

Relationship between pelagic larval duration and geographic distribution of Mediterranean littoral fishes

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ABSTRACT: We examined the relationship between pelagic larval duration (PLD)—a predictor of a species' dispersal potential—and the geographic distribution range of 62 Mediterranean littoral fishes. We found a significant, positive, weak relationship between PLD and distribution range. This relationship was observed in species with long PLDs that can cross the few dispersal barriers (Macaronesian Islands) present in the Mediterranean, and in endemic Mediterranean species with short PLDs. Species with inshore larvae exhibited a shorter PLD than species with offshore larvae. Species with larvae living in spring-summer had shorter PLDs than those developing in autumn-winter. Mean geographic range was clearly smaller for species with inshore larval distributions than for species with offshore larval distributions. However, the geographic range of species with benthic eggs was smaller than that of pelagic spawners. The size of the distribution range of fishes is probably not controlled only by the PLD. The inshore/offshore position and the season of planktonic life play an important role in ensuring the return of larvae to their settlement habitats. Consequently, these factors also affect the size of the species' distribution range.

KEY WORDS: Early life history · Geographic range size · Pelagic larval duration · Mediterranean fishes · Biogeography · Dispersal

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INTRODUCTION

The range of a species' geographic distribution and its dispersal capabilities are still central issues in marine ecology and biogeography. Recent studies have emphasized the importance of this relationship (Muss et al. 2001, Heads 2005). Most studies have revealed that it is difficult to apply common rules. However, several authors have shown that, in general, species with high dispersal capabilities have a larger geographic range than those with low dispersal potential (Kinlan & Gaines 2003).

Pelagic larval duration (PLD) in fishes is considered a predictor of a species' dispersal potential. However, the existence of numerous exceptions in the dispersal-range size relationship indicates that additional aspects of early life fish biology should be researched (Armsworth et al. 2001, Shanks et al. 2003). Daily in-

cremental marks on otoliths can be used to determine the duration of the larval phase. This provides a method for evaluating the relationship between PLD and a species' geographic distribution (Victor & Wellington 2000, Lester & Ruttenberg 2005). Despite several studies, no clear patterns have emerged to explain the relationship between these 2 factors. Some studies demonstrated a positive relationship between PLD and range (Zapata & Herron 2002, Lester & Ruttenberg 2005). In contrast, other studies found no significant relationship (Wellington & Victor 1989, Victor & Wellington 2000). Other reports have demonstrated a positive relationship between gene flow and PLD, suggesting that larval strategies may be effective predictors of population genetic structure (Planes 2002).

Studies relating PLD and distribution range have used tropical reef fishes; see review by Lester & Ruttenberg (2005). These authors suggested that the posi-

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tive relationship between these 2 variables in the Indo-Pacific can only be found in species with long PLDs that can cross significant dispersal barriers. These barriers are numerous in tropical reef systems, particularly in the Indo-Pacific and East Pacific, where the habitat is distributed among islands. Some of these islands are isolated by thousands of kilometres between patches of reef habitats. The habitat distribution in the Indo-Pacific and East Pacific tropical reef systems is quite different from that in temperate areas (e.g. the Mediterranean Sea). Therefore, it would be interesting to assess whether the patterns observed in tropical reef fishes can be generalized to other areas. The Mediterranean and eastern temperate Atlantic is characterised by a continuous coastline around the perimeter. There are a few oceanic islands (the Macaronesian Islands: Azores, Madeira and the Canaries), and few significant open-ocean barriers to dispersal (Macpherson 2002). Hence, we would expect to find no relationship between PLDs and range size distributions.

Dispersal potential can also be influenced by mechanisms other than PLD, such as inshore or offshore larval distributions and benthic or pelagic spawning strategies. Several studies document stronger transport currents offshore than inshore (Tintore et al. 1995, Largier 2003). Thus, larvae situated near the coastline would have lower dispersal possibilities than those situated along the continental shelf and slope (Shanks & Eckert 2005). Furthermore, other studies show that larvae from benthic eggs are larger, better swimmers, and have more developed sensory systems than larvae from pelagic spawners (Blaxter 1986). The combination of these characteristics may make retention more likely for larvae from benthic spawners than for larvae from pelagic eggs, thereby affecting their dispersal capabilities (Hickford & Schiel 2003). However, these aspects have not been considered in the context of the relationship between PLD and range size, with the exception of a recent study on California Current fishes (Shanks & Eckert 2005). These authors suggested the existence of strong selective pressure to facilitate larval return to adult habitats, thus closing the larval pelagic phase. They called this problem the 'drift paradox'. They also suggested that selective pressure to solve this problem may involve the adaptation of early life traits to local oceanography, influencing the geographic range distribution of the species.

The Mediterranean Sea is inhabited by some 300 littoral fish species. Nearly 100 of these normally dwell at depths <50 m. There is a high proportion of endemic species (ca. 25%) (Macpherson 2002). The geographic distribution and reproductive patterns of these species are well known (Whitehead et al. 1986) and, in addition, much is known about the planktonic larval distri-

butions of numerous species (Sabatés 1990, Sabatés et al. 2003, A. Sabatés pers. comm.).

The western Mediterranean is characterized by a narrow continental shelf (100 m isobath, usually situated no more than 10 km from the coastline) and a permanent shelf/slope frontal system parallel to the bathymetry of the shelf. This front separates high-salinity open ocean water (greater than 38) from low-salinity coastal water, partially as a consequence of continental discharges. The front runs along the continental slope and extends to a depth of some 400 m, and the associated geostrophic current flow is 10 km wide at the surface, parallel to the front on its coastal side. The dynamics of the front displays a mesoscale activity, with formation of filaments, eddies and oscillations. The front has been found to delimit shelf and oceanic fish larvae and act as a barrier preventing dispersal of fish larvae out to the open sea (see Sabatés & Olivar 1996, Sabatés et al. 2003 and references therein). The coastal area is also strongly influenced by seasonal changes in the predominant air masses. The predominant air mass blowing over the western Mediterranean basin is a dry, continental wind (Astraldi & Gasparini 1992). During winter, strong winds are more frequent and can persist for several days, inducing intense water mixing and changes in the direction of flow, and bringing nutrients to the surface. In summer the pattern is very different, with weak onshore or shoreward winds.

In this study, the relationship between PLD and geographic range distribution of 62 littoral fishes was examined. We compared whether patterns observed in Mediterranean littoral fishes are similar to those observed in tropical reef fishes (Lester & Ruttenberg 2005 and references therein). We also extended the analysis of Shanks & Eckert (2005) by investigating whether combinations of early life traits (inshore/offshore distributions of larvae, spawning strategies and length of planktonic life) are related to local oceanography. Such a relationship would facilitate the closure of the larval pelagic phase and influence the geographic distribution of species.

MATERIALS AND METHODS

Sampling was performed along the coast off Blanes, Spain (ca. 42°02' N, 3°13' E, north-west Mediterranean) between spring 2001 and autumn 2004. Additional samples were taken in the western Mediterranean Sea, from the north-east of Spain to the Straits of Gibraltar. Following the methodology described in Raventos & Macpherson (2001), a minimum of 3 samples were taken weekly during the settlement period for most of the species (spring-summer). One or 2 samples were

taken weekly in autumn-winter (Garcia-Rubiés & Macpherson 1995, Raventos & Macpherson 2001, 2005, Macpherson & Raventos 2005, authors' unpubl. data for settlement period identification). Samples were collected at depths of between 0 and 20 m (occasionally as far down as 30 m) by SCUBA divers using hand nets. New settlers were identified according to different authors and by personal observations made in previous studies (see Raventos & Macpherson 2001 and references therein). Fish were measured in the laboratory within 1 h of capture. Otoliths (sagittae and lapilli) were removed and preserved in 96% ethanol. The size of newly settled individuals ranged from 4 to 20 mm, depending on the species (see Raventos & Macpherson 2001). In all cases, the size of post-settlers was under 40 mm at no more than 30 d after settlement.

PLDs were estimated using the daily otolith increment technique. Otoliths (lapillus and sagitta) were mounted on microscope slides using Eukitt as the mounting medium. After mounting, otoliths were polished to expose all the daily increments within the same plane. Readings were made using a light microscope connected to a digital camera and an image analysis system. PLD was defined as the number of increments occurring from the centre of the otolith outwards to the settlement mark. All individuals examined had a settlement mark (see Wilson & McCormick 1999, Raventos & Macpherson 2001 for settlement mark identifications). Sub-daily increments (i.e. faint increments occurring between dark, well-defined increments) were found on the otoliths of some species. However, we followed the criteria used by Wellington & Victor (1989) and Raventos & Macpherson (2001) for interpreting which increments constitute daily growth increments. As previous authors have done (e.g. Wellington & Victor 1989), we assumed that increments formed during the larval stage represented daily increments. However, as Brothers et al. (1983) noted, the initiation time for daily increments in our study species was not known. Thus, our counts could slightly over- or underestimate the length of larval life, depending on the exact timing of the growth-increment initiation. For some species (*Symphodus roissali*, *S. tinca*, *Chromis chromis* and *Lipophrys trigloides*), we observed that increment deposition in laboratory-reared larvae started on the first day of hatching (Macpherson & Raventos 2005, Raventos & Macpherson 2005).

PLD was estimated from 2389 otoliths from 59 littoral species. We also considered data obtained in previous papers (Vigliola 1998, Raventos & Macpherson 2001). In all, we examined 62 species (3046 otoliths) belonging to 13 families (see Table 1).

For each species we examined: mean, minimum and maximum PLD; the spawning strategy (benthic or pelagic broadcast spawners); larval distribution (inshore

or offshore waters); the season of pelagic larval life; and the geographic distribution range (Table 1). We collected spawning type and geographic range size information for each species from Whitehead et al. (1986) and the FishBase data bank (www.fishbase.org/home.htm). The larval distributions of both inshore (<100 m depth) and offshore (>100 m depth) plankton were collected from different studies covering the coastal area and continental shelf and slope of the north-west Mediterranean. Such studies were carried out over several years, and included Sabatés (1990) and Sabatés et al. (2003) and references therein (additional information was obtained from A. Sabatés pers. comm.). The distinction between inshore and offshore zones was made by differences in physical oceanography between the 2 habitats, and was based primarily on the distance from the shore. Inshore waters are dominated by waves and bottom stress and have slower alongshore flows (Largier 2003). Shanks & Eckert (2005) used the inshore area (<30 m depth) and shelf/slope (>30 m depth) to separate species by adult habitat. These authors used the 30 m isobath because each group of fishes released larvae into water with different oceanographic conditions. However, in the present study, as a narrow coastal shelf characterizes the study area, we used a more conservative distance (the location of the 100 m isobath) for larval distribution. The season of each species' larval pelagic life was estimated using the PLD and settlement period (see Garcia-Rubies & Macpherson 1995, Raventos & Macpherson 2001, and present data). Most species only spawn in one season. However, for those species that spawn in 2 seasons (e.g. *Lipophrys trigloides* in late autumn and winter; *Sarpa salpa* in spring and autumn) we considered only the season in which most larvae were found (Garcia-Rubies & Macpherson 1995, Macpherson & Raventos 2005).

Distribution range size was calculated following the examples of previous studies (Victor & Wellington 2000, Lester & Ruttenberg 2005). We estimated 3 measures of range size: latitudinal range, longitudinal range, and maximum linear surface distance (km) of the furthest 2 points of the known species range. The maximum linear distance was determined from the surface of the globe and not from a flat projection. Adult mobility might influence range distribution independently of early life characteristics. However, most species have littoral benthic habitats and probably do not cross large coastal discontinuities (e.g. between the continent and islands). Only atherinids show pelagic behaviour, mostly along the littoral zone.

We regressed all range size measurements against PLD. In all analyses, measurements were log-transformed to attain normality. Analyses were conducted: (1) using all data; and (2) by limiting analyses to sam-

Table 1. Pelagic larval duration (mean, SD, maximum and minimum) in days, and maximum geographic range of littoral species in the Mediterranean Sea; N = total no. of ind., Np = no. of ind. from previous papers (Vigliola 1998 [*] and Raventos & Macpherson 2001). Distribution of each species in biogeographic provinces is listed. NECS = Northeast Atlantic Continental Shelf (50–65°N), CNRY = Canary Current Coastal (20–50°N), GUIN = Guinea Current Coastal (15°S–20°N), MAC = Macaronesian Islands (25–40°N; see Macpherson 2002); I = inshore (<1 mile) larval distribution, O = offshore (>1 mile) larval distribution, B = benthic eggs, P = pelagic eggs; season of planktonic life: W = winter, S = spring, SU = summer, A = autumn

Species	N	Mean	SD	Min.	Max.	Np	Larval dist.	Eggs	Season	NECS	CNRY	GUIN	MAC	Range (km)
Apogonidae														
<i>Apogon imberbis</i>	63	21.3	1.4	18	24	8		B	SU		+	+	+	5480
Atherinidae														
<i>Atherina boyeri</i>	72	10.4	0.9	9	12	17	I	B	SU		+		+	4805
<i>Atherina hepsetus</i>	83	11.4	1.3	9	14	24	I	B	SU		+		+	4384
Bleniidae														
<i>Aidablennius sphyinx</i>	61	41.2	2.5	35	45	11	O	B	SU		+			3625
<i>Coryphoblennius galerita</i>	30	25.8	1.1	24	28	2	O	B	S		+		+	5480
<i>Lipophrys adriaticus</i>	5	23.0	1.7	21	24	2		B	SU					2951
<i>Lipophrys canevei</i>	24	30.7	1.0	28	34	3	O	B	SU					3625
<i>Lipophrys trigloides</i>	299	67.2	10.7	39	89	15		B	W		+		+	4384
<i>Parablennius incognitus</i>	54	23.8	1.6	21	30	10		B	SU		+		+	4384
<i>Parablennius pilicornis</i>	2	28	–	28	28		O	B	S		+	+		7778
<i>Parablennius sanguinolentus</i>	2	33	1.4	32	34	1	I	B	S		+	+		4667
<i>Parablennius zvonimiri</i>	2	24	–	24	24			B	SU					2951
Bothidae														
<i>Arnoglossus thori</i>	14	31.4	3.7	25	39		O	P	A		+			3778
<i>Bothus podas</i>	41	33.7	2.6	28	38		O	P	A		+	+		3889
Clinidae														
<i>Clinitrachus argentatus</i>	53	26.2	1.1	23	29	4		B	S					3625
Gadidae														
<i>Gaidropsarus mediterraneus</i>	1	43	–	43	43	1	O	P	W	+	+			4047
Gobiesocidae														
<i>Apletodon dentatus</i>	21	14.4	0.7	13	15	3	I	B	S		+			2361
<i>Apletodon incognitus</i>	20	14.1	1.1	12	15		I	B	SU					2361
<i>Diplecogaster bimaculata</i>	11	11.8	1.1	10	14		I	B	SU	+	+			3334
<i>Gouania wildenowi</i>	23	13.1	1.6	11	17	1	I	B	SU					2951
<i>Lepadogaster candollei</i>	12	13.2	0.9	12	15	1	I	B	SU	+	+		+	3445
Gobiidae														
<i>Gobius bucchichi</i>	22	19.2	1.0	17	21	10		B	SU		+			4047
Labridae														
<i>Coris julis</i>	75	28.1	3.6	21	34	23	O	P	SU	+	+	+	+	7223
<i>Ctenolabrus rupestris</i>	66	20.9	2.0	18	28	12	I	P	S	+	+			4445
<i>Labrus viridis</i>	22	31.3	2.5	27	35	1	I	B	S		+			3625
<i>Symphodus cinereus</i>	54	11.6	1.0	10	14	3	I	B	SU		+			3625
<i>Symphodus doderleini</i>	56	13.0	0.9	11	15	3	I	B	SU					3372
<i>Symphodus mediterraneus</i>	72	13.6	1.1	11	16	9	I	B	SU					3625
<i>Symphodus melops</i>	2	15.0	0.0	15	15	2	I	B	S	+	+		+	3334
<i>Symphodus ocellatus</i>	220	10.1	1.1	8	13	23	I	B	S					3372
<i>Symphodus roissali</i>	292	12.6	1.6	9	18	106	I	B	S					3625
<i>Symphodus rostratus</i>	10	14.8	1.6	13	17	2	I	B	S					3372
<i>Symphodus tinca</i>	82	10.8	1.0	9	13	4	I	B	S					3625
<i>Thalassoma pavo</i>	71	38.9	5.2	30	48	11	O	P	SU		+		+	5480
<i>Xyrichtis novacula</i>	33	34.2	6.0	28	55	1		P	A		+	+		4445
Mullidae														
<i>Mullus surmuletus</i>	52	30.1	2.1	28	35		O	P	S		+			4047
Pomacentridae														
<i>Chromis chromis</i>	425	18.6	1.6	15	25	17	O	B	SU		+	+		5556
Sciaenidae														
<i>Sciaena umbra</i>	3	22.5	0.7	22	23			P	S		+		+	4890
Scorpaenidae														
<i>Scorpaena porcus</i>	1	29	–	29	29	1	O	P	S		+		+	5901
<i>Scorpaena scotra</i>	1	25	–	25	25		O	P	S		+		+	5901

Table 1 (continued)

Species	N	Mean	SD	Min.	Max.	Np	Larval dist.	Eggs	Season	NECS	CNRY	GUIN	MAC	Range (km)
Serranidae														
<i>Epinephelus marginatus</i>	21	24.6	1.3	22	30		O	P	SU		+	+	+	10001
<i>Serranus cabrilla</i>	54	24.3	1.8	21	28	3	O	P	S		+	+	+	9445
<i>Serranus hepatus</i>	22	18.0	0.9	16	22		O	P	SU		+		+	2223
<i>Serranus scriba</i>	12	28.2	1.6	26	32		O	P	S		+	+	+	9445
Sparidae														
<i>Boops boops</i>	23	16.9	0.9	16	20	14	O	P	SU	+	+	+	+	6112
<i>Diplodus annularis</i>	74	18.3	1.4	16	21	15	O	P	SU		+		+	4468
<i>Diplodus cervinus</i>	3	18.3	1.5	17	20	1	O	P	S		+		+	4890
<i>Diplodus puntazzo</i>	80	32.7	4.8	19	48	80*	O	P	A		+	+	+	4805
<i>Diplodus sargus</i>	80	27.6	4.3	19	37	80*	O	P	S					4047
<i>Diplodus vulgaris</i>	80	40.8	5.7	29	58	80*	O	P	W		+	+	+	5889
<i>Oblada melanura</i>	55	16.2	1.3	14	18	25	O	P	SU		+	+	+	5556
<i>Pagellus erythrinus</i>	10	43.9	2.8	40	49		O	P	S	+	+		+	4384
<i>Pagrus pagrus</i>	1	38	–	38	38	1	O	P	S		+		+	4384
<i>Sarpa salpa</i>	74	31.7	2.5	27	38	11	O	P	W		+		+	4778
<i>Spondyliosoma cantharus</i>	12	33.7	2.9	29	38	2	O	B	S	+	+	+	+	7556
Syngnathidae														
<i>Nerophis ophidion</i>	2	21.5	0.7	21	22		I	B	S	+	+			4047
<i>Syngnathus typhle</i>	2	15.0	0.0	15	15		I	B	S	+	+			4047
Trachinidae														
<i>Trachinus draco</i>	10	12.9	0.7	12	14		O	P	SU	+	+		+	4805
Triglidae														
<i>Trigla lucerna</i>	12	19.1	1.2	18	21		O	P	W	+	+			5001
Tripterygiidae														
<i>Trypterygion delaisi</i>	25	17.3	1.1	16	21	3	I	B	S		+			3625
<i>Trypterygion melanurus</i>	53	17.6	2.3	15	25	6	I	B	S					3625
<i>Trypterygion tripteronotus</i>	39	18.4	2.8	16	27	5	I	B	S					3625

ples that comprised over 20 ind. per species (Victor & Wellington 2000, Lester & Ruttenberg 2005). A Bonferroni correction was used to correct for multiple comparisons.

PLD differences among species with different spawning strategies (benthic and pelagic spawners), larval distributions (inshore and offshore), and seasons of planktonic life were tested using ANOVA. We also compared differences between Medi-terranean endemic and non-endemic species, and between species that have colonized oceanic islands (the Macaronesian Islands: Azores, Madeira and Canaries) and those that are only distributed along the continental coast. These islands are situated at ca. 1880, 760 and 100 km from the nearest continental coast, respectively. Mediterranean endemic species are defined as those living in the Mediterranean and waters around the Straits of Gibraltar (Gulf of Cadiz and north-west Morocco). We used the full dataset (using counts of individual otoliths), but only included species with more than 5 individuals. We ran these tests as nested ANOVAs, nesting species within type (e.g. inshore or offshore larvae, benthic or pelagic spawner) as a random factor. A Bonferroni correction was used to account for multiple tests of these analyses.

We also tested whether larval distributions and spawning characteristics of the species were related to their distribution range size. Pairwise comparisons (*t*-tests) were used to compare maximum geographic range sizes of species with inshore vs. offshore larvae, and benthic vs. pelagic eggs.

RESULTS

The life traits of the 62 species (Table 1) showed that 35 species produce demersal eggs and 27 are pelagic spawners; 23 species were identified to have inshore larvae, whereas 30 species were identified to have offshore larvae (data were not available for 9 species). Most species with inshore larvae (92%) were benthic spawners. The larvae of most species had their planktonic period in spring (28 species) and summer (25 species). Four species had their planktonic period in autumn, and 5 in winter. Eighteen species were endemic to the Mediterranean, and 28 species can be found in the Macaronesian Islands.

Correlation results showed that all 3 geographic range measurements were highly significant: $r = 0.89$ and 0.83 ($p < 0.0001$) for maximum linear distance vs. longitudinal

and latitudinal range, respectively; 0.62 ($p < 0.0001$) for longitudinal vs. latitudinal range. Therefore, in accordance with Lester & Ruttenberg (2005), we used maximum linear distance as the measure of a species' geographic extent. Correlations between mean PLD vs. maximum and minimum PLD were also highly co-linear (0.94 and 0.89, $p < 0.0001$, respectively). We used mean PLD as the measure of a species' pelagic larval duration (Victor & Wellington 2000).

The relationship between PLD and geographic ranges was positive across species (and thus significant; $r = 0.30$, $p < 0.01$). However, this only explained a low proportion of variance (Fig. 1). When analyses were limited to samples comprised of over 20 ind. per species, the relationship was positive but non-significant (Table 2). However, values differed between families; they were highly positive and significant for Labridae ($r = 0.65$, $p = 0.01$) and non-significant for Blenniidae and Sparidae. A significantly positive relationship was also observed in those species with benthic spawning strategies ($r = 0.36$, $p = 0.003$; Table 2). The other relationships were non-significant after Bonferroni correction. We considered these 2 relationships (spawning strategies and larval distributions) separately. However, benthic spawners have predominantly inshore larvae, and pelagic spawners mostly offshore larvae (Table 1).

Species with inshore larvae exhibited a shorter PLD (mean = 13.4 d) than species with offshore larvae (mean = 26.3 d, ANOVA, $p < 0.001$). Furthermore, mean PLD was shorter for benthic spawners than for

pelagic spawners. PLD was also shorter for Mediterranean endemic species than for non-endemics. However, the results were not significant after Bonferroni correction (Table 3). The species that have colonized oceanic islands (the Macaronesian Islands: Azores,

Table 2. Correlation analyses of PLDs and distribution ranges, using maximum linear distance (km). Analyses include all species (left columns) and those with sample sizes >20 ind. (right columns). N = number of species, ns = not significant (p-values calculated after Bonferroni correction)

	N	R	p	N	R	p
	All			>20 ind.		
All species	62	0.30	0.01	38	0.27	ns
Families						
Blenniidae	9	0.02	ns	5	0.28	ns
Labridae	13	0.65	0.01	11	0.64	0.03
Sparidae	11	-0.06	ns	7	-0.16	ns
Ecological characteristics						
Inshore larvae	23	0.23	ns	16	0.28	ns
Offshore larvae	29	-0.02	ns	16	-0.04	ns
Benthic eggs	35	0.36	0.003	20	0.43	ns
Pelagic eggs	27	-0.03	ns	18	-0.03	ns
Endemics	18	0.26	ns	15	0.40	ns
Non-endemics	44	0.24	ns	23	0.13	ns
Macaronesian colonizers	38	0.25	ns	17	0.01	ns
Non-colonizers	24	0.29	ns	21	0.37	ns

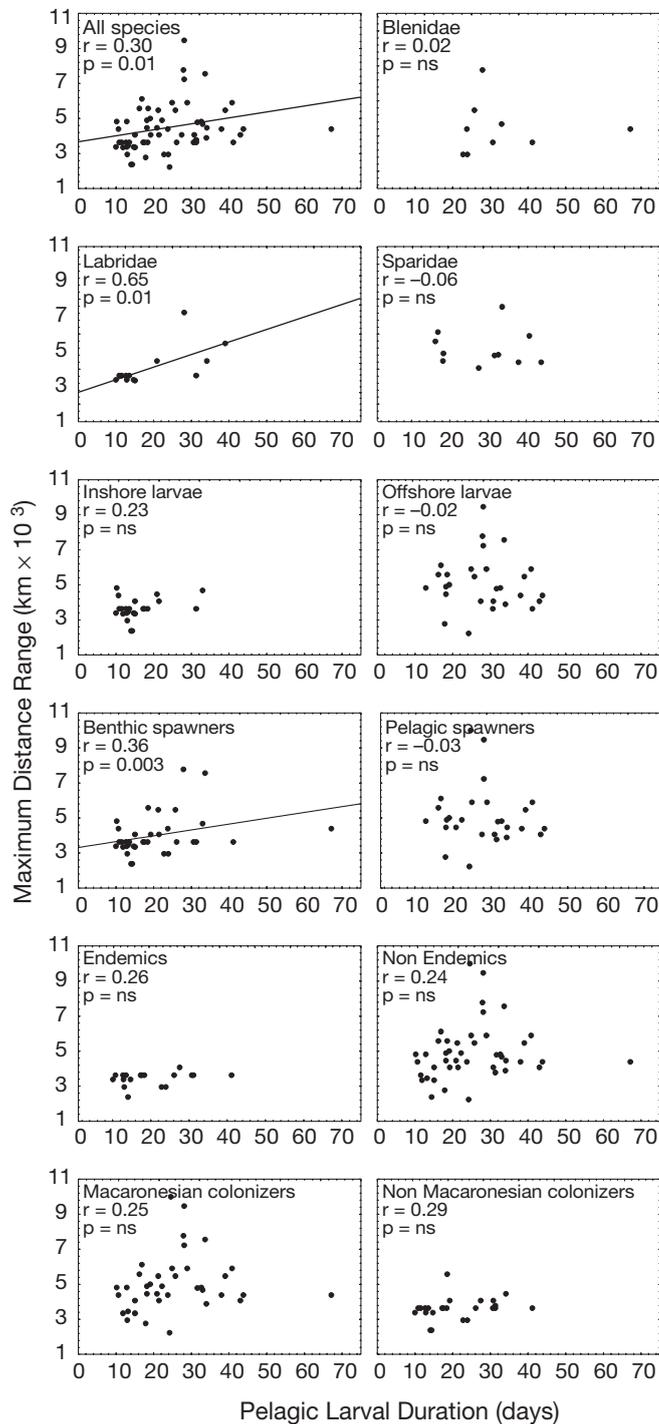


Fig. 1. Relationships between mean planktonic larval duration (PLD) and maximum geographic range for different groups of species. ns = not significant

Table 3. PLD differences among species, taking into account ecological distribution characteristics. Values are results of nested ANOVAs using the full dataset (counts of individual otoliths) excluding species with <5 ind. Species within type (e.g. inshore or offshore, benthic or pelagic eggs) are used as a random factor. N = number of species, NO = number of otoliths, *a*, *b*, *c* = post hoc Newman-Keuls test results (p-values calculated after Bonferroni correction)

Group	N	NO	Mean PLD	SD	MS	F	p
Inshore larvae	19	1150	13.4	4.12	8046.1	13.08	<0.001
Offshore larvae	23	1388	26.3	8.87			
Benthic eggs	30	2135	23.9	19.1	30146.3	0.44	0.509
Pelagic eggs	22	959	28.4	8.5			
Mediterranean endemics	18	1140	16.7	8.6	38251.2	3.49	0.067
Non-endemics	34	1954	30.3	18.1			
Macaronesian Is. colonizers	28	1356	34.7	19.9	32429.9	6.62	0.013
Non-colonizers	24	1738	17.9	8.0			
Winter (<i>a</i>)	4	465	55.8	18.8	15408.2	11.68	<0.001
Spring (<i>b</i>)	19	1174	18.8	9.3			
Summer (<i>b</i>)	25	1287	19.2	6.9			
Autumn (<i>c</i>)	4	168	33.2	4.6			

a > *c* > *b*

Madeira and the Canaries) had significantly longer PLDs than those living exclusively along the European and African coasts.

Species characterised by planktonic life in spring and summer showed a significantly shorter PLD (mean = 18.8 and 19.2 d, respectively) than those developing in winter (mean = 55.8 d) and autumn (mean = 33.2 d) (Table 3). All species found in winter and autumn (except *Lipophrys trigloides*), in periods with strong winds and changes in the direction of flow had an offshore distribution and pelagic eggs (Table 1).

Finally, mean geographic range was clearly smaller for species with inshore larval distributions than for species with offshore larval distributions (*t*-test, $p < 0.001$). However, species with benthic eggs had range sizes smaller than those of pelagic spawners (*t*-test, $p < 0.001$; Table 4). To further explore the relationship among geographic range, larval distribution and spawning characteristics, we examined the relationship between residuals from regressions of PLD against range size. These residuals (factoring out PLD) were also significantly related (for inshore-offshore larvae, *t*-test: $t = -2.668$, $df = 50$, $p = 0.01$; for benthic-pelagic eggs: $t = -2.985$, $df = 60$, $p \leq 0.004$). This further supports the notion that some factors that are correlated with spawning characteristics and larval position act as important controls on geographic range size.

DISCUSSION

We observed a weak, positive relationship between PLD (as a proxy of potential dispersal) and distribution range of Mediterranean littoral fishes. Species with a long PLD tended to have a larger geographic range than those with a short PLD. This supports the results of some studies on tropical reef fishes (e.g. Zapata & Heron 2002, Lester & Ruttenberg 2005). However, the low proportion of variance accounted for by this relationship suggests that PLD is not a strong predictor of the distribution range size. Other mechanisms may also influence the distribution patterns exhibited by fishes.

Lester & Ruttenberg (2005) suggested that the positive relationship between PLD and range size in Indo-Pacific reef fishes is generated by species with long PLDs that can cross dispersal barriers. In our study, species whose ranges extend to oceanic islands (Azores, Madeira,

Canaries) have significantly longer larval durations. This suggests that there is a certain relationship between PLD and island colonization capabilities (Victor & Wellington 2000, Zapata & Heron 2002). Furthermore, endemic Mediterranean species usually have a short PLD and small geographic ranges. They mostly cluster in the lower-left corner of each plot, and may also be the cause of the significance of this relationship.

Endemic Mediterranean species showed different characteristics to those in isolated islands in the tropics, e.g. PLDs in the Mediterranean were clearly shorter than those in these islands (Robertson 2001). Most insular, endemic tropical water species have PLDs of around 1 mo or more (Victor & Wellington 2000). This is clearly longer than that of most Mediterranean endemics. For instance, endemic Mediterranean labrids

Table 4. Pairwise comparisons (*t*-test) among maximum distribution ranges (Max. distr., km) of species, taking into account their ecological characteristics. Analyses include all species (left columns) and those with sample sizes >20 ind. (right columns). N = number of species (p-values calculated after Bonferroni correction)

Group	N	Max. distr.	p	N	Max. distr.	p
	All	Mean		SD	>20 ind.	
Inshore larvae	23	3679	628	16	3641	688
Offshore larvae	29	6104	2055	16	6345	2033
Benthic eggs	32	4058	1511	20	3762	799
Pelagic eggs	30	5964	2008a	18	6494	2070

$p < 0.001$ (for Inshore vs Offshore larvae and Benthic vs Pelagic eggs)

have PLDs that are significantly shorter (mean = 19.7 d) than labrids from the eastern Pacific (mean = 46.6 d, *t*-test, $p < 0.0001$) (Victor & Wellington 2000). Furthermore, other Mediterranean endemics belong to taxa with PLDs that are shorter than 1 mo and that have inshore larvae (e.g. *Gobiesocidae*, *Tripterygiidae*). The PLDs of Mediterranean nearshore fishes are also shorter than those of other temperate nearshore fishes, e.g. California Current species (Shanks & Eckert 2005).

The source of these differences is not easy to explain. However, the characteristics of the Mediterranean littoral fishes and their distribution patterns can be influenced by events that are not directly related to PLD, e.g. historical processes. Such processes (e.g. the closing and opening of the Mediterranean Sea and periodic glaciation events over the past 1 million yr) have favoured speciation events and the geographic distribution of numerous extant species in the North Atlantic (Mix et al. 2001). These historical processes have conditioned endemism, e.g. as exhibited by labrids (Hanel et al. 2002). They have also affected species flow, both between oceanic islands and mainland areas, and between Mediterranean and Atlantic basins (Bargelloni et al. 2003). The effects of these processes can be observed in the gene flow between fish populations from mainland areas and oceanic islands. Genetic studies have demonstrated that short-PLD species from oceanic islands (e.g. *Tripterygion delaisi*) were isolated by such climatic fluctuations (Carreras-Carbonell et al. 2005). Other species with longer PLDs could capitalize on an unobstructed gene flow between mainland areas and oceanic islands (Muss et al. 2001). Although genetic studies on this topic remain scarce, findings suggest that historical processes should be taken into account when comparing potential dispersal abilities and distribution ranges (Heads 2005).

The results obtained using residuals and factoring out PLD showed that range size distributions can be controlled by larval position and spawning strategies. Armsworth et al. (2001) showed that incorporation of larval biology and behavioural considerations into dispersal models markedly changes their predictions. Additionally, larvae residing near the bottom disperse short distances, thus affecting predictions from PLD (Shanks et al. 2003). The larval behaviour of Mediterranean species is mostly unknown, and further studies may clarify its influence on dispersal capabilities. Furthermore, species with larvae situated inshore showed shorter PLDs and smaller ranges than species with larvae situated offshore. Larvae from demersal eggs are usually more abundant inshore, whereas larvae from pelagic spawners are more common offshore (Sabatés 1990, Suthers & Frank 1991, but see Hickford & Schiel 2003). As different authors have pointed out (Blaxter 1986), pelagic eggs produce smaller larvae with less-

developed sensory systems and poorer swimming abilities. Indeed, they usually require a longer planktonic period to reach settlement size. This combination of factors, together with stronger transport events offshore (Tintore et al. 1995), may make retention less likely for these larvae. This leads to higher dispersion capabilities and larger geographic range sizes.

The differences in life history traits of species that have planktonic larvae in spring-summer or in autumn-winter suggests that these species were well adapted to local oceanography, as indicated by Shanks & Eckert (2005) for California Current species. Mediterranean species that have their planktonic life in autumn and winter had significantly longer PLDs than those developing in spring and summer. The spawning and planktonic life of most littoral species in the Mediterranean takes place in spring and summer, when water temperature and phyto- and zooplankton productivities are higher (Estrada et al. 1985). These environmental conditions are more favourable for larval survival. Furthermore, the wind regime in spring-summer (low inshore winds) facilitates the closure of the pelagic phase of larvae with short PLDs. Larvae with PLDs shorter than 2 wk (most inshore larvae) would have great difficulties in surviving and returning to settlement habitats in offshore wind conditions (e.g. winter). Furthermore, wind conditions have significant effects on the spawning strategies of the species. The reproductive season of most benthic spawners is in late spring and summer, when strong winds are less frequent and their negative effects on nests lower (Raventos & Macpherson 2005). As Shanks & Eckert (2005) pointed out, the early life traits of the species may show an adaptation to the local oceanography to avoid alongshore loss of larvae, thus promoting settlement of larvae into their parental habitats. This trend was observed in Mediterranean littoral fishes in the present study, and suggests that the hypotheses made by Sinclair (1988) and Shanks & Eckert (2005) for California Current species could be extrapolated to other areas.

In conclusion, PLD is not a strong predictor of the range size distribution of Mediterranean littoral fishes. The positive relationship between these 2 variables can be generated by: species with long PLDs, which can cross the few barriers to dispersal (Macaronesian Islands), and Mediterranean endemic species, with short PLDs. These results agree with those observed in the Indo-Pacific tropical reef system (Lester & Ruttenberg 2005). However, the range size distribution of fishes is not only controlled by PLDs. The inshore/offshore position and season of planktonic life play an important role in ensuring the return of larvae to their settlement habitats. Consequently, these factors also affect a species' distribution range size.

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