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Productivity and sea surface temperature are correlated with the pelagic larval duration of damselfishes in the Red Sea

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ABSTRACT

We examined the variation of pelagic larval durations (PLDs) among three damselfishes, *Dascyllus aruanus*, *D. marginatus*, and *D. trimaculatus*, which live under the influence of an environmental gradient in the Red Sea. PLDs were significantly correlated with latitude, sea surface temperature (SST), and primary production (CHLA; chlorophyll *a* concentrations). We find a consistent decrease in PLDs with increasing SST and primary production (CHLA) towards the southern Red Sea among all species. This trend is likely related to higher food availability and increased metabolic rates in that region. We suggest that food availability is a potentially stronger driver of variation in PLD than temperature, especially in highly oligotrophic regions. Additionally, variations in PLDs were particularly high among specimens of *D. marginatus*, suggesting a stronger response to local environmental differences for endemic species. We also report the first average PLD for this species over a broad geographic range (19.82 ± 2.92 days).

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1. Introduction

The time a fish larva spends in the plankton before recruiting onto a reef, known as its pelagic larval duration (PLD), is a valuable source of information on how ecological and oceanographic processes affect a fish's early life. Such information can help to better understand organisms with complex life cycles, such as many coral reef inhabitants; subsequently, this fundamental life history information can be used to improve management of marine ecosystems and their natural resources. PLDs of coral reef fishes are known to exhibit variation driven by a wide range of intrinsic and extrinsic factors (McCormick and Molony, 1995; Searcy and Sponaugle, 2000; Sponaugle, 2010; Wellington and Victor, 1992; Wilson and Meekan, 2002). Two of the most relevant extrinsic factors that cause intraspecific variations in larval growth and development are temperature and food availability (Heath, 1992; Houde and Zastrow, 1993; Mcleod et al., 2011; Takahashi and Watanabe, 2005), which can be estimated from remote sensing satellite data on sea surface temperature (SST) and chlorophyll *a* (CHLA) concentrations respectively. Warmer temperatures increase metabolic rate and growth rates (Green and Fisher, 2004; Meekan et al., 2003; Sponaugle et al., 2006), which can lead to shorter PLDs (Bergenius et al., 2005; Green and Fisher, 2004; Grorud-Colvert and Sponaugle, 2011; McCormick and Molony, 1995; Sponaugle et al.,

2006). Similarly, higher food availability can increase larval growth (Biktashev et al., 2003; Fontes et al., 2010; Houde and Hoyt, 1987; Houde, 1989; Landaeta and Castro, 2006; Sponaugle, 2009, 2010) and potentially decrease the time a fish larva spends in the pelagic before recruiting onto a coral reef (Sponaugle and Grorud-Colvert, 2006). Variations in PLDs can be indicative of differences in dispersal potential, growth rates, and survival of fish larvae. Furthermore, the conditions a fish larva experiences during its PLD seem to even influence success, fitness, and growth in later life stages as juvenile and adult fish (Cushing and Horwood, 1994; Houde and Hoyt, 1987; Houde, 1989; Rankin and Sponaugle, 2011; Sponaugle and Grorud-Colvert, 2006; Sponaugle et al., 2011). However, most studies that have assessed the influence of temperature and food availability on the larval stage of fishes have focused on larval growth rate (Mcleod et al., 2015), size at settlement (McCormick and Molony, 1995), or recruitment cohort size (Lo-Yat et al., 2011) rather than on the length of PLDs in the standing population, and still fewer of these studies target coral reef fishes. In our study we focus specifically on PLD variations within the standing populations (i.e., post-settlement and adult fishes, as opposed to recruitment cohorts) of three congeneric coral reef damselfishes present in the Red Sea.

The Red Sea is an ideal location to study the effect of a variety of environmental parameters on coral reefs (Berumen et al., 2013). The Red Sea harbors thriving and continuous coral reefs along both sides of its narrow basin. Due to its shape, location, and only a single shallow and narrow connection to the Indian Ocean, it displays a unique

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environmental gradient of temperature, salinity, productivity, turbidity, and essentially reef-scape (Racault et al., 2015; Raitzos et al., 2013). These physical and environmental characteristics have made the Red Sea a natural location to assess the environmental impact on several coral reef organisms (e.g., Froukh and Kochzius, 2007; Giles et al., 2015; Lozano-Cortés and Berumen, 2015; Nanninga et al., 2014; Ngugi et al., 2012; Roberts et al., 1992; Robitzch et al., 2015; Sawall et al., 2014a, 2014b).

Here, we focus on the two seemingly major parameters that may drive PLD variations in the environmental gradient of the Red Sea: temperature and food availability. For this purpose we use the three *Dascyllus* species that live in the Red Sea (*D. aruanus*, *D. marginatus*, and *D. trimaculatus*). These species serve as a good model group to study PLD variations in coral reef fishes for several reasons. They are biologically similar, small in size, and commonly present along the entire environmental gradient of the Red Sea at overlapping depth ranges. They are zooplanktivorous, demersal spawners, and have relatively similar recruitment periods and larval development times (PLD). However, they have subtly different ecological preferences, which make them an interesting group to study the effect of the environment on early life history traits in the context of ecological specialization. We consider *D. trimaculatus* as the most ecologically versatile species within this group. It can be found on exposed reef walls, sheltered backside-reefs, and lagoons; it is not dependent on live coral; and it only uses reef structure for shelter, recruitment, and as spawning habitat. While *D. trimaculatus* mostly recruits onto anemones in the Red Sea, it can also recruit into branching corals, sea urchins, and other microhabitats. Once they reach juvenile stages, *D. trimaculatus* leave their settlement substrate, range throughout the entire reef structure, and spend most of their lifetime foraging in the water column. Intermediate on the ecological specialization ranking is *D. aruanus*. This species shows stronger habitat preferences, only recruiting to and living its entire life in branching live corals that are located in sheltered sandy reefs and lagoons. *Dascyllus aruanus* and our third species, *D. marginatus*, both show similar habitat preferences and occasionally even co-inhabit the same coral colony. However, the degree of ecological specialization is stronger in *D. marginatus*, which cannot be found on very shallow reef-tops and lagoons, nor can it be found on offshore reefs in most of the Red Sea. Therefore, we refer to *D. marginatus* as the most ecologically specialized species in our group.

The *Dascyllus* model also seems suitable to study variation in PLDs in the context of biogeography of coral reef associated fishes. Of the three species that occur in the Red Sea, *D. marginatus* is an Arabian endemic while *D. trimaculatus* and *D. aruanus* are both widespread species, common in most of the Indo-Pacific. In general, pomacentrid species with restricted distributions have shorter PLDs than wide-ranging species (Cowen and Sponaugle, 1997; Wellington and Victor, 1989), although the opposite is observed for labrids (Cowen and Sponaugle, 1997; Victor, 1986). The expected trend is that endemic or geographically-constrained species have shorter PLDs potentially restricting dispersal (Lester and Ruttenberg, 2005; Macpherson and Raventos, 2006; Mora et al., 2003). However, in endemic pomacentrid species the PLDs seem to have a rather non-linear relationship with range size (Thresher et al., 1989). Similarly, most studies assessing correlations between PLDs and biogeographic ranges over a number of species find no link between the two (Macpherson and Raventos, 2006; Victor and Wellington, 2000; Zapata and Herrón, 2002). The exact nature of PLD vs. biogeography remains an open question.

Thus, the objectives of our study are to use the model species-group of *D. marginatus*, *D. aruanus*, and *D. trimaculatus* to 1) assess the influence of environmental parameters such as SST and CHLA on the PLDs of coral reef associated damselfishes with different degrees of ecological specialization in a natural environment inside the Red Sea; 2) investigate variations in PLDs related to differences in biogeographic ranges among closely related species; 3) provide the first PLD-measurements for *D. trimaculatus* and *D. aruanus* from the Red Sea and additional

measurements from two sites outside the Red Sea as well as 4) provide the first PLD-measurements the first PLDs for *D. marginatus* from a wide geographic range.

2. Materials and methods

2.1. Fish sampling

Clove oil, tweezers, hand nets, and spears were used to collect juvenile and adult specimen from the three *Dascyllus* species (*D. aruanus*, *D. marginatus*, and *D. trimaculatus*) present in the Red Sea (RS) (Fig. 1). Fishes of different sizes (Fig. 2) and/or from different sampling years (Table 1) were collected for PLD assessment to cover potential temporal variations as much as possible. These were caught at 18 reef sites off the Saudi Arabian coastline and at two sites outside the RS (Indian Ocean “IO” and Indo-Australian-Archipelago “IA”; Table 1 and Fig. 1). Samples were immediately preserved in 90% ethanol. The sampling range (> 1600 km of coastline) covers most of the latitudinal span of the RS.

Whenever possible, specimens from all three species were collected from the same reef site for coherent interspecific comparisons. In case of absence of any of the species, specimens from the nearest possible site were sampled. The sampling sites were divided into four major Red Sea (RS) regions: “GAQ” (Gulf of Aqaba), “NCRS” (north-central RS), “SCRS” (south-central RS); “SRS” (southern RS) (in consensus with Raitzos et al., 2013; Fig. 1 and Table 1).

2.2. Otolith preparation and PLD assessment

PLDs for all three species were estimated from daily increments up to the settlement marks of sagittal otoliths. Sagittae were extracted and mounted onto a microscopy glass slide with thermoplastic resin, then ground and polished (following Wilson and McCormick, 1997) using aluminum oxide lapping films (South Bay Technology, Inc.) of three different thicknesses (30, 12, and 5 μm). Three to ten pictures were taken of each polished otolith with the program AxioVision Rel. (V. 4.8.2.0; copyright 2006–2010 Carl Zeiss Micro Imaging GmbH) utilizing a Zeiss AXIO Scope A1 microscope (200 \times magnification) and a Zeiss AxioCam ICc1. From the pictures, three independent PLD readings were made and if the counts deviated by less than 10% the mean count for each individual was calculated and included in the analyses. The same reader calculated PLDs for all species and lacked any information or metadata about the origin of the sample. A total of 28 *D. trimaculatus*, 56 *D. marginatus*, and 92 *D. aruanus* otolith readings were used for the statistical analyses (Table 1).

2.3. Chlorophyll *a* (CHLA) and sea surface temperature (SST) correlations

Two environmental parameters of the Red Sea were tested for correlations to PLD data: Chlorophyll *a* (CHLA) and sea surface temperature (SST). CHLA content is a good proxy for phytoplankton biomass (Håkanson et al., 2007) and is herein used as a proxy of food availability for the pelagic larva of the three studied species. Validated regional averages of CHLA concentrations (mg m^{-3}) and SST ($^{\circ}\text{C}$) were provided by D. Raitzos, based on Raitzos et al. (2013) for the regions NRS, NCRS, SCRS, and SRS; and by D. Dreano for the Gulf of Aqaba (GAQ). These estimates were produced from a 10-year high-resolution data set of satellite remote-sensing CHLA estimates (see Raitzos et al. (2013) for a detailed description of data acquisition). These estimates were subsequently used for Pearson correlations with PLD for each species.

2.4. Statistical analyses

All data were tested for normality (Kolmogorov–Smirnov test) and homoscedasticity (Levene’s test) prior to analyses. The differences in PLD among the three species in the four Red Sea regions (GAQ, NCRS, SCRS, and SRS) were explored with a factorial ANOVA. The spatial

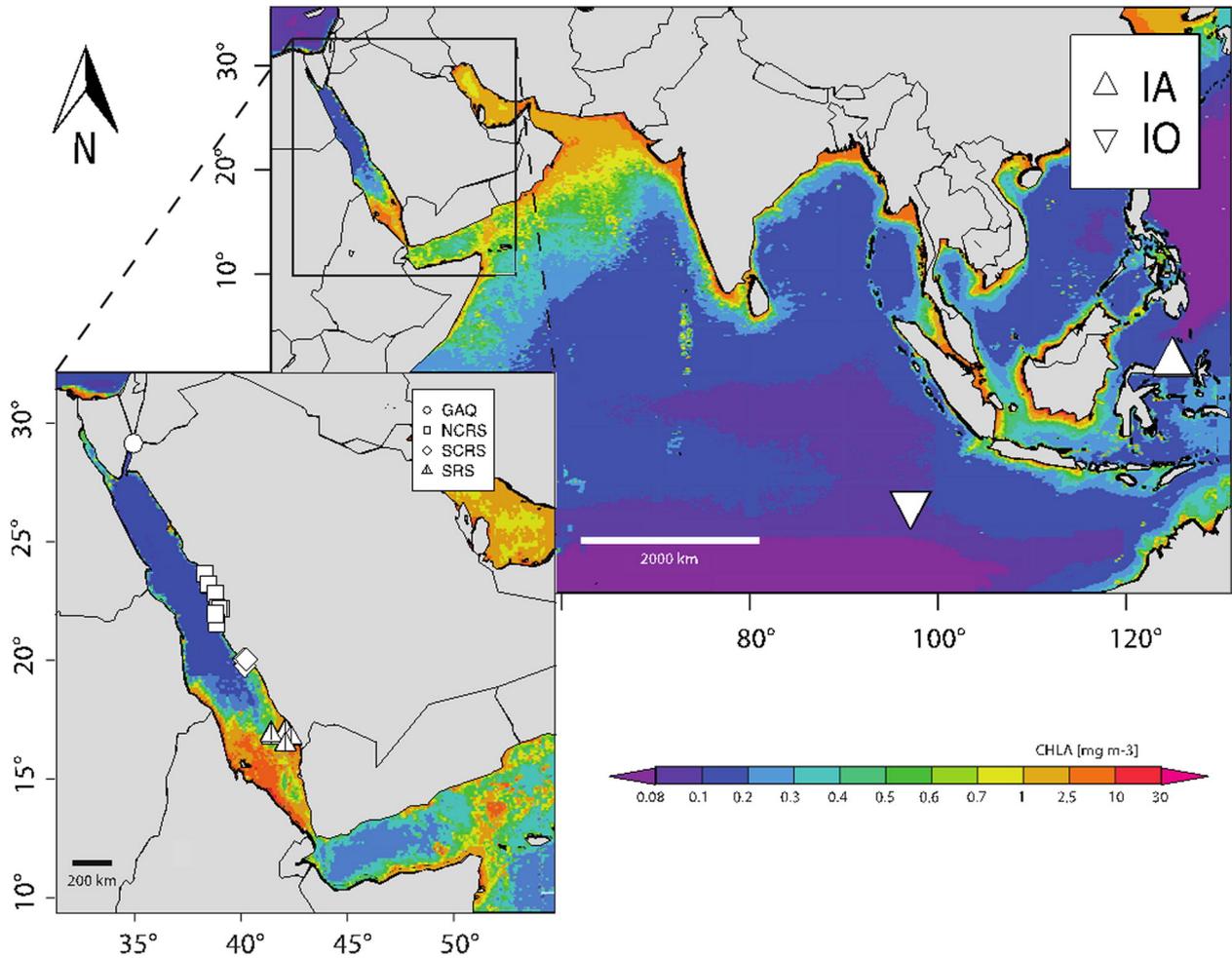


Fig. 1. Sampling sites of *Dascyllus marginatus*, *D. aruanus*, and *D. trimaculatus*. A total of 20 sites are grouped into four regions within the Red Sea (RS) and two outside the Red Sea (IA: Indo-Australian Archipelago; and IO: Indian Ocean). Those inside the Red Sea are represented by white circles (GAQ: Gulf of Aqaba), squares (NCRS: north-central RS), diamonds (SCRS: south-central RS), or sails (SRS: southern RS) according to the respective region. The regions were assigned in consensus with those in Raitos et al. (2013). The two locations outside the Red Sea are represented by a white naba and a white triangle (IO: Indian Ocean and IA: Indo-Australian-Archipelago, respectively). Map axes indicate latitude (°N) and longitude (°E). Additional information on exact number of samples and coordinates for each site can be found in Table 1. The chlorophyll *a* (CHLA, in mg m^{-3}) concentrations of the Indo-Pacific and Red Sea are displayed from the NASA Giovanni website (<http://oceancolor.gsfc.nasa.gov>) to visualize approximate differences between locations.

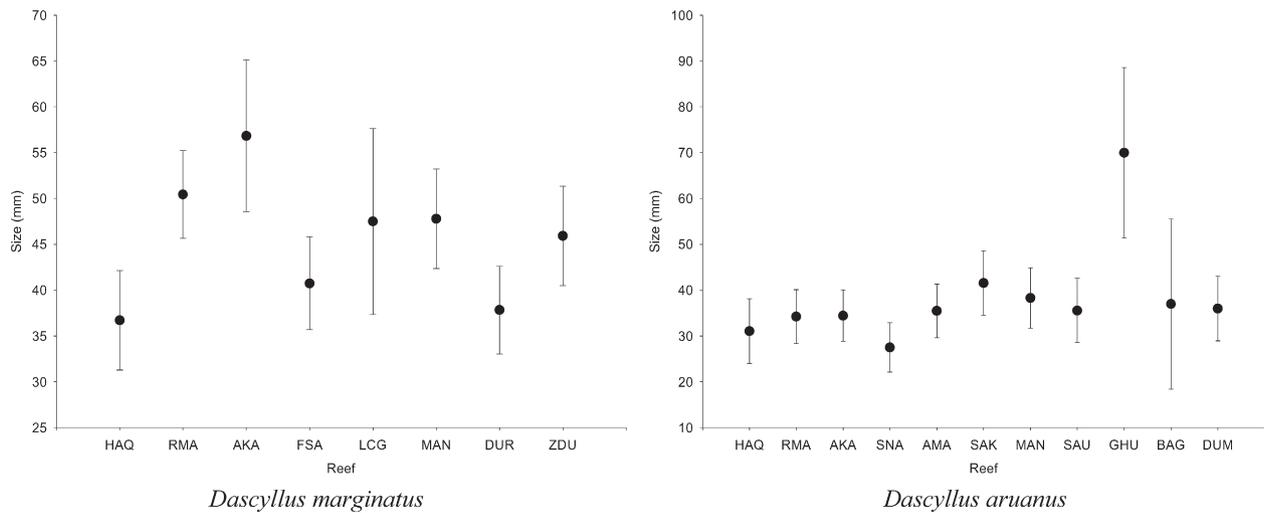


Fig. 2. Distribution of fish sizes (total length, in mm) of *Dascyllus marginatus* (left panel) and *D. aruanus* (right panel) used for PLD measurements from each site. Sites are given with three letter abbreviations on the x-axis (reef names can be found in Table 1). The sites are in latitudinal order from north to south from left to right, respectively along the axis. Black circles represent mean sizes and the whiskers display the maximum and minimum sizes of the fishes.

Table 1
Sampling sites, including number of samples, reef names and coordinates.

Location	Region	Site	N (Dt)	N (Dm)	N (Da)	Latitude	Longitude	Reef Name
RS	GAQ	HAQ	2	7	7	29°15'11.45"N	34°56'20.11"E	Haql
		YRM	1	–	–	23°46'21.12"N	38°16'34.02"E	Yanbu-Ras Majiz
		RMA	–	9	10	23°18'36.12"N	38°26'12.48"E	Ras Masturah
		AKA	–	3	11	22°56'15.90"N	38°45'56.58"E	Shib Al Karrah
		SNA	2	–	12	22°20'51.96"N	38°51'09.42"E	Shib Nazar
		FSA	–	8	–	22°17'46.80"N	39°04'26.64"E	Inner Fsar
		AFA	4	–	–	22°17'49.20"N	38°57'32.40"E	Al Fahal
		SAK	–	–	7	21°40'16.53"N	38°50'36.60"E	Shib Al Kabir
		AMA	–	–	10	22°04'25.75"N	38°46'40.26"E	Abu Madafi
		Total	7	20	50			
	NCRS	MAN	4	7	8	20°08'05.10"N	40°06'04.39"E	Manila Bay
		SAU	2	–	7	19°53'15.43"N	40°09'23.94"E	Saut Reef
		LCG	–	2	–	20°09'44.52"N	40°13'36.72"E	Coast Guard Reef
	NSRS	Total	6	9	15			
		GHU	–	–	1	17°06'37.20"N	42°04'03.10"E	Ghurab
		DAH	2	–	–	16°52'22.60"N	41°26'24.50"E	Dhi Dahaya
		ZDU	1	7	–	16°50'03.30"N	42°18'38.20"E	Zahrat Durakah
		BAG	1	–	1	16°58'44.00"N	41°23'05.60"E	Al Baglah
		DUR	–	13	–	16°51'36.20"N	42°19'18.00"E	Durakah
		DUM	4	–	11	16°33'50.80"N	42°03'30.60"E	Dumsuq
Total		8	20	13				
SRS	IND	–	–	7	02°11'11.04"N	118°32'55.33"E	Manado Nth Sulawesi	
IA	OUT	–	–	–	12°7'42.24"S	96°55'0.42"E	Cocos Keeling	
	IO	COC	5	–	–			
Total			28	56	92			

The three main geographic locations are the Red Sea (RS), the Indo-Australian-Archipelago (IA), and the Indian Ocean (IO). The RS location is subdivided in four major regions (GAQ: Gulf of Aqaba, NCRS: north-central RS, SCRS: south-central RS, and SRS: south RS). The sites represent the reefs sampled for each region (three letter codes based on the reef names). The IA and IO locations are represented by one sampling site each: Mandando in North Sulawesi, Indonesia (IND) and the island of Cocos Keeling, Australia (COC) respectively. N represents the number of individuals for which pelagic larval durations (PLDs) were assessed for statistical analyses of each studied species: *D. trimaculatus* (Dt), *D. marginatus* (Dm), and *D. aruanus* (Da). Samples from the RS were collected in 2013, 2014, and 2015; from the IO in 2010 and 2014; and from the IA in 2003.

variation of the PLD within each species was tested using an independent one-way ANOVA for each of the three *Dascyllus* species. A post-hoc test applying the unequal N Tukey's HSD means comparisons was used to detect any significant differences within the two aforementioned analyses. Subsequently, the PLD data was correlated (Pearson correlation) with latitude, SST, and CHLA (i.e., food availability) measurements to assess the impact of the latitudinal environmental gradient of the Red Sea. Finally, the PLDs from the Red Sea sites were compared against those from locations outside the Red Sea for the two widespread species (*D. trimaculatus* and *D. aruanus*). For this analysis, data from the four Red Sea regions for each of the two species was merged and compared independently with the IO (*D. trimaculatus*) and the IA (*D. aruanus*) using a t-student test. All analyses were conducted with STATISTICA 8.0 (StatSoft, Inc. 2007).

3. Results

3.1. PLD measurements

3.1.1. Within the Red Sea

The total mean PLDs of all three species differed significantly from each other ($F_{(2,144)} = 50.453$, $p < 0.001$, Fig. 3). Overall, *D. trimaculatus* showed the highest mean PLD (24.33 ± 2.02), followed by *D. aruanus* (23.09 ± 1.92), while *D. marginatus* exhibited the lowest (19.82 ± 2.92) (Table 2). Significant interspecific differences in PLDs were found among regions ($F_{(3,144)} = 31.723$, $p < 0.001$, Fig. 5) and intraspecific differences among all three species: between sampling regions ($F_{(3,144)} = 31.723$, $p < 0.001$, Fig. 5) and sites (only assessed for *D. marginatus* ($F_{(7,44)} = 10.099$, $p < 0.001$) and *D. aruanus* ($F_{(11,76)} = 7.6954$, $p < 0.001$ due to low number of *D. trimaculatus* specimen per site; see Fig. 5). The interaction between species and regions was not significant. In addition, a consistent latitudinal decrease in PLD was found to be present from north to south among all of the species between the four regions (see Fig. 4). PLD ranges were the largest for the endemic species *D. marginatus* (15–28 d; 13 d difference) and almost double of the ranges found in *D. aruanus* (19–27 d; 8 d difference) and

D. trimaculatus (20–27 d; 7 d difference). Within sampling sites, individuals of the endemic species also showed the highest PLD range (19–28 d, 9 d difference in HAQ) compared to those of the two widespread species (*D. aruanus*: 6 d difference in MAN; *D. trimaculatus*: 4 d difference in AFA).

3.1.2. Inside vs. outside the Red Sea

We report the PLD measurements for *D. aruanus* and *D. trimaculatus* from sites outside the Red Sea (RS) (*D. aruanus*: 21.05 ± 1.10 in the IA; *D. trimaculatus*: 24.40 ± 1.25 in the IO) and compare these to our measurements from inside the Red Sea. The mean PLD of both widespread

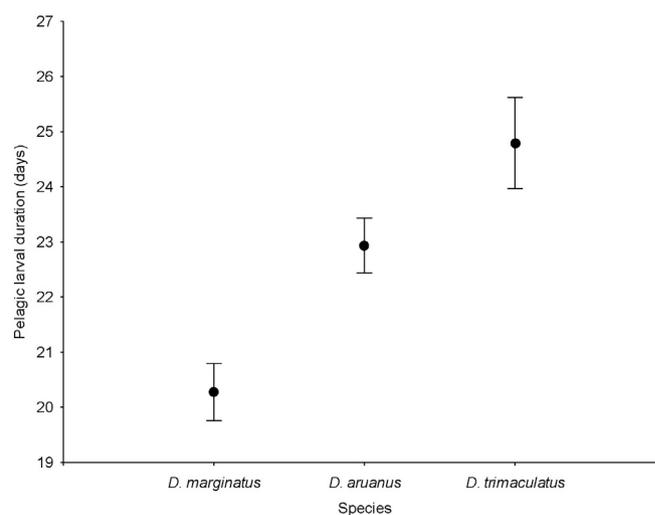


Fig. 3. Mean pelagic larval duration (PLD, in days) for *Dascyllus marginatus*, *D. aruanus*, and *D. trimaculatus* averaged among all study sites in the Red Sea. Whiskers represent 95% confidence intervals around the mean (black circle).

Table 2

Average pelagic larval durations (PLD in days; mean ± standard deviation) of *Dascyllus marginatus*, *Dascyllus aruanus*, and *Dascyllus trimaculatus* based on replicate counts of daily growth increments from otoliths.

Locat.	Region	Site	PLD Dm	PLD Da	PLD Dt	Lat.	Mean SST [°C]	Mean CHLA [mg m ⁻³]	
RS	GAQ (NRS)	HAQ	23.43 ± 2.89	25.10 ± 0.94	26.50 ± 1.17	29.253	24.2	0.20	
							25.8	0.15	
		NCRS	YRM	–	–	27.00	23.773		
			RMA	19.56 ± 1.97	23.77 ± 1.32	–	23.310		
			AKA	24.55 ± 2.04	24.61 ± 1.89	–	22.938		
			SNA	–	23.45 ± 1.46	26.67 ± 0.94	22.348		
			FSA	21.67 ± 1.00	–	–	22.296		
			AFA	–	–	24.92 ± 2.06	22.297		
			SAK	–	23.24 ± 1.33	–	21.671		
			AMA	–	23.73 ± 1.37	–	22.074		
			Total	20.65 ± 2.33	23.79 ± 1.52	25.72 ± 1.81		27.2	0.14
		SCRS	MAN	19.29 ± 2.69	21.95 ± 1.77	24.58 ± 1.20	20.135		
			SAU	–	22.52 ± 1.14	24.84 ± 0.23	19.888		
			LCG	20.67 ± 0.94	–	–	20.162		
			Total	19.59 ± 2.43	22.22 ± 1.48	24.67 ± 0.94		28.8	0.27
		SRS	GHU	–	21.00	–	17.110		
			DHI	–	–	22.00 ± 0.95	16.873		
			ZDU	20.09 ± 0.71	–	20.33	16.834		
			BAG	–	24.00	25.33	16.979		
			DUR	17.83 ± 1.63	–	–	16.860		
			DUM	–	20.09 ± 0.71	22.17 ± 1.57	16.564		
			Total	17.34 ± 1.43	20.63 ± 1.44	22.29 ± 1.76		28.9	1.64
		Total	19.82 ± 2.92	23.22 ± 1.96	24.32 ± 2.17				
	IO			–	–	24.40 ± 1.25	12.128		
		IA		–	21.05 ± 1.10	–	2.186		
	All			19.82 ± 2.92	23.09 ± 1.92	24.33 ± 2.02			
	R ² [%]	Dm					43.6	39.4	33.0
Da						34.8	30.6	27.6	
Dt						46.2	30.1	50.1	

Average PLDs for each species (*D. marginatus* (Dm), *D. aruanus* (Da), and *D. trimaculatus* (Dt)) are given among all (All) and within each geographic location: of the Indian Ocean (IO), the Indo-Australian-Archipelago (IA), and the Red Sea (RS); of each region within the RS (GAQ: Gulf of Aqaba, NCRS: north-central RS, SCRS: south-central RS, and SRS: south RS); and of each site within the RS (three-letter coded reef name). The latitude (Lat., in decimal degrees) is given for each site as used for correlation analysis. Estimates of mean surface sea temperature (mean SST, in °C) and chlorophyll *a* content (CHLA, in mg m⁻³) are provided by D. Raitsos and D. Dreano from 10-years satellite remote sensing high-resolution data (in consensus with Raitsos et al., 2013).

species is longer outside the Red Sea than within the Red Sea but only significantly longer for *D. aruanus* (*D. aruanus*: RS vs. IA: t-value = 2.88, df = 86, p = 0.04; *D. trimaculatus*: RS vs. IO: t-value = 0.07, df = 26, p = 0.93; see Fig. 5).

3.2. Environmental correlations with PLD in the Red Sea

Regional means of SST and CHLA concentrations were used as environmental data for Pearson correlations (Table 2). Their respective mean annual profiles are visualized in Fig. 6. The profiles of each region display a similar trend-curve except for SRS and GAQ. The SRS has

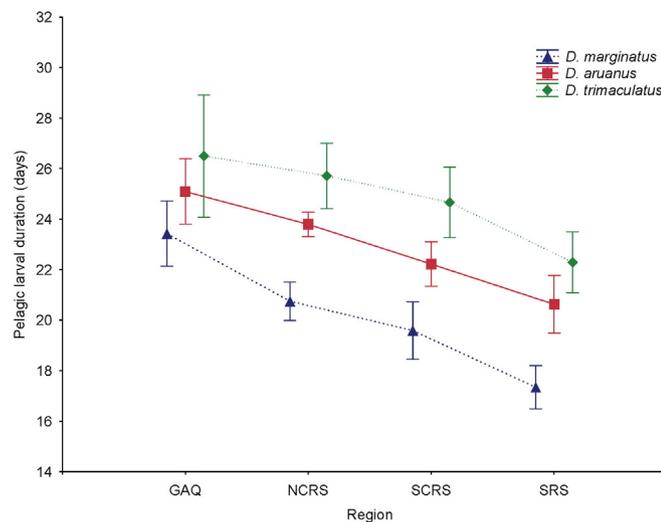


Fig. 4. Mean pelagic larval durations (PLD, in days) of three *Dascyllus* species in the four regions of the Red Sea (RS) (GAQ: Gulf of Aqaba, NCRS: north-central RS, SCRS: south-central RS, and SRS: south RS). Average PLDs are given by blue triangles for *D. marginatus*, red squares for *D. aruanus*, and green diamonds for *D. trimaculatus*. Whiskers represent 95% confidence intervals around the mean. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

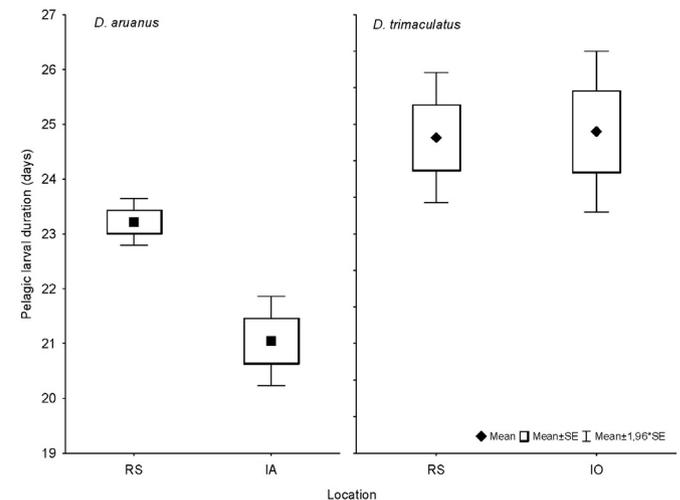


Fig. 5. Mean pelagic larval duration (PLD, in days) of *Dascyllus aruanus* and *D. trimaculatus* from locations inside the Red Sea (RS) and outside the Red Sea (Indo-Australian Archipelago (IA) and Indian Ocean (IO)). Whiskers represent 95% confidence intervals and boxes represent one standard error around the mean. Mean PLDs are given by black squares for *D. aruanus* and diamonds for *D. trimaculatus*.

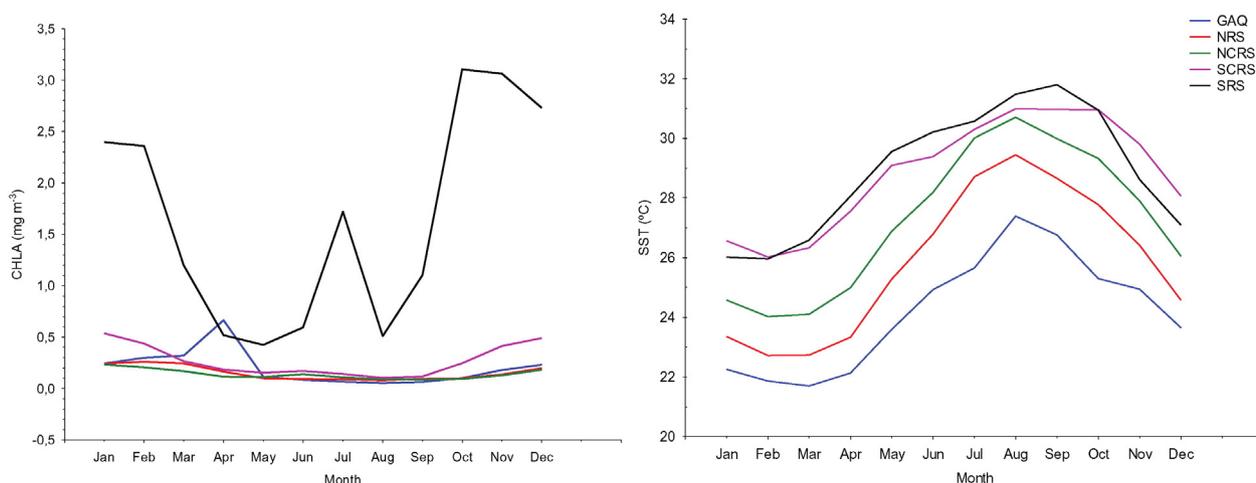


Fig. 6. Validated monthly regional averages of chlorophyll *a* concentrations (CHLA, in mg m^{-3} , left panel) and sea surface temperature (SST, in $^{\circ}\text{C}$, right panel). Each panel shows monthly mean averages for an average calendar year (three-letter coded months, x-axis) for each region (GAQ: Gulf of Aqaba, NCRS: north-central RS, SCRS: south-central RS, and SRS: south RS). Averages were produced from 10-year high-resolution data of satellite remote-sensing CHLA and SST estimates provided by D. Raitsos (for the regions NRS, NCRS, SCRS and SRS; sensu Raitsos et al. (2013)) and D. Dreano for the Gulf of Aqaba (GAQ). The trend lines are color-coded for each region.

overall much higher CHLA concentrations and its average annual CHLA profile has an additional peak in the summer. Different from all other regional CHLA profiles, the GAQ displays a sharp peak later in the spring and has both the highest concentrations of CHLA over the entire Red Sea during the spring and the lowest during the summer (Fig. 6). These unique seasonal changes of CHLA in GAQ result in one of the largest regional ranges ($>0.6 \text{ mg m}^{-3}$) in CHLA concentrations in the Red Sea (besides the southernmost SRS region; Table 2 and Fig. 6, left panel). In contrast, the SST profiles for all regions have similar ranges of about 6°C (Fig. 6, right panel).

3.2.1. Correlations with/latitude

Pearson correlation tests show a positive highly significant ($p < 0.001$) correlation between latitude and PLD among all species (Fig. 7). Latitude is also significantly negatively correlated with both CHLA and SST, indicating the latitudinal character of the Red Sea environmental gradient ($p < 0.001$). Even though latitude shows the highest correlations with PLDs (except among *D. trimaculatus*, $R^2 = 46.2\%$, Table 2), latitude itself is most likely not the driving factor but the correlation is rather a result of the combined effects of the environmental parameter at each site (e.g. SST and CHLA).

3.2.2. Correlations with SST

Temperature (SST) is significantly negatively correlated with PLDs of all three species (longer PLDs at lower SST) and shows the second highest R^2 values (except among *D. trimaculatus*, $R^2 = 30.1\%$, Table 2). This correlation is negative and significant for all species (Fig. 7).

3.2.3. Correlations with CHLA

CHLA concentration is significantly ($p < 0.001$) negatively correlated to the PLDs of all three *Dascyllus* species. The correlation is the strongest for *D. trimaculatus* ($R^2 = 50.1\%$; Table 2, Fig. 7). However, the sample size for this species is low and limits the overall interpretation of this result. Moreover, the R^2 values of SST and CHLA do not differ much and make it difficult to interpret which of the two parameters has the stronger influence on PLDs.

4. Discussion and conclusions

Our study shows that there is a significant link between the pelagic larval duration (PLD) of *Dascyllus* species and environmental parameters such as mean sea surface temperature (SST) and chlorophyll *a* (CHLA) content in the Red Sea. In all three study species, we found a

gradual and consistent decrease in mean PLD with decreasing latitude along the environmental gradient. Moreover, intra-specific differences in PLD between sampling regions along this gradient were higher in *D. marginatus* than the other two widespread species (*D. aruanus* and *D. trimaculatus*), suggesting that the endemic species might be more responsive to environmental differences within its habitat potentially related to a higher degree of specialization. We provide the first PLD estimate for a broad geographic range of the endemic *D. marginatus* ($19.8 \pm 2.9 \text{ d}$), which displays a consistently lower PLD at all sites in comparison to PLDs of *D. aruanus* and *D. trimaculatus*. Our results suggest that environmental factors can act as drivers of biogeography (as well as endemism) and dispersal among coral reef fishes. We also find the PLDs within species to be overall spatially and potentially also temporally highly plastic, which should be considered when evaluating correlations of PLDs and other parameters.

4.1. Pelagic larval durations (PLDs) in the chlorophyll *a* (CHLA) and sea surface temperature (SST) gradient of the Red Sea

The Red Sea is a good living laboratory for examining the effect of strong environmental gradients on various aspects of community ecology (Roberts et al., 1992; Ngugi et al., 2012; Sawall et al., 2014a, 2014b) and genetic connectivity (Froukh and Kochzius, 2007; Nanninga et al., 2014; Giles et al., 2015; Reimer et al., in review; Robitzch et al., 2015). However, very few studies have examined variation in life history traits or demographics (e.g., growth rates or PLD). In our study, we specifically look at the influence of SST and CHLA levels on early life stages of three *Dascyllus* species and find both to be consistently negatively correlated to PLDs of the studied fishes. A reduction in PLDs can be the result of an increase in the metabolic rate of larvae in warmer waters (Atkinson et al., 1996; Björnsson et al., 2001; Green and Fisher, 2004; Hunt et al., 1996) or of higher availability of food (Sponaugle and Grorud-Colvert, 2006) or of a combination of the two. In this context, CHLA explained up to 50% of the variation in PLD data (e.g., of *D. trimaculatus*), suggesting it is a strong environmental driver of PLDs in *Dascyllus*. Nevertheless, the coefficients of correlation (R^2 values) for both SST and CHLA are quite similar, which makes it difficult to infer which parameter has a stronger effect on PLDs, and a higher metabolic rate in warmer waters also demands more energy and higher food consumption (Houde and Zastrow, 1993; Houde, 1989). Since both SST and CHLA co-vary with latitude in the Red Sea, it is not surprising that the strongest significant correlation was a between PLD and latitude. However, latitude itself is unlikely to be influencing the PLD of coral reef

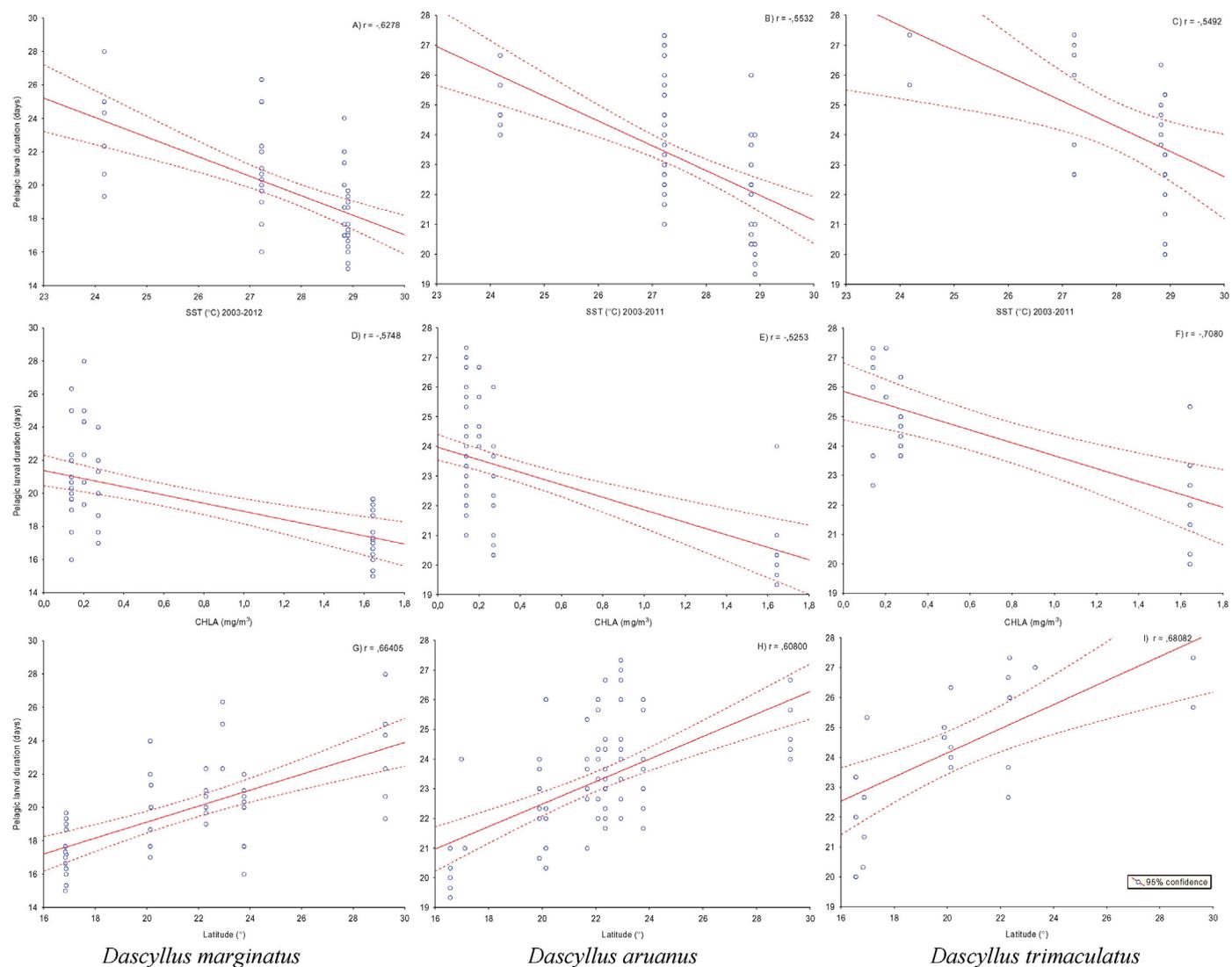


Fig. 7. Plots of Pearson correlations of pelagic larval durations (PLD, in days, y-axis) of three *Dascyllus* species (*Dascyllus marginatus*, *D. aruanus*, *D. trimaculatus*, from left to right) to: A–C) regional means of sea surface temperature (SST in °C, first row), D–F) regional means of chlorophyll *a* concentrations (CHLA, in mg m⁻³, middle row), and G–I) latitude (in degrees, last row; values in Table 2). The plots are arranged in columns according to species (i.e., *D. marginatus* shown in panels A, D, G; *D. aruanus* in panels B, E, H; and *D. trimaculatus* in panels C, F, I) and regional means of SST, CHLA, and latitude. The blue circles represent the measured PLD values of each species (y-axis, in days). The regression line is in red and the dotted curves represent the respective 95% confidence intervals of the correlation tests.

fishes (Booth and Parkinson, 2011). We interpret our findings as the synergic effect of greater food availability (higher CHLA concentrations) and higher metabolism (higher SST) on larval growth rates, subsequently reducing PLDs for all species in the warmer and more productive southern regions unique to the Red Sea. Furthermore, the decrease of PLDs along the SST and CHLA gradient seems to be stronger and more significant among individuals of the endemic and ecologically more specialized *D. marginatus* in comparison to *D. aruanus* and *D. trimaculatus*. We thus propose that the influence of small-scale regional changes in the environment might be stronger and positively correlated with the degree of ecological specialization and habitat range of damselfishes.

This is best illustrated in our study by the observation of large differences in PLDs among the endemic species, *D. marginatus* at one specific site in the Gulf of Aqaba (GAQ) (a 9 d range of difference in HAQ). These differences in PLDs were the highest among all *Dascyllus* in the Red Sea. If we then focus on the regional seasonal changes of the two environmental parameters SST and CHLA, the range of seasonal changes of CHLA concentrations for the GAQ region is distinctly higher compared to adjacent regions to the south, further suggesting that the GAQ is a variable environment itself. In contrast, the seasonal changes in SST in

all other regions are rather homogeneous. In other words, larvae that hatch during the spring/early summer in GAQ have up to six times more food available compared to cohorts hatching during other seasons. The extreme variability in the food available to these cohorts could be responsible for the large range of PLDs within the GAQ region. We therefore hypothesize that if the range of PLD differences within sites is a result of seasonal changes in the pelagic environment, seasonal changes in CHLA (food availability) rather than SST could more likely be the driver of differences in PLDs of *Dascyllus* in the Red Sea. However, the proposed hypothesis warrants further investigation in view of the correlation between temperature and food availability (CHLA) (McCormick, 1994; Lo-Yat et al., 2011) and the implementation of statistical models to discretely analyze the influence of these two environmental parameters on coral reef fishes. In terms of biological data, recruit collections could be targeted at different times of the year to assess whether longer PLDs correlate with seasons of lower productivity. For the more “homogeneously” productive regions of the Red Sea one could assess if the differences in PLDs are also more homogeneously distributed throughout the year. Unfortunately, we were unable to reliably back-calculate birthdates for our individual samples to determine specific intra-annual patterns. Alternate hypotheses that could explain

the large within-region differences in PLDs include seasonal changes in survival strategies and/or competition during the larval stage. For example, there may be a benefit in early settlement if there is seasonal variability in settlement habitat availability and early settlement increases the opportunity to secure space on the reef. Alternatively, delayed recruitment may confer a benefit due to larger size-at-settlement if post-settlement competition varies seasonally. During seasons that may have less settlement competition, delaying settlement may confer advantages in the form of decreased post-settlement mortality (bigger-is-best hypothesis, Anderson, 1988; Miller et al., 1988).

4.2. Pelagic larval durations (PLDs) of *Dascyllus* and the biogeography of coral reef fishes

It is thought that spatial-temporal variation in the environment can select for or against dispersal (Duputié and Massol, 2013), ultimately shaping specialization, evolutionary processes, and the biogeography of species (Berdahl et al., 2015; Heinz et al., 2009). In theory, endemic species should have reduced dispersal potentially linked to a shorter PLD than widespread species, and biogeographic provinces with steep environmental gradients may thus have higher rates of endemism than more homogeneous environments.

The Red Sea has long been recognized as a hotspot of endemism (Roberts et al., 1992; DiBattista et al., 2015a, 2015b) and in its sharp environmental gradient (Raitsos et al., 2013) the endemic damselfish species *D. marginatus* consistently exhibits shorter PLDs than the two widespread species. Of the two more ecologically versatile species, *D. trimaculatus* shows the longest PLD and the global average for this species is even longer (Luiz et al., 2013, Dataset S1). From a biogeographical point of view, this might indicate a successive increase of average PLD with spatial distribution among the three *Dascyllus* species in our study.

The relationship between dispersal potential and biogeographic distribution of marine species has long been an open discussion and many studies have approached this question using PLD data. However, most of these studies have found either weak, non-linear, or no correlation between distribution ranges and PLDs at different geographic scales and for a wide number of species. There can be several reasons for conflicting results among studies on the relationship between dispersal potential and biogeography of marine species. From our data we find it important to point out the extreme plasticity observed in PLDs of *Dascyllus* in relation to the environment and how such variations can radically change the outcome of the study. For instance, in our study, *D. marginatus* consistently has a shorter PLD than *D. aruanus* at the same geographic site (i.e., spatially coherent data) and we thus find a positive correlation between distribution range and dispersal potential. However, if our reference PLDs for the two species within the Red Sea were not spatially coherent but we instead use a reference PLD for *D. marginatus* from the northern Red Sea (GAQ; the only measurement available in previous literature) and a reference PLD for *D. aruanus* from the southern Red Sea (SRS), we would conclude the opposite, that is, we would find that the endemic species has a longer PLD than the widespread species. Broad comparisons of PLDs to range sizes may therefore be complicated by large intraspecific variations in PLD among sampling locations (see also Victor, 1991).

We suggest that appropriately designed studies may still have the potential to provide insight into the unresolved relationship of PLD and biogeography. The cautious collection of adequate temporal and spatial data is crucial. A study focused on long-term/evolutionary processes like biogeography in relation to contemporary demographic data like PLDs, would ideally meet the following criteria: A) address closely related species to eliminate variation related to phylogenetic effects, B) sample from standing (adult) populations to capture as much temporal variation as possible, also to ensure that the data represent the 'effective' population's PLD (from adults from different recruitment cohorts), and C) sample with spatial coherency in order to isolate extrinsic environmental variables from intrinsic biological differences.

The genus *Dascyllus* may offer an opportunity to address such questions. The genus has an endemic representative almost in every biogeographic province in the Indo-Pacific, which will allow future comparative studies using this genus to further assess the relationship between PLD and biogeography over a wide geographic range. Other genera (e.g., *Chaetodon*, *Thalassoma*, *Eviota*, etc.) may provide similar opportunities for congeneric comparison of endemic vs. widespread species. We further advocate the importance of analyzing PLD data accounting for sources of temporal and spatial variation at small scales.

Much work remains to be done to resolve the many potential drivers of plasticity in the PLDs of larval reef fishes at both ecological and evolutionary timescales. The role of various environmental factors and the inclusion of genetic, biological, and ecological data are a prime target for future studies, particularly in connection with understanding how ecological specialization of a species interacts with these factors.

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