Endemism and the pelagic larval duration of reef fishes in the eastern Pacific Ocean

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ABSTRACT: We examined the relationship between pelagic larval duration (PLD) and species range for the wrasses and damselfishes of the eastern Pacific Ocean. This region and these species are particularly appropriate for this analysis, since there is huge variation in the biogeographic range among these reef fishes, from endemics to islands a few kilometers in diameter to pan-Indo-Pacific ranges of 25 000 km or more. Furthermore, this variation in range occurs between pairs of congeners. We found no correlation between the mean (or maximum) PLDs measured from daily otolith increments and biogeographic range, for either family of reef fishes, and even after restricting the analysis to species with sample sizes over 50 individuals. A pairwise comparison of congeners showed, if anything, a significant inverse relationship between larval duration and range. The correlation between mean PLD and maximum PLD was very strong, even for large sample sizes (r = 0.987), indicating that mean PLD may be a good proxy measure for maximum PLD. We conclude that, at least within this region and within the limitations of this technique, larval duration appears not to determine species range.

KEY WORDS: Reef fish · Biogeography · Pelagic larval duration · Otolith aging

INTRODUCTION

The tropical eastern Pacific region is remarkable for having a few widely separated island groups and a thin strip of continental shelf. Perhaps as a result of this unusual geography, there is a relatively high rate of endemism among the reef-associated fishes. Unlike comparable reef areas, such as the Caribbean Sea, the biogeography of reef fishes in this region shows a curious pattern of wide-ranging species coexisting with congeners with exceptionally small ranges. This pattern applies across many major reef fish taxa, including the wrasses, damselfishes, angelfishes, and groupers (Allen & Robertson 1994, Robertson & Allen 1996). The result is high regional fish diversity, especially relative to total reef area, as well as some of the most restricted geographic ranges known for marine fishes (Rosenblatt 1967, Allen & Robertson 1994). The

pattern of sympatric congeners with vastly differing ranges provides a powerful testing ground for hypotheses explaining the biogeography of reef fishes.

In this study we compare endemics and wide-ranging congeners of wrasses (family Labridae) and damselfishes (family Pomacentridae) and focus on variation in pelagic larval duration (PLD) and its relationship with species range. The time a fish larva spends in the plankton before settling onto a reef is the simplest proxy measure of dispersal ability and few theories on the determinants of range in reef fishes would discount the importance of this feature of early life history. The eastern Pacific region contains reef fishes with some of the longest recorded larval durations as well as some genera with perhaps the largest and smallest geographic ranges known for reef fishes (Victor 1986a). The razorfish genus *Xyrichtys*, for example, contains *X. pavo*, found from East Africa to Baja California, while *X. wellingtoni* is apparently endemic to Clipperton Atoll in the eastern Pacific, which measures only 4 km in diameter (at the 50 m depth contour; Glynn et

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al. 1996). If dispersal ability indeed plays a role in determining range then it would be expected that some relationship would be found between range and PLD.

A variety of other factors can affect dispersal ability, such as larval behavior and distribution (Leis 1991) as well as larval swimming speeds and orientation abilities (Stobutzki & Bellwood 1994, 1997, Leis & Carson-Ewart 1997). In addition, many other important ecological and physical determinants of range can be proposed. Nevertheless, we focus on PLD because, unlike virtually all the others, it can be easily estimated by otolith aging techniques (Victor 1991). Clearly, an analysis of PLD should be the preliminary step in understanding the biogeography of fishes in this region. Since the otolith aging method has been validated for some members of both wrasses and damselfishes, and we have collected almost all of the eastern Pacific members of these families, we chose to explore the relationship between PLD and biogeographic range for these reef fishes.

METHODS AND MATERIALS

We surveyed wrasses and damselfishes in the eastern Pacific Ocean from Baja California south, including the Revillagigedos Islands, Clipperton Atoll, Cocos Island, the Galápagos Archipelago, and at the continental shelf in Panamá (Table 1). Collections were made between November 1982 and July 1999, with multiple collections over many years from Baja California, Panamá, and the Galápagos Islands, including collections described in Victor (1986a) and Wellington & Victor (1989, 1992).

Ranges were assigned according to Allen & Robertson (1994), as well as our own observations. Additional species lists for the island of Malpelo and mainland Ecuador are provided by Rubio et al. (1992), Bearez (1996), and Fernando Rivera of the Estacion Charles Darwin, Galápagos (F. Rivera pers. comm.). For the wrasses, we note the following changes from and additions to ranges reported by Allen & Robertson (1994): *Halichoeres chierchiae* to the Galápagos (authors' pers. obs.), *H. insularis* to Baja California (Gotshall 1998), *H. nicholsi* to Malpelo and mainland Ecuador (Rubio et al. 1992, F. Rivera pers. comm.), *Stethojulis bandanensis* to Baja California (authors' pers. obs.) and to Panamá (D. Ross Robertson pers. comm.), *Thalassoma lucasanum* to mainland Ecuador (F. Rivera pers. comm., authors' pers. obs.), *T. purpureum* to Galápagos, Cocos, Panamá and Clipperton (Randall 1995, McCosker & Humann 1996, D. Ross Robertson pers. comm., authors' pers. obs.), *T. virens* to Baja California (authors' pers. obs.), *Xyrichtys mundiceps* from the Sea of Cortez (Thomson et al. 1979) and Panamá (Victor et al. in press), *X. wellingtoni* from Clipperton Atoll

(Robertson & Allen 1996), and *X. victori* to Cocos (Grove & Lavenberg 1997). New species include an additional, presumably endemic, *Xyrichtys* species from the Galápagos (authors' pers. obs.) and a new species of *Halichoeres* replacing *H. melanotis* at Cocos Island (D. Ross Robertson pers. comm.).

Among the damselfishes, we note *Stegastes acapulcoensis* to Galápagos and Malpelo (Rubio et al. 1992, Grove & Lavenberg 1997, authors' pers. obs.) and *S. arcifrons* to mainland Ecuador (F. Rivera authors' pers. comm.). We do not include single observations as range extensions (e.g. *S. flavilatus* to Galápagos; Grove & Lavenberg 1997).

Range was calculated as the linear surface distance in kilometers between the furthest 2 points of the known world-wide range of the species calculated from the surface of the globe and not from a flat projection. It could be argued that areas should be used, or some weighted mean, taking into account isolation versus contiguous habitats. Nevertheless, we used this simple measure of range, realizing that some subtleties may be lost. The extraordinary variation in biogeographic range for the species we analyzed, almost 4 orders of magnitude, ensures that any real relationship should make itself evident, regardless of the methodology of calculating range.

We also calculated an additional estimate of required dispersal distance: the 'gap traversed'. This distance was measured as the greatest gap within the range without shallow hard substrate, thus taking into account the actual distance larvae would need to travel to maintain their present range. For species found along the coast throughout the region, the largest gap is between Puerto Angel, Mexico and the Golfo de Fonseca of Honduras (about 920 km on the global projection). The largest gap between islands in the northern group is about the same distance (Clipperton Atoll to the Revillagigedos Islands). For trans-Pacific species, the largest gap was calculated from the Marquesas to the Galápagos (the 'East Pacific Barrier'; about 5000 km on the global projection).

For pairwise comparisons in the eastern Pacific region, we define a widespread species as one whose range includes Baja California in the north and extends to Peru, Galápagos, or mainland Ecuador in the south or is trans-Pacific. Endemic species are defined as those who are limited to 1 or 2 island groups and/or the Gulf of California (Gulf endemics).

Pelagic larval durations were estimated with the use of the daily otolith increment technique. Otolith increments have been demonstrated directly to be daily in new recruits of representatives of these 2 families of reef fishes and we assume this phenomenon is generally true for other labrid and pomacentrid species and before as well as after settlement. The procedure for

preparing otoliths and counting increments and calculating PLDs is described for wrasses in Victor (1986a) and for damselfishes in Wellington & Victor (1989).

RESULTS

An overall comparison of mean PLD and biogeographic range for eastern Pacific wrasses and damselfishes shows no significant relationship between these variables in either family (Fig. 1, Table 2). Refining the analysis by using the recorded maximum PLD in our samples did not improve the relationship (Fig. 2, Table 2). Limiting the analysis to sample sizes over 50 per species did not change the conclusions (Table 2). Despite huge differences in species' ranges, there was no trend to longer larval durations in species with wide biogeographic ranges; in fact, the slope was occasion-

Table 1. Biogeographic range and pelagic larval duration (PLD) of the tropical eastern Pacific wrasses (family Labridae) and damselfishes (family Pomacentridae). All species found in the region are listed. Ranges: WP = western Pacific, BA = Baja California, RE = Revillagigedos Islands, CL = Clipperton Atoll, CO = Cocos Island, PA = Panamá, MA = Malpelo, GA = Galápagos Islands, EC = Ecuadorian mainland

| | | Biogeographic range | | | | | | | | | Larval duration | | | | |
		WP	BA	RE	CL	CO	PA	MA	GA	EC	Range (km)	Mean PLD (d)	Min.	Max.	SD	n
Family Labridae																
Bodianus	*diplotaenia*	–	+	+	+	+	+	+	+	+	7192	40	31	51	4.7	138
Bodianus	*eclancheri*	–	–	–	–	–	–	–	+	+	3308	32.3	31	35	2.3	3
Decodon	*melasma*	–	+	?	–	+	?	?	+	+	4885	–	–	–	–	–
Halichoeres	*adustus*	–	–	+	–	+	–	–	–	–	3077	33	29	38	2	35
Halichoeres	*aestuaricola*	–	+	–	–	–	+	–	–	–	4115	–	–	–	–	–
Halichoeres	*chierchiae*	–	+	+	–	–	+	–	+	–	4231	28.5	21	38	3.5	117
Halichoeres	*discolor*	–	–	–	–	+	–	–	–	–	6	32	29	38	2.4	28
Halichoeres	*dispilus*	–	+	+	–	+	+	?	+	+	5192	39.4	30	50	4	147
Halichoeres	*insularis*	–	+	+	–	–	–	–	–	–	1269	35.5	32	39	1.8	20
Halichoeres	*malpelo*	–	–	–	–	–	–	+	–	–	2	–	–	–	–	–
Halichoeres	*melanotis*	–	+	–	–	–	+	–	–	–	3846	35.7	31	40	3.1	10
Halichoeres	*nicholsi*	–	+	+	–	–	+	+	+	+	4346	30.4	24	38	2.8	71
Halichoeres	*notospilus*	–	+	+	–	+	+	+	+	+	5192	37.9	29	47	4.4	41
Halichoeres	*semicinctus*	–	+	–	–	–	–	–	–	–	1692	29.9	24	36	3.6	7
Halichoeres	sp. nov.	–	–	–	–	+	–	–	–	–	6	37	34	40	2.6	4
Novaculichthys	*taeniourus*	+	+	+	+	+	+	–	+	–	25269	50.3	44	57	4.4	7
Semicossyphus	*darwini*	–	–	–	–	–	–	–	+	+	3231	37	35	38	1.4	2
Semicossyphus	*pulcher*	–	+	–	–	–	–	–	–	–	1346	37.4	34	52	5.1	10
Stethojulis	*bandanensis*	+	+	+	+	+	+	–	+	–	17423	35	31	44	3.6	10
Thalassoma	*grammaticum*	–	+	+	+	+	+	+	+	–	3808	61.8	45	94	8.3	76
Thalassoma	*lucasanum*	–	+	+	–	+	+	+	+	+	4115	70.2	37	104	11.1	721
Thalassoma	*purpureum*	+	–	–	+	+	+	–	+	–	23923	57.7	50	62	6.7	3
Thalassoma	*robertsoni*	–	–	–	+	–	–	–	–	–	4	58.6	45	70	5.4	52
Thalassoma	*virens*	–	+	+	+	–	–	–	–	–	1308	68.8	49	96	8.2	59
Xyrichtys	*mundiceps*	–	+	–	–	–	+	–	–	–	3846	59.2	55	67	4.3	10
Xyrichtys	*pavo*	+	+	+	?	?	+	–	+	–	24885	51	42	67	6.6	14
Xyrichtys	sp. nov.	–	–	–	–	–	–	–	+	–	100	70.7	66	75	4.5	3
Xyrichtys	*victori*	–	–	–	–	+	–	–	+	–	1038	73.7	69	76	2.1	3
Xyrichtys	*wellingtoni*	–	–	–	+	–	–	–	–	–	4	68	66	70	1.6	5
Family Pomacentridae																
Abudefduf	*concolor*	–	–	–	–	+	+	+	+	+	2308	19.7	15	24	2.6	24
Abudefduf	*declivifrons*	–	+	?	–	–	–	–	–	–	1615	21.9	17	28	2.5	60
Abudefduf	*troschelii*	–	+	+	?	+	+	+	+	+	7115	18.1	16	22	1.6	11
Azurina	*eupalama*	–	–	–	–	+	–	–	+	–	1038	–	–	–	–	–
Azurina	*hirundo*	–	+	+	–	–	–	–	–	–	1654	–	–	–	–	–
Chromis	*alta*	–	+	+	+	?	+	–	+	–	4346	18.7	18	20	1.2	5
Chromis	*atrilobata*	–	+	+	–	+	+	+	+	+	5308	28.9	23	38	3.1	23
Chromis	*limbaughi*	–	+	–	–	–	–	–	–	–	692	22.8	20	27	1.5	15
Hypsypops	*rubicundus*	–	+	–	–	–	–	–	–	–	1808	20	18	22	2.8	2
Microspathodon	*bairdii*	–	+	+	–	+	+	+	+	+	4308	28.9	27	30	1.4	7
Microspathodon	*dorsalis*	–	+	+	–	+	+	+	+	+	4308	25.9	20	34	4.5	31
Nexilosus	*latifrons*	–	–	–	–	–	–	+	+	+	3115	29.2	28	33	1.8	10
Stegastes	*acapulcoensis*	–	+	+	–	+	+	+	+	+	4808	22.7	17	29	2.9	233
Stegastes	*arcifrons*	–	–	–	–	+	–	+	+	+	1269	29.8	20	35	2.5	103
Stegastes	*baldwini*	–	–	–	+	–	–	–	–	–	4	26	23	29	1.4	52
Stegastes	*flavilatus*	–	+	+	–	+	+	–	–	+	4500	25.8	20	39	3.8	250
Stegastes	*leucorus beebei*	–	–	–	–	+	+	+	+	–	1769	33.4	27	36	2.1	40
Stegastes	*leucorus leucorus*	–	+	+	–	–	–	–	–	–	1269	34	31	47	3.2	30
Stegastes	*rectifraenum*	–	+	–	–	–	–	–	–	–	923	21.5	17	25	2	51
Stegastes	*redemptus*	–	+	+	–	–	–	–	–	–	692	32.3	29	35	1.7	15

ally negative which, if significant, would represent a reduction in PLD with increasing range (e.g. for damselfish PLD vs range, and in both analyses of wrasse
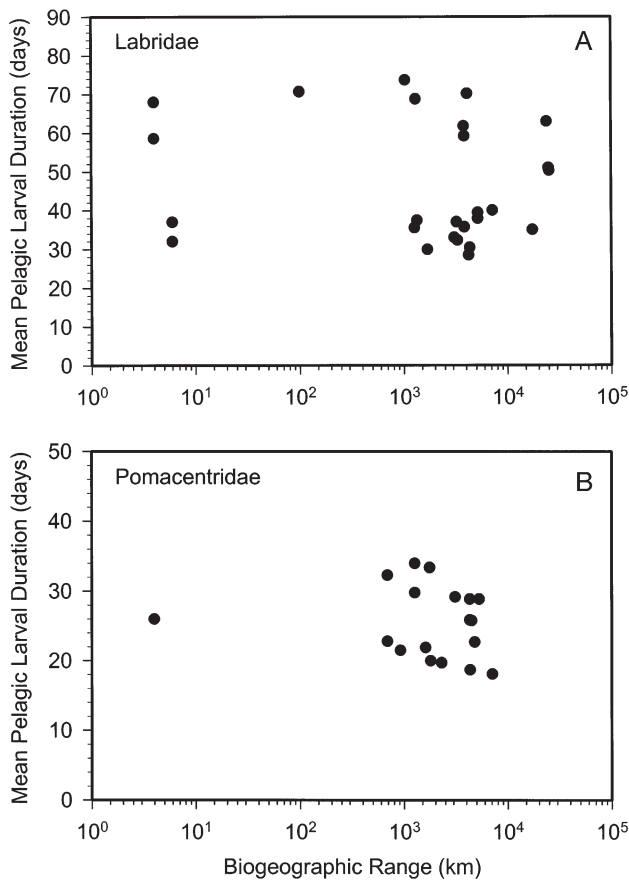

Fig. 1. Relationship between biogeographic range and mean pelagic larval duration (PLD) for (A) eastern Pacific labrid and (B) pomacentrid reef fishes

species with sample sizes over 50). Use of the 'gap traversed' instead of overall range also did not improve the relationship (Table 2). The most derived analysis, the combined families' maximum PLD of samples over 50 versus gap traversed, does show a weak trend to a positive relationship. However, combining families introduces a bias in that several endemic wrasse species with long larval lives were not included (e.g. the razorfishes) while the short-lived damselfishes were included. Clearly, when families (or sometimes genera) are combined in an uneven fashion any kind of artifactual relationship can be introduced.

A more precise comparison can be made for closely related pairs of congeners with different-sized ranges. The pairwise comparisons can be made for 2 different forms of congeneric biogeography. One is sympatry, where 2 closely related species coexist in a locality and, for some reason, the endemic does not disperse or survive elsewhere while its congener is widespread. All other things held equal, a dispersal-based hypothesis to explain this pattern would be a short PLD for the endemic and a relatively long PLD for the widespread species.

The second pattern is allopatry, where there is a widespread congener and an endemic congener that replaces the widespread species in an isolated locality. The origin of this pattern is presumably the genetic divergence of an isolated local population with subsequent restricted gene flow between the geminates, as well as some barrier to recolonization by the widespread species and a barrier to spread by the endemic. All other things held equal, a dispersal-based hypothesis to explain this pattern would be a short PLD for the endemic and a moderate PLD for the widespread species, with the short PLD preventing dispersal away from the locality by the endemic, and the moderate

Table 2. Regression analyses of PLDs and range for labrids and pomacentrids (Poma); using mean, maximum, and maximum with sample size over 50 for PLD and simple range and 'gap traversed' as measures of range. The bottom row represents the results of regression of the pairwise comparisons listed in Table 3 using mean PLD, maximum PLD, and maximum PLD with each member of the pair having sample sizes over 30 (therefore total n > 60)

| | Mean PLD (d) | | Max. PLD (d) | | Max. PLD (n > 50) (d) | | |
	Labrid	Poma	Labrid	Poma	Labrid	Poma	Combined
Range (km)	0.09×10^{-3}	-0.74×10^{-3}	0.15×10^{-3}	-0.52×10^{-3}	-5.15×10^{-3}	0.71×10^{-3}	0.62×10^{-3}
	$p = 0.83$	$p = 0.25$	$p = 0.78$	$p = 0.55$	$p = 0.3$	$p = 0.5$	$p = 0.87$
	$r^2 = 0.002$	$r^2 = 0.083$	$r^2 = 0.003$	$r^2 = 0.023$	$r^2 = 0.176$	$r^2 = 0.123$	$r^2 = 0.002$
	$n = 26$	$n = 18$	$n = 26$	$n = 18$	$n = 8$	$n = 6$	$n = 14$
Gap traversed (km)	0.04×10^{-3}	1.38×10^{-3}	0.23×10^{-3}	2.68×10^{-3}	-12.1×10^{-3}	6.27×10^{-3}	19.52×10^{-3}
	$p = 0.98$	$p = 0.69$	$p = 0.93$	$p = 0.56$	$p = 0.7$	$p = 0.13$	$p = 0.3$
	$r^2 < 0.001$	$r^2 = 0.01$	$r^2 < 0.001$	$r^2 = 0.021$	$r^2 = 0.024$	$r^2 = 0.473$	$r^2 = 0.09$
	$n = 26$	$n = 18$	$n = 26$	$n = 18$	$n = 8$	$n = 6$	$n = 14$
Pairwise comparison (families combined)	Slope = 0.70, intercept = 7.6 $p < 0.001$ $r^2 = 0.73$ $n = 33$		Slope = 0.77, intercept = 7.6 $p < 0.001$ $r^2 = 0.74$ $n = 33$		Slope = 1.04, intercept = −1.2 $p < 0.002$ $r^2 = 0.81$ $n = 8$		

PLD sufficient for some dispersal but not enough to recolonize the isolated locality.

We collected a set of congeneric pairs for this comparison (Table 3). Many of the PLDs for sympatric pairs of congeners were compared for collections from the same site and the same time, to avoid any complications of geographic and seasonal variation in PLD. Regional and seasonal variations in PLD have been documented to occur at Baja California for both wrasses and damselfishes; however little variation has been detected in the rest of the region (Wellington & Victor 1992). For sympatric species pairs, we obtained pairwise comparisons with mostly simultaneous collections (7 wrasse pairs, 2 damselfish pairs) and pairs that we could not collect from the same site (11 wrasse pairs, 5 damselfish pairs). For this latter group we compared from the closest region and time that was possible. Some species were used more than once in the pair comparisons.

Allopatric species pairs were less common (4 wrasse pairs, 4 damselfish pairs), especially since so many

recently recorded range extensions have reduced the observed rate of allopatry. Some pairs are obvious geminates, e.g. *Thalassoma robertsoni* and *T. lucasanum*, and *Chromis limbaughi* and *C. alta*, while others are only presumed. By definition, allopatric pairs could not be compared from the same collections, and therefore samples of the widespread species of the pair were collected when possible from about the same latitude.

The mean PLD of the appropriate sample of the endemic species was plotted against the mean PLD of the corresponding sample for the widespread congener (Fig. 3). If there were a tendency for endemics to have shorter larval lives, then the resulting plot should have a slope more than 1 and/or an intercept greater

Fig. 2. Relationship between biogeographic range and maximum PLD for (A) eastern Pacific labrid and (B) pomacentrid reef fishes

Table 3. List of endemic and widespread species pairs of eastern Pacific labrids and pomacentrids and the sites of collection for a pairwise comparison of PLD. Site abbreviations as in Table 1
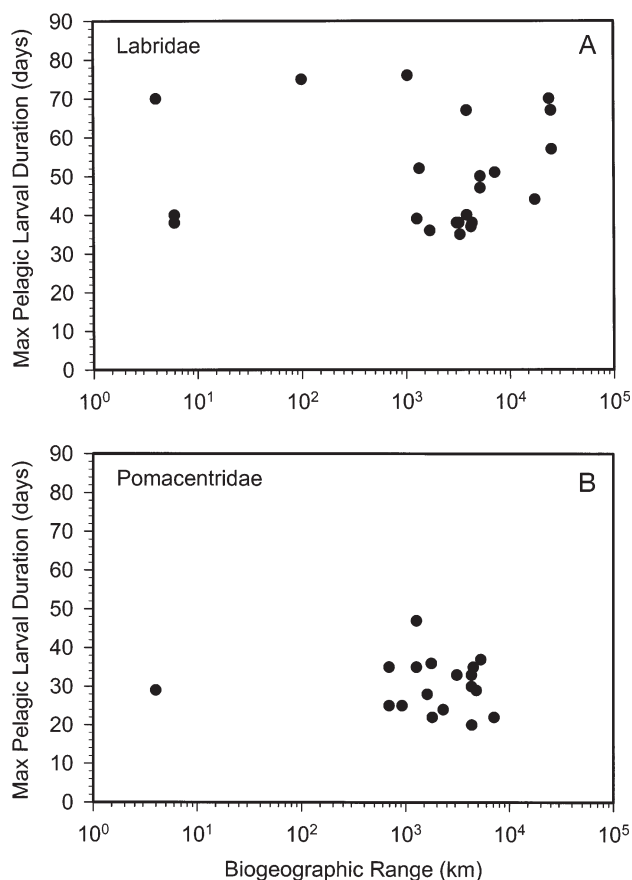
| Species pair (endemic × widespread)	Location of collections
Sympatric pairs	
Halichoeres adustus × H. dispilus	CO
H. discolor × H. dispilus	CO
Thalassoma robertsoni × T. grammaticum	CL
T. virens × T. grammaticum	CL
T. virens × T. lucasanum	BA
Xyrichtys victori × X. pavo	GA
Xyrichtys sp. nov. × *X. pavo*	GA
Stegastes rectifraenum × S. flavilatus	BA
S. rectifraenum × S. acapulcoensis	BA
Sympatric pairs (different collection sites)	
Halichoeres adustus × H. chierchiae	CO/PA
H. adustus × H. melanotis	CO/PA
H. adustus × H. nicholsi	CO/PA
H. adustus × H. notospilus	CO/PA
H. discolor × H. notospilus	CO/PA
H. insularis × H. chierchiae	RE/PA
H. insularis × H. dispilus	RE/CO
H. insularis × H. nicholsi	RE/PA
H. insularis × H. notospilus	RE/PA
Halichoeres sp. nov. × *H. notospilus*	CO/PA
Xyrichtys wellingtoni × X. pavo	CL/GA
Stegastes arcifrons × S. acapulcoensis	GA/PA
S. leucorus beebei × S. acapulcoensis	GA/PA
S. leucorus leucorus × S. acapulcoensis	RE/BA
S. leucorus leucorus × S. flavilatus	RE/BA
S. redemptus × S. flavilatus	RE/PA
Allopatric pairs	
Halichoeres discolor × H. nicholsi	CO/PA
Halichoeres sp. nov. × *H. melanotis*	CO/PA
Thalassoma robertsoni × T. lucasanum	CL/PA
T. virens × T. purpureum	CL/GA
Chromis limbaughi × C. alta	BA/GA
Stegastes baldwini × S. acapulcoensis	CL/PA
S. baldwini × S. flavilatus	CL/PA
S. redemptus × S. acapulcoensis	RE/PA
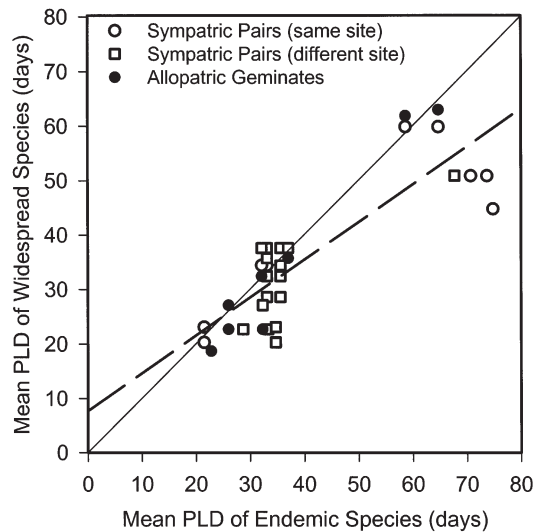
Fig. 3. Pairwise comparisons of mean PLD for paired endemic versus widespread congeners of the eastern Pacific labrid and pomacentrid reef fishes listed in Table 3. Not all individuals listed in Table 1 for the relevant species are utilized: only subsets from simultaneous collections or those paired in time and region. The solid line represents the line of unity (equal PLDs); the broken line represents the regression line for the 3 sets combined: PLD (widespread) = 0.7 PLD (endemic) + 7.6 d (p < 0.001, r^2 = 0.73, n = 33)

than 0 (an intercept greater than 0 in the absence of a slope differing from 1 would be obtained if the widespread species had a constant additional larval life regardless of mean PLD). If there were no overall difference, then the slope should be no different from 1 and the intercept should be 0. This method assesses whether there is a general trend, rather than focusing on specific comparisons. We used this method in place of detailed pairwise analysis of variance, since the data were heterogeneous, often with small and varying sample sizes. Furthermore, some significant species differences were to be expected in the complex groupings we used, and it would be difficult to interpret relative numbers of shorter versus longer larval durations in the pairwise comparisons.

The slope was, in fact, significantly less than 1, indicating some tendency for endemics to have longer larval durations than widespread species (slope of 0.7, p < 0.001, r^2 = 0.73; slope significantly different from 1, p < 0.05) (Fig. 3, Table 2). The intercept was at 7.6 d (significantly greater than 0, p < 0.03), although this would have more meaning if the slope were 1 or greater. When maximum PLD is used, the slope is still significantly less than 1 (p < 0.05), and the intercept becomes no different from 0. This counter-intuitive finding (slope less than 1) is likely driven by the presence of several endemics who have particularly long larval

lives, such as *Xyrichtys* species. When these species are removed by requiring a sample size of at least 30 per species, the slope reverts to 1.04 and is not significantly different from 1 and the intercept gets close to 0 (Table 2). These results indicate that even for matched pairs of species, there is clearly no tendency for widespread species to have longer larval durations.

DISCUSSION

There is, at present, no coherent theory explaining the complex biogeographic patterns exhibited by eastern Pacific reef fishes. Historically, vagility, or dispersal ability, has been postulated as the primary determinant of range for marine organisms with pelagic larvae (e.g. Scheltema 1968). Vagility is determined by a number of factors. The most obvious components of vagility comprise PLD, swimming ability, and larval behavior and ecology (Leis 1991). In addition, the ability to delay larval metamorphosis, remain pelagic as a juvenile, or even re-enter the pelagic realm as an adult directly affect vagility (e.g. Robertson & Foster 1982). Other independent factors, including local abundance, spawning frequency and seasonality, and the size of adults could also have an influence on dispersal rates. Alternatively, it has been suggested that ecological constraints, perhaps competition or presence of specific habitats, determine which species colonize which sites, regardless of their ability to get there. There even may be specific ecological requirements for larvae, independent of the ability of adults to persist in a habitat (Leis 1986). Unfortunately, there is little evidence for any unifying hypothesis and the more data are gathered, the less clear the picture becomes.

Our survey of eastern Pacific reef fish biogeography showed that PLDs, as inferred from otolith counts, are not correlated with species range in this region. This finding does not directly demonstrate that dispersal ability does not determine range, since larval duration is only a proxy measure of dispersal ability. A variety of complicating issues could hamper the analysis. It could be that the otolith aging technique is inappropriate for measuring larval durations and some as yet undetected artifact is producing increments on larval otoliths. Alternatively, sampling error may hide the true larval duration (McCormick 1994). It may be necessary to sample sufficiently intensively to discern the degree to which some few larvae can delay metamorphosis, for it is these larvae that would colonize new areas (Victor 1986b, Cowen 1991, McCormick 1994). It has been pointed out that maximum larval durations should be used when dealing with evolutionary or zoogeographic questions (Leis 1991). When we limited the analysis to the maximum PLD for those species for

which we had large samples (over 50), there was still no significant relationship with range. Using averages, however, is not as reckless as it may first appear. Indeed, the mean may be a good indicator of the maximum since there is a strong correlation between mean PLD and maximum PLD regardless of sample size: for our data set the correlation coefficient gets stronger with increasing sample size; $r = 0.951$ overall, $r = 0.984$ for samples over 30, and $r = 0.987$ for samples over 50 (Fig. 4). It also should be noted that the rare maximum may not be biologically relevant, since colonization requires survival to adulthood of sufficient numbers to establish a breeding population and the rare solitary individual that occasionally arrives would never be able to colonize.

Geographic and seasonal variations in larval duration could easily compromise the accuracy of PLD estimates, although studies of geographic variation in other areas have shown at most only minor differences in average PLDs (but see Victor 1986a for Hawaii vs western Pacific and McCormick 1994 for goatfishes). In the past we have found 1 significant anomaly: a regional and seasonal difference in PLD in Baja California (Wellington & Victor 1992, unpubl.). In this study, we have tried to take most of these factors into account by repeated sampling, using large sample sizes where possible, and controlling for known geographic variation. The clear absence of any apparent relationship between our estimates of PLD and range argues that some methodological shortcoming is not responsible for the lack of a correlation.
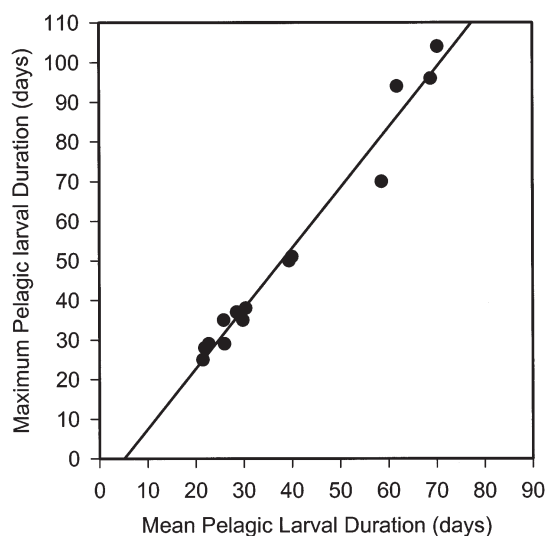

Fig. 4. Relationship between mean and maximum PLD for eastern Pacific labrid and pomacentrid reef fishes with sample sizes greater than 50 individuals. The solid line represents the regression line

It is certainly possible that length of larval life is not the primary determinant of dispersal ability. Recent studies have shown that reef fish larvae have strong swimming abilities and orientation abilities (at least during later stages; Leis et al. 1996, Leis & Carson-Ewart 1997), and these characteristics may affect how far larvae disperse from their natal region. Indeed, at least 1 recent study has shown puzzling genetic heterozygosity between reef fish populations within a single island group, suggesting that long-distance pelagic dispersal may not be automatic in reef fish with long-lived larval stages (Planes et al. 1998).

Any radical reinterpretation of the long-distance dispersal abilities of reef fishes must, however, take into account the vast ranges of some reef fish species. Furthermore, the documented arrival of vagrants from distant regions clearly indicates that many reef fish species do have long-distance dispersal abilities, even within the short period of recent scientific investigations. Crossing of the eastern Pacific Barrier, the widest tract of tropical ocean without stepping stones, is occasionally observed. A number of Central Pacific reef fish species have recently been reported in the Galápagos Islands and Clipperton Atoll, usually associated with the El Niño-Southern Oscillation event (Merlen 1988, McCosker & Humann 1996, Robertson & Allen 1996, Grove & Lavenberg 1997). This phenomenon is not limited to fishes: Lessios et al. (1996, 1998) have documented the recent invasion of the western Pacific sea urchin *Echinothrix diadema* at several sites in the eastern Pacific. Fish larvae of some of the genera in our study have been captured both in the middle of the eastern Pacific Barrier (*Thalassoma*; Leis 1983), as well as 400 km east of the Galápagos Islands (*Halichoeres*, *Thalassoma*, *Xyrichtys*, *Stegastes*; Victor 1987). Clearly, these fish larvae do disperse far into the open ocean in great numbers, sufficient to show up in small plankton nets.

Although PLD does not correlate with range within the eastern Pacific region, there is certainly some overall relationship between ocean-wide dispersal and PLD. The species that cross the Pacific Ocean to Hawaii and the eastern Pacific tend to have long PLDs (e.g. Victor 1986a). Generally, species that cross the Pacific come from families with long-lived larvae such as labrids (wrasses), acanthurids (surgeonfishes), and muraenids (moray eels), while families with shorter-lived larvae do not cross, e.g. pomacentrids (damselfishes), haemulids (grunts and relatives), and all but 1 lutjanid (snappers) (Leis 1984, Allen & Robertson 1994, Robertson & Allen 1996). Beyond this simple tendency, no relationship appears to exist: species with long PLDs can be endemic to a single island and, within the region, the correlation between measured PLD and range is non-existent.

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