates ranged from 0.971 to 0.955 day⁻¹.

Discussion

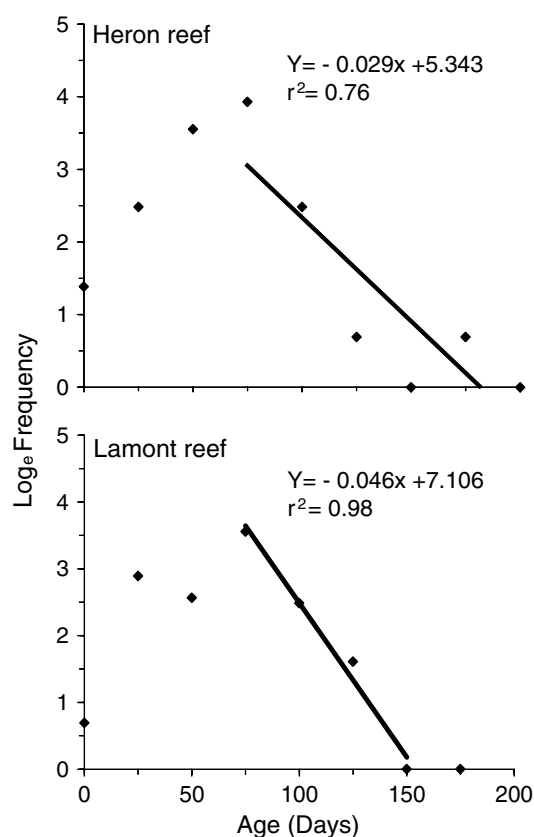
Ostorhinchus doederleini had a short PLD and once they settled, grew fast and died young. High mortality rates within days of settlement are common for reef fishes (Sale and Ferrell 1988) and low age maxima have been found in other apogonids (Longenecker and Langston 2006). Our study has demonstrated that *O. doederleini* has a high mortality (2.9–4.6 % day⁻¹) and a low age maxima. Ages of 1 year or less clearly put these tropical apogonids

Table 4 von Bertalanffy growth parameters for four reefs and estimates of age maxima for individual fish from samples at each location and average age of the oldest 5 and 10 % of fish (i.e., maximum%)

Reef	n	L_{∞}	K	r^2	Age maxima	Max. 5 % (n) SE	Max. 10 % (n) SE
Heron	122	76.24	0.008	0.86	215	173 (6) 13	144 (12) 11
One Tree Island	257	60.76	0.012	0.88	284	255 (13) 4	240 (26) 4
Lamont	91	83.84	0.006	0.82	368	213 (5) 6	176 (9) 27
Fitzroy	123	70.48	0.009	0.77	282	224 (6) 12	207 (12) 8
All reefs	593	65.04	0.010	0.89	368	249 (30) 5	226 (59) 4

Table 5 Size, age and sex differences for *Ostorhinus doederleini* collected at One Tree Island, October 2010

	Female	Male
<i>n</i>	55	70
Mean (SL)	53.27 mm	52.09 mm
SE	0.535	0.596
Min. (SL)	43 mm	41 mm
Max. (SL)	60 mm	66 mm
Mean (age)	191 days	190 days
Min. (age)	139 days	132 days
Max (age)	258 days	263 days

**Fig. 6** Age-based 'catch-curves' that provide estimates of mortality for *O. doederleini* for Heron and Lamont reefs in the Capricorn-Bunker group, Great Barrier Reef, Australia; each data point indicates Log_e frequency of each age class

at the lower end of the longevity spectrum for tropical fishes along with the Gobiidae and Blenniidae (Table 6). Although some taxa such as gobies may live for less than a year and have high mortality rates (e.g., *Eviota silligata* has an age maxima of 59 days, mortality rate 7.8 % day⁻¹; Depczynski and Bellwood 2005), species from families of common reef fishes such as the Pomacentridae (e.g., Doherty and Fowler 1994; Kingsford and Hughes 2005),

Labridae (Choat et al. 2006), Scaridae (Choat et al. 1996; Gust et al. 2002), Serranidae, Lutjanidae (Kingsford 2009) and Acanthuridae (Choat and Axe 1996) live for years and sometimes decades (Munday and Jones 1998; Fowler 2009) Table 6. Fishes with the lowest age maxima were generally small and represented three different trophic groups: nocturnal planktivores, micro/meso-carnivores and herbivores/detrital feeders. Although short-lived reef fish appear to be small, not all small fish are short lived (e.g., *Pomacentrus mollucensis* maximum SL 90 mm (TL) and age maxima 18 years; Doherty and Fowler 1994).

To the best of our knowledge, this is the first study to report information on the growth rates of *O. doederleini* prior to settlement and immediately after settlement. Further, it is the first to provide data on longevity (age maxima) of the species in the tropics. Some families had data on multiple stages of life history when multiple species were pooled (e.g., omnivorous/herbivorous damselfishes), but given the differences in demographic characteristics within a family, general patterns would be crude or simply inaccurate. There was an abundance of data on age, growth and mortality of representatives of families that are the focus of fisheries, especially macrocarnivores and piscivores such as lutjanids, serranids and carangids. However, data on pre-settlement growth, PLDs and post-settlement growth were comparatively rare. In other families, the focus has only, or primarily, been on early life history stages (e.g., Holocentridae, Pomacentridae). For many important families, we found no data at all on age and growth (e.g., Holocentridae, Pempheridae, Caesionidae and Pomacanthidae). The paucity of data is due in part to a relatively recent understanding that the otoliths of tropical species can provide reliable estimates of age (Meekan et al. 2001). Despite this, there is a clear need to increase knowledge in this area for the management reef assemblages and tropical fisheries.

We concluded that accurate estimates of age could be obtained from daily increments. Evidence that counts were accurate included the following: The technique was validated, daily increments were easily observed (Fig. 2), the asymptote for age/length relationship for all reefs was beyond 200 days, and adult fish were collected from a size of 49 mm and 132 days or older (based on brooding fish and macroscopic examination of gonads).

The oldest fish we found was 368 days (*n* = 581); at 23°35'S), and unpublished data by Michael Marnane at One Tree Island also indicated that some *O. doederleini* can reach an age of over 1 year. Similar to our study, Longenecker and Langston (2006) found that *O. rubrimacula* (Apogonidae) lived to a maximum of 280 days in Fiji (17°15'S). However, there are great differences between our results for *O. doederleini* and other data from temperate waters in Japan. Okuda et al. (1998) concluded age estimates of up to 7 years in Shikoku Island, Japan

Table 6 Comparison with examples of demographic characteristics among multiple families of tropical reef fishes, by trophic groups (adapted from Randall et al. 1990); in some cases, we found more references than listed, but the age range was within the other publication listed

Family	Species	Presettlement growth	PLD (range)	Settlement mark	Early post-settlement growth	Life time growth	Age maxima	Estimates of mortality	Country	Source
Nocturnal planktivores/piscivores										
Apogonidae	<i>Apogon cyanosoma</i>	N	18–19 days	ND	ND	ND	ND	ND	GBR, Australia	Brothers et al. (1983)
	<i>Cheilodipterus quinqueleatus</i>	N	17–29 days	ND	ND	ND	ND	ND	GBR, Australia	Brothers et al. (1983)
	<i>O. doederleini</i>	Y	16–26 days	ND	Y	Y	<1 year	Y	GBR, Australia	This study
	<i>O. rubrimacula</i>	N	N	ND	Y	Y	<1 year	ND	Fiji	Longenecker and Langston (2006)
Holocentridae	Multiple (7)	Y	32–56 days	ND	ND	ND	ND	ND	Western Atlantic	Tyler et al. (1993)
Pempheridae		ND	ND	ND	ND	ND	ND	ND		
Diurnal planktivores										
Caesionidae		ND	ND	ND	ND	ND	ND	ND		
Pomacentridae	Multiple (8)	ND	8–32 days	Y	Y	ND	ND	ND	GBR, Australia	Bay et al. (2006); Green and McCormick (2005)
Acanthuridae	<i>Naso</i> sp. (6)	ND	ND	ND	ND	Y	9–30 years	ND	GBR, Australia	Choat and Robertson (2002)
Serranidae	E.g., <i>Anthias</i> spp. and <i>Pseudanthias</i> spp	ND	ND	ND	ND	ND	ND	ND		
Micro-meso-carnivores										
Balistidae	Multiple (2)	ND	ND	ND	ND	Y	11–14 years	Y	Brazil	de Albuquerque et al. (2011); Bernardes 2002
Chaetodontidae	Multiple (8)	Y	23–45 days	Y	Y	Y	6–20 years	Y	GBR, Australia	Fowler (1989); Berumen (2005); Berumen et al. (2012)
Gobiidae	Multiple (3)	ND	24–26 days	Y	Y	Y	59–100 days	Y	GBR, Australia	Depczynski and Bellwood (2006)
Labridae	<i>Coryphopterus kuna</i>	ND	45–74 days	Y	Y	Y	120 days	Y	Caribbean	Victor et al. (2010)
	<i>Eviota sigillata</i>	ND	23–27 days	Y	Y	Y	59 days	Y	GBR, Australia	Depczynski and Bellwood (2005)
	Multiple (9)	ND	21–50 days	Y	ND	Y	15–36 years	Y	GBR, Australia	Brothers et al. (1983); Choat et al. (2006)
	<i>Thalassoma bifasciatum</i>	Y	40–72 days	Y	Y	ND	ND	ND	Caribbean	Victor (1982)

Table 6 continued

Family	Species	Presettlement growth	PLD (range)	Settlement mark	Early post-settlement growth	Life time growth	Age maxima	Estimates of mortality	Country	Source
Nemipteridae	<i>Scopelogadus bimaculatus</i>	ND	ND	ND	ND	Y	16	Y	GBR, Australia	Boaden and Kingsford (2012)
Pomacanthidae	<i>Pomacanthus imperator</i>	ND	ND	ND	ND	Y	16	ND	China	Chung and Woo (1999)
Macrocarinidae/piscivore										
Carangidae	Multiple (2)	ND	ND	ND	ND	Y	6–10 years	ND	Hawaii	Sudekum et al. (1991)
	<i>Caranx bucculentus</i>	ND	ND	ND	ND	Y	ND	Y	Northern Australia	Brewer et al. 1994
Lethrinidae	Multiple (7)	ND	ND	ND	ND	Y	15–36 years	Y	GBR, Australia	Currey et al. (2013); Brown and Sumpton (1998)
Lutjanidae	Multiple (11)	ND	ND	ND	ND	Y	12–55 years	Y	Northern Australia, Indonesia	Marriott et al. (2007); Newman et al. (1996); Newman et al. (2000); Heupel et al. (2010a)
Scorpaenidae	<i>Lutjanus carponotatus</i>	ND	ND	ND	ND	Y	18 years	Y	GBR, Australia	Kingsford (2009)
	<i>Pterois volitans</i>	ND	20–35 days	ND	ND	ND	ND	ND	Bahamas	Ahrenholz and Morris (2010)
Serranidae	<i>Cephalopholis cyanostigma</i>	ND	ND	ND	ND	Y	45 years	Y	GBR, Australia	Mosse et al. 2002
	<i>Cromileptes altivelis</i>	ND	ND	ND	ND	Y	19 years	Y	GBR, Australia	Williams et al. (2009)
	<i>Epinephelus fuscoguttatus</i>	ND	ND	ND	ND	Y	42 years	Y	GBR, Australia	Pears et al. (2006)
	<i>Plectropomus laevis</i>	ND	ND	ND	ND	Y	16 years	Y	GBR, Australia	Heupel et al. (2010b)
	<i>Plectropomus leopardus</i>	ND	ND	ND	ND	Y	15 years	Y	GBR, Australia	Kingsford (2009)
Omnivores/herbivores/scrapers and detrital feeder										
Acanthuridae	Multiple (5)	ND	84 days	Y	ND	Y	21–70 years	ND	GBR, Australia	Choat and Axe (1996)
Blenniidae	Multiple (3)	ND	12–33 days	Y	ND	ND	ND	ND	GBR, Australia	Beldade et al. (2007); Brothers et al. (1983)
	<i>Salarias patzneri</i>	ND	ND	Y	Y	ND	350 days	ND	GBR, Australia	Wilson 2004

Table 6 continued

Family	Species	Presettlement growth	PLD (range)	Settlement mark	Early post-settlement growth	Life time growth	Age maxima	Estimates of mortality	Country	Source
Pomacentridae	Multiple (100)	Y	12–39 days	Y	ND	ND	ND	ND	GBR, Australia; Pacific, Atlantic	Bay et al. (2006); Wellington and Victor 1989
	<i>Acanthochromis polyacanthus</i>	ND	ND	Y	Y	N	9–11 years	Y	GBR, Australia	Kingsford and Hughes (2005)
	<i>Pomacentrus amboinensis</i>	Y	15–23 days	ND	ND	ND	ND	ND	GBR, Australia	Kerrigan (1996)
	<i>Pomacentrus coelestis</i>	Y	15–27 days	Y	Y	ND	ND	ND	GBR, Australia	Kingsford et al. (2011)
	<i>Pomacentrus moluccensis</i>	ND	ND	ND	Y	Y	18 years	Y	GBR, Australia	Doherty and Fowler (1994)
	<i>Stegastes acapulcoensis</i>	ND	ND	ND	ND	Y	12–32 years	Y	Panama, Galapagos	Meekan et al. (2001)
	Multiple (7)	Y	30–50 days	Y	ND	Y	5–20 years	Y	GBR, Australia	Brothers et al. (1983); Gust et al. (2002); Choat et al. (1996)
Scaridae	<i>Sparisoma viride</i>	ND	ND	ND	ND	Y	7–9 years	Y	Caribbean	Choat et al. (2003)

A Yes (Y) indicates that some information is available; ND—no data, y—years, d—days. Brothers et al. (1983) provided estimates of PLD for many of the groups listed, but they relied on the presence of settlement marks that are not found in some families such as apogonids. Some families appear in more than one trophic group (e.g., Pomacentridae). Data from temperate regions are not included

(33°40'N). The fish sampled in Japan grew to a maximum SL of 86 mm SL, whereas we only found fish to a size of 74 mm (93 mm TL). The maximum size of *O. doederleini* recorded for the GBR is 90 mm TL–74 mm SL, but no location is given by Randall et al. (1990) for this specimen. Okuda et al. (1998) had few data on fish less than 1 year for us to make comparisons of age versus a fish of known size. There are three possibilities to explain latitudinal variation in *O. doederleini* age and growth: (1) There are great differences in age (as there are for maximum size) over 10° difference in latitude (from the equator) between the two studies; (2) a methodological issue where the accuracy of aging techniques varies; Okuda et al. (1998) used scales, whereas we used daily increments in otoliths; and (3) mortality rates vary greatly between latitudes. With respect to options one and two, we favor option one as latitudinal variation in growth and age maxima are common in fishes (growth, Conover et al. 1997; age maxima, Boehlert and Kappenman 1980). Furthermore, scales tend to underestimate not overestimate ages. In Japan, Okuda et al. (1998) fin clipped some fish that were monitored for up to 2 years, so they clearly get older than their tropical conspecifics. The apogonid *Apogon ruepillei* found in estuaries near Perth (~32°S) were over a year old (Chrystal et al. 1985). All of the evidence from tropical waters indicates that small *O. doederleini* have age maxima of a year or less. Estimates of L_{∞} would be most reliable for all reefs combined (Table 4) as very large fish were rare. Our comparisons of the size/age of fish among reefs in the 80–90 mm SL range would be robust, but beyond 200 days would be weak. Latitudinal gradients in growth and life span would be interesting to examine. Conover et al. (1997), for example, demonstrated a strong positive correlation between the latitude of origin of *Morone saxatilis* and growth. Further, it is common for there to be positive relationships between life span and latitude in ectotherms, including fishes (Boehlert and Kappenman 1980; review, Munch and Salinas 2009). At present, there are no comparative data on growth by latitude for *O. doederleini*. The presettlement phase of *O. doederleini* was 16–26 days and fish settled at 9.5–13 mm SL. Settlement marks were not observed, and the age of settling fish was determined from potential settlers collected in nets at night and new arrivals to patch reefs. Ishihara and Tachihara (2011) estimated the PLDs of six *O. doederleini* in Japan at ~16–24 days and 10–11.5 mm SL, which fell within the ranges of values we had from the southern GBR; these authors also collected fish in channel nets. The range of ages over which fish settled was 38 % of the maximum age at settlement, a little less than that recorded for the damselfish *Pomacentrus coelestis* (45 %; Kingsford et al. 2011). Although many damselfishes spend a similar period of time in the plankton to *O. doederleini*, there are many other taxa that have longer PLDs. For example, scarids have

PLDs of 34–58 days; chaetodonts 25–40; and acanthurids 80 + days (Brothers et al. 1983).

Ostorhinchus doederleini have strong olfactory senses and can respond to the presence of lagoonal waters (Atema et al. 2002). Presettlement fish swim and/or are carried over the reef crest at night (Kingsford 2001) into One Tree lagoon where they find suitable settlement habitat to settle. *O. doederleini* commonly settle away from continuous reef on sections of substratum, potentially to avoid predatory adults (Finn and Kingsford 1996). We demonstrated that during this phase, fish had linear growth; this is typical of other fishes during the early juvenile phase (Kingsford and Milicich 1987).

Although reef fishes often have a mark in their otoliths related to settlement from pelagic to benthic environments (Brothers et al. 1983; Kingsford et al. 2011), 'settlement marks' were absent in the otoliths of *O. doederleini*. Brothers et al. (1983) also concluded that *O. doederleini* settle at 16 to 27 days ($n = 5$) and did not mention a settlement mark (= 'transition'). Settlement marks are not found in all fishes, and it has been speculated that the eco-behavioral transitions are less traumatic in these circumstances (e.g., monacanthids settling from drift algae to algae attached to the substratum, Kingsford and Milicich 1987). *O. doederleini* may experience less post-settlement trauma by not settling on continuous reef, where the risk of predation (and stress) is high. Further, they usually settle with conspecifics (pers. obs.) and they already have an established ability to feed in low light (Job and Bellwood 2000).

There is strong evidence that population structure within a metapopulation of *O. doederleini* can be complex at spatial scales of kilometers to tens of kilometers. Despite having a PLD of 16–26 days, a combination of favorable oceanography and larval behavior means that a disproportionately high number of fish return to natal reefs, and this can result in significant genetic differences among reefs (Gerlach et al. 2007). The robustness of population structures through time is likely to depend on larval survival, physical forcing (Sissenwine 1984), post-settlement processes (Jones 1991; Almany and Webster 2006) and demographic characteristics. It is critical to consider age for numerical modeling of ecological variation in population size and genetic robustness. For short-lived species such as *O. doederleini*, there is a great vulnerability to recruitment failure, especially if they do not have a prolonged spawning season. This in turn could compromise the resistance and resilience of a local genotype to change. Information on the timing and duration of spawning of *O. doederleini* is largely anecdotal, but does suggest a prolonged spawning season. Mouth brooding fish have been observed in October and January–February and peak recruitment is in January to February (i.e., from spawning in December and January). Further, the collection of *O. doederleini* larvae

in June by Kingsford (2001) indicates that at least some spawning occurs in winter, and backdating the age of fish collected in January and February puts many birthdates in the Austral winter to spring.

In conclusion, *O. doederleini* have a short PLD, and they settle onto sand and rubble away from continuous reefs and grow quickly. They reach asymptotic size beyond 200 days, but few fish reach 200 days old and the age maximum we found at four reefs was 368 days. These small fish were characterized by high mortality rates and presumably have a high population turn over; this should be considered in models relating to the trophodynamics of reefs and the population biology of *O. doederleini*. A review of the literature indicated that other fishes with similar demographic characteristics are small gobies and blennies.

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