META-ANALYSIS

Pelagic propagule duration and developmental mode: reassessment of a fading link

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ABSTRACT

Aim As the main or sole motile stage of many aquatic taxa, propagules play a central role in their population dynamics, macroevolution and biogeography. The premises of studies concerned with dispersal, on issues as diverse as marine protected areas, sustainable fisheries and invasive species, commonly make simplified assumptions linking larval development mode (planktotrophic, lecithotrophic) and pelagic propagule duration (PPD) or pelagic larval duration. Because general empirical tests of these connections have yielded equivocal results, we critically examined the relationship between larval mode and PPD in light of regional and taxon-specific criteria.

Location Oceans world-wide.

Methods We collated data from 190 species from the phylum Echinodermata and used two-way and one-way ANOVA to compare PPD among larval modes, taxonomic classes, geographic regions and climate zones. We also assessed the contribution of egg size, temperature and other continuous predictors using multiple regressions and ANCOVA, and examined whether geographic range size differed among larval modes.

Results Our results depart from the common assumption that planktotrophs have longer PPDs than lecithotrophs. Instead, we detected a synergistic influence of phylogeny and climate. No significant difference in PPD between planktotrophs and lecithotrophs occurred in two of the four classes and only four out of nine major ocean basins contained species with significantly different PPDs on the basis of larval mode. Species from colder climates displayed relatively constant PPDs regardless of larval mode, whereas temperate and warm-water species displayed a clearer dichotomy. PPD did not correlate with geographic range size nor did planktotrophs and lecithotrophs exhibit significantly different range sizes.

Main conclusions Our findings indicate that larval mode is not a reliable predictor of PPD across broad geographic and taxonomic scales. Instead developmental strategies may instigate shorter or longer PPDs in schemes that are influenced by evolutionary and environmental pressures.

Keywords

Benthic invertebrates, dispersal, echinoderms, larval development, lecithotrophy, oceans, planktotrophy, propagules, range size, reproductive strategy.

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INTRODUCTION

Early life-history strategies, and larval ecology in particular, have a critical role in our understanding of the maintenance and dynamics of marine benthic populations. While these topics have long inspired fundamental research (Young, 1990), a fresh interest in the characteristics of early life stages is being fuelled by novel motivations related to the threat of invasive species, the

sustainable management of fisheries, the design of conservation measures and the impact of climate change (Levin, 2006; Cowen & Sponaugle, 2009). The literature is filled with examples of the functional role and ecological significance of propagules in a diversity of marine taxa (e.g. Hughes *et al.*, 2008; Rius *et al.*, 2010) and their role in population persistence and ecological resilience.

Marine benthic invertebrates display a rich array of larval forms and functions. Among species with development via a pelagic stage, this diversity is often simplified to a dichotomy between two developmental, or nutritional, modes: feeding (planktotrophy) and non-feeding (lecithotrophy). While a number of intermediate larval forms exist in some phyla (Allen & Pernet, 2007), the planktotrophy–lecithotrophy dichotomy remains useful when considering the general implications of life-history patterns in marine invertebrates.

In this context, the relationships between larval development mode (hereafter larval mode), egg size and egg-to-juvenile period (EJP), often equated to pelagic larval duration (PLD), have been the subject of much theoretical debate (Vance, 1973; Emlet *et al.*, 1987; Strathmann, 1987; Havenhand, 1993; Emlet, 1995; Levitan, 2000). The long-held paradigm has been that larval modes and pelagic propagule duration (PPD, i.e. combined embryonic and larval development times) are correlated, and that pelagic and non-pelagic lecithotrophs are less dispersive than planktotrophs (Calow, 1983; Jablonski & Lutz, 1983; Emlet *et al.*, 1987; Strathmann, 1987; Emlet, 1995; O'Connor *et al.*, 2007). This simple prediction has been questioned (Young *et al.*, 1997), as has the notion that pelagic larvae and the length of PLD are directly or exclusively linked to dispersal (Paulay & Meyer, 2006; Strathmann, 2007; Shanks, 2009; Weersing & Toonen, 2009). Recent studies have shown that PLD is not a general determinant of a species' geographic range size (Lester *et al.*, 2007), and is a poor predictor of both the level of variation in population fluctuation (Eckert, 2003) and the magnitude of gene flow and geographic scale of population structure in marine invertebrates, i.e. PLD is poorly correlated with F_{ST} (Weersing & Toonen, 2009) but shows a higher correlation ($r^2 \sim$ 0.3) with 'isolation-by-distance' (IBD) slope or global F_{ST} (Selkoe & Toonen, 2011).

Nevertheless, oversimplified assumptions about the relationship between egg size, larval mode and dispersal are often included in the introductions of papers that focus on larval ecology and life-history strategies (e.g. Jeffery & Emlet, 2003; Botello & Krug, 2006; Allen & Pernet, 2007; Moran & McAlister, 2009). The 'widely accepted' assertion is that species with small eggs have long-lived planktonic larvae that disperse broadly, whereas species with large eggs tend to have non-feeding larvae with a short planktonic existence and reduced dispersal potential. It has even been recently proposed that 'for marine invertebrates, passive dispersal via planktotrophic larvae represents the most effective means of achieving long-distance transport' (Rundle *et al.*, 2007).

The present study, which combines a thorough review, a critical assessment of the literature and presentation of new empirical data, has two main aims. Firstly, we wish to uncouple the

assumptions about larval mode and dispersal potential by assessing whether species with feeding and non-feeding larvae exhibit consistently longer or shorter PPDs, and whether the length of the obligate non-feeding embryonic phase (to gastrula) is correlated to PPD. Secondly, we examine the relationship between larval mode and PPD (with and without covariates) in the light of regional and taxon-specific criteria, and we probe the link between larval mode and range size to identify key trends and formulate new hypotheses with respect to the significance of the pelagic propagule phase in benthic macroinvertebrates. Recent studies on PPD-related questions have either been carried out at the subphylum level, mainly using fish, or across extreme taxonomic scales, i.e. kingdoms and phyla (Lester *et al.*, 2007; O'Connor *et al.*, 2007; Bradbury *et al.*, 2008; Shanks, 2009; Weersing & Toonen, 2009; Selkoe & Toonen, 2011). Here we adopted an intermediate position that allowed us to obtain complete multi-parameter data sets for a sizeable number of species spanning a relatively broad taxonomic range (a whole phylum). We focused on the Echinodermata because its representatives are ubiquitous in the marine environment and display a rich diversity of reproductive patterns.

METHODS

Data collection

We collected published time series of embryonic and larval development for 190 species of echinoderms (64 Echinoidea, 70 Asteroidea, 39 Holothuroidea, 16 Ophiuroidea, 1 Crinoidea) with different larval modes (Table S1 in Supporting Information). Further data selection was undertaken to obtain single values for species that were studied by multiple investigators. (1) In general, we used the most complete data set, with the greatest details on development, location and rearing temperature. (2) For comparably complete data sets from the same location, we used either the most recent data, when the interval between investigations was significant, or the mean values when it was not. (3) Multiple values for a species were kept only when similarly detailed data were obtained from distinct regions or for distinct larval modes in that species. New empirical data were also collated for under-represented temperate-cold species (see methods and data in Table S1). Subsets of data were used in the different analyses, i.e. those entries for which the specific parameters required (e.g. egg size, time to gastrula, latitude, temperature) were available, as indicated in the Results.

Range size

Studies often try to establish links between PPD (viewed as a proxy of dispersal) and species geographic ranges (e.g. Lester *et al.*, 2007). Here we also examined whether range sizes differ significantly between planktotrophs and lecithotrophs, both globally and separately, in species with long (> 30 days) or short PPDs. For this analysis we could only use available databases on geographic occurrences, which are subject to two caveats: (1) taxonomic issues (misidentification) that lead to erroneous

distribution ranges; and (2) the potential impact of evolutionary time (planktotrophy is considered to be the ancestral developmental mode, and thus species with this mode may have had a longer time to extend their range). Additionally, this type of analysis cannot consider extinction or extirpation events that may have occurred or the potential differences in fecundity among reproductive strategies.

Data on species distributions were obtained from the World Register of Marine Species (Appeltans *et al.*, 2010) and the Ocean Biogeographic Information System (OBIS, 2010). We used the extent of occurrence as a proxy for range size, and measured it in two ways: (1) the distance between the outermost limits of occurrence, calculated using the 'measure line' tool of Google Earth (Google Inc., Menlo Park, CA, USA), and (2) the area that encloses the limits of the range (Gaston, 1996), calculated with Google Planimeter (http://www.acme.com/planimeter).

Data analysis

Assumptions of normality and homogeneity of variance were verified using normal probability plots of data and residuals, and predicted versus residual scores; data were transformed using natural log (ln) if necessary. PPDs were compared with two-way analyses of variance (ANOVAs; class, larval mode), using Student–Newman–Keuls (SNK) post hoc tests where appropriate. This was done on the complete data set (including NP, non-pelagic development; LP, lecithotrophic pelagic; PP, planktotrophic pelagic), and then restricted to species of known origin with pelagic development (LP; PP). A final subset was retained where time to gastrula was available, to separately test PPD and PLD. The determinants of PPD were explored by adding relevant predictors (egg size, temperature, latitude) as covariates in ANCOVAs (after verifying within-group distributions and slopes of each covariate). Results led to class-specific analyses in which comparisons between PP and LP were made on the basis of egg size, temperature and time to gastrula using *t*-tests or Mann–Whitney rank sum tests (where unequal variance could not be corrected). Relationships between egg size and time to gastrula and PPD, and between PPD and temperature and latitude were probed using Spearman's rank correlation. Multiple linear regressions were used to assess the combined effects of temperature and egg size on PPD (after verifying the absence of collinearity between predictors). Analyses were also conducted based on regions (Table S2), climate zones (tropical, temperate-warm, temperate, temperate-cold, polar; defined in Results) and range size. Data analysis was conducted using the software STATISTICA 10 (StatSoft, Inc.).

RESULTS

The initial data set comprised 228 entries from 190 species (Table S1). As per the data selection criteria (Table S1), the full data set had 179 entries, including 101 PP, 56 LP and 22 NP (69 Asteroidea, 60 Echinoidea, 36 Holothuroidea, 14 Ophiuroidea; Fig. 1). There was a significant interaction between class and
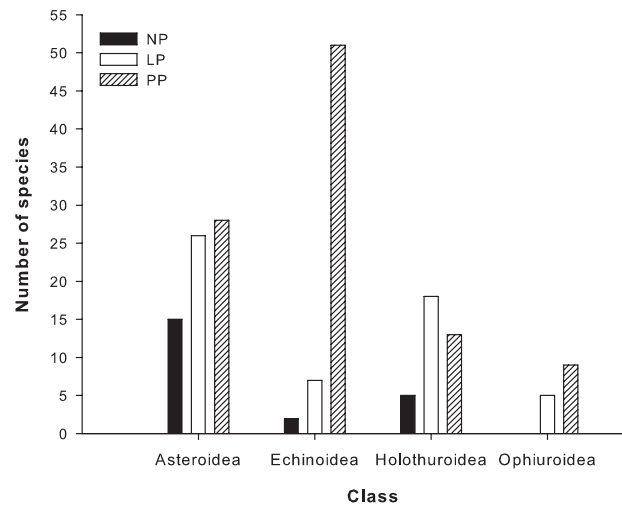

Figure 1 Distribution of species into classes and larval modes (NP, non-pelagic; LP, lecithotrophic pelagic; PP, planktotrophic pelagic) in the main data set ($n = 179$).

larval mode on PPD ($F_{5,168} = 3.38$, $P = 0.006$). Separate one-way ANOVAs and post hoc tests (Fig. 2) revealed: (1) significant differences only between NP and LP in asteroids ($F_{2,66} = 4.01$, $P = 0.023$; SNK, $P = 0.011$); (2) significant differences between LP and the two other larval modes in echinoids ($F_{2,57} = 16.20$, $P < 0.001$; SNK, $P < 0.003$); (3) no significant differences in PPD among larval modes in holothuroids ($F_{2,33} = 1.14$, $P = 0.331$); and (4) significant differences between LP and PP (NP mode absent) in ophiuroids ($F_{1,12} = 22.54$, $P < 0.001$; SNK, $P < 0.001$).

Once narrowed down to the two pelagic larval modes (56 LP; 101 PP), the data set comprised 54 Asteroidea, 58 Echinoidea, 31 Holothuroidea and 14 Ophiuroidea. A graphical illustration of PPD ranges is shown in Fig. 3. This subset still showed a significant interaction between class and larval mode ($F_{3,149} = 4.62$, $P = 0.004$). For further analyses we retained only species where time to gastrula was available ($n = 87$; Table S3) in order to separate the embryonic from the larval phase. Tests on this subset showed consistency with earlier results, i.e. a significant effect of the interaction term (class × larval mode) on PPD ($F_{3,79} = 4.94$, $P = 0.003$), with PP and LP modes showing comparable PPDs in asteroids and holothuroids, and significantly different PPDs in echinoids and ophiuroids (Fig. 4). The same interaction occurred when using shortest PPD instead of mean PPD ($F_{3,79} = 4.25$, $P = 0.008$) or when testing the pelagic larval duration (PLD) consisting of the PPD minus time to gastrula ($F_{3,79} = 4.72$, $P = 0.004$).

ANCOVAs (Table S4) were used in an effort to further tease out mediators of PPD. As expected, egg size was significantly smaller in PP than LP (mean of 136 vs. 530 μm; $t = 9.21$, d.f. = 82, $P < 0.001$). Therefore, distributions of egg sizes within each larval mode differed and regression slopes were highly heterogeneous among larval modes and classes (Fig. S1), prompting the use of a separate slope analysis. This revealed a significant interaction among class, larval mode and egg size on PPD ($F_{8,68} = 2.16$, $P = 0.042$). Slopes of predictor versus PPD were not parallel
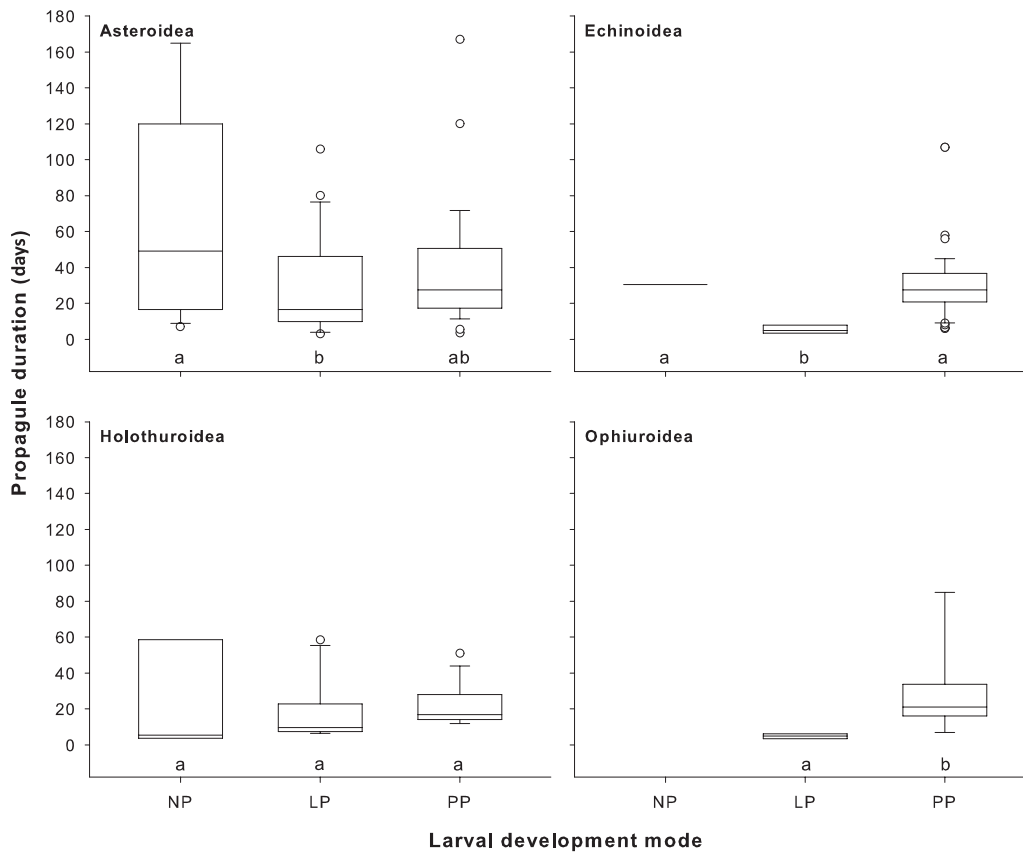
Figure 2 Propagule duration (= PPD for pelagic propagules) in days for the different larval modes (NP, non-pelagic; LP, lecithotrophic pelagic; PP, planktotrophic pelagic) in the four echinoderm classes. Different letters indicate significant differences in mean PPD (see text for statistical results based on ln-transformed data). The upper and lower boundaries of the boxes denote lower and upper quartiles, respectively; the line across the box indicates the median; whiskers show 5th/95th percentiles; open circles are outliers.

among groups for temperature (Fig. S2) and for latitude; results of separate slope analyses showed significant trivariate interactions in both cases (class × larval mode × temperature, $F_{8,64}$ = 11.89, $P < 0.001$; class × larval mode × latitude, $F_{8,68}$ = 4.54, $P < 0.001$). Combining egg size and temperature as covariates confirmed the above-mentioned trivariate interactions and the absence of any other significant effect on PPD (Table S4). Comparable results were obtained when the three continuous predictors (egg size, temperature, latitude) were included as covariates. Combined with the ANOVA results, these findings emphasized the need for taxon-specific and region-specific approaches.

Analysis by class

Table 1 provides a summary of the class-specific results obtained using mean PPD. Asteroidea (16 PP; 13 LP) did not exhibit any significant difference in PPD between larval modes ($t = -1.11$, d.f. = 27, $P = 0.276$). Time to gastrula did not vary significantly between larval modes ($U = 71.50$, $P = 0.160$) but ratio of time to gastrula to PPD was greater in LP than in PP (mean of 11.4 vs. 2.5%; $t = 4.01$, $P < 0.001$). There was no significant difference in rearing temperature between the larval modes ($t = -1.94$, $P =$

0.062). A significant negative correlation between PPD and temperature ($r_s = 0.74$; $P < 0.001$) and a positive correlation between PPD and latitude ($r_s = 0.68$, $P < 0.001$) were found. There was no relationship between egg size and time to gastrula ($P = 0.088$) and no correlation between egg size and PPD ($P = 0.431$). A multiple linear regression showed that both temperature and egg size ($F_{2,25} = 27.54$, $P < 0.001$) accounted for the predicted PPD in this class ($r^2 = 0.69$), although egg size was only influential across pooled larval modes, not within PP ($P = 0.446$) or LP ($P = 0.292$).

Echinoidea (16 PP; 4 LP) showed longer PPDs for PP than for LP (mean of 42 vs. 10 days; $t = 4.60$, d.f. = 18, $P < 0.001$). Time to gastrula was not significantly related to larval mode ($t = -0.19$, $P = 0.849$) but ratio of time to gastrula to PPD was greater in LP than PP (mean of 15.3 vs. 3.2%; $t = -3.94$, $P < 0.001$). Temperature did not differ significantly between larval modes ($U = 16.00$, $P = 0.221$). However, there was a significant negative correlation between PPD and temperature ($r_s = 0.69$, $P = 0.001$) and a positive one between PPD and latitude ($r_s = 0.58$, $P = 0.013$). There was no significant relationship between egg size and time to gastrula ($P = 0.962$) nor between egg size and PPD ($P = 0.061$). A multiple linear regression ($F_{2,15} = 8.40$, $P = 0.004$, $r^2 = 0.53$) revealed that temperature ($P = 0.005$) but not egg size
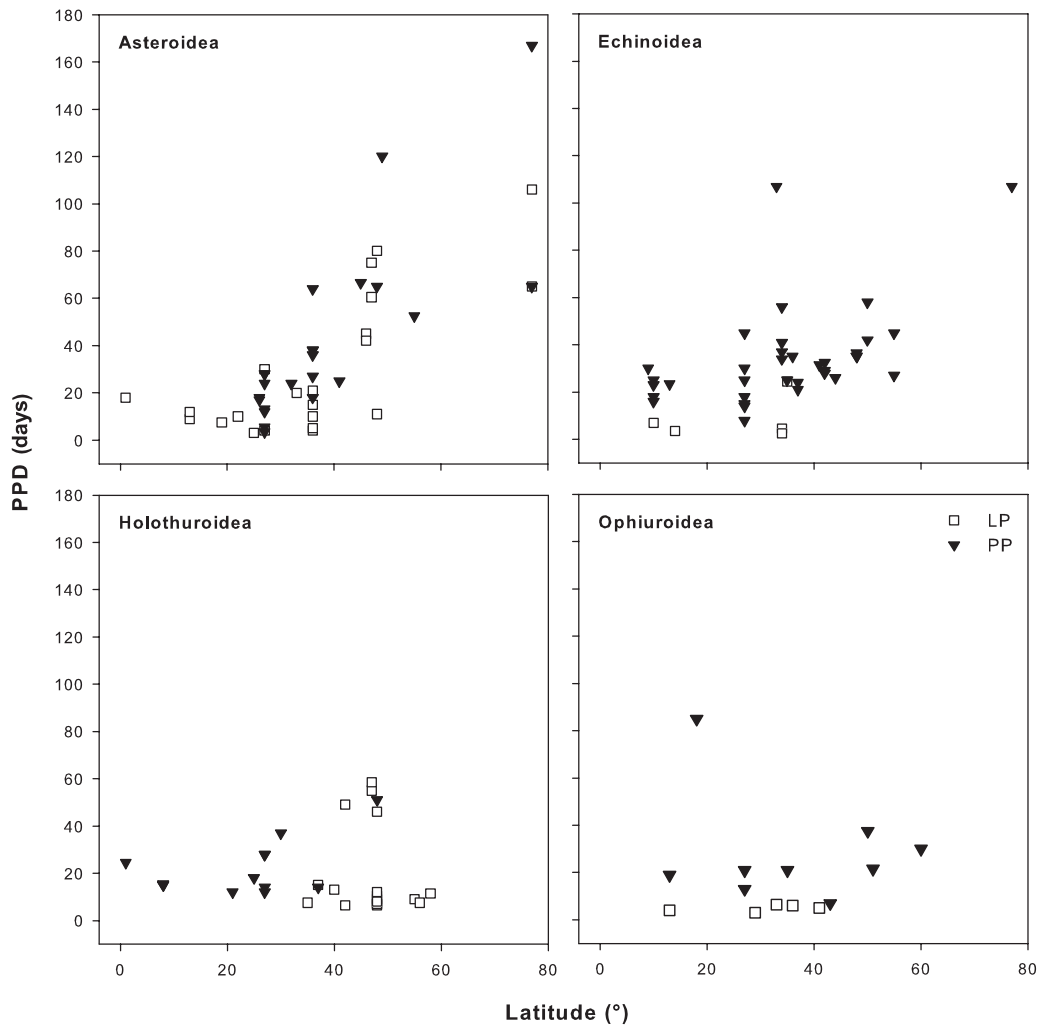
Figure 3 Scatter plots of pelagic propagule duration (PPD) across latitude in the four echinoderm classes. Data for the two main larval modes (LP, lecithotrophic pelagic; PP, planktotrophic pelagic) are shown.

($P = 0.052$) accounted for the predicted PPD. Sample size in LP was too low to examine within-mode results.

In Holothuroidea (11 PP; 14 LP) there was no significant difference in PPD between larval modes ($U = 52.0$, d.f. = 23, $P = 0.180$). Both time to gastrula ($t = -4.66$, d.f. = 23, $P < 0.001$) and the ratio of time to gastrula to PPD ($t = -4.44$, $P < 0.001$) were significantly greater in LP (mean of 64.6 h and 19.2%) than in PP (17.3 h; 4.5%). Furthermore, PP modes were associated with significantly warmer temperatures than PL modes (mean of 25.3 vs. 9.9 °C; $t = 9.73$, d.f. = 19, $P < 0.001$). There was no significant correlation between PPD and latitude ($P = 0.154$), temperature ($P = 0.863$) or egg size ($P = 0.843$), but there was a positive relationship between egg size and time to gastrula ($r_s = 0.61$, $P = 0.002$). A multiple linear regression could not predict PPD using egg size and temperature ($F_{2,16} = 1.60$, $P = 0.232$). Neither factor was a significant predictor of PPD within PP ($P > 0.737$), whereas both factors were significant predictors of PPD within LP ($P < 0.027$).

In Ophiuroidea (10 PP; 4 LP) PPDs were significantly longer in PP than in LP (mean of 34 vs. 5 days; $t = 4.33$, d.f. = 12, $P <$

0.001). Larval mode did not have any effect on time to gastrula ($t = 0.32$, $P = 0.756$), whereas the ratio of time to gastrula to PPD was significantly greater in LP than in PP (mean of 19.9 vs. 4.6%; $t = -4.11$, d.f. = 12, $P = 0.001$). Larval modes did not show a significant difference in rearing temperature ($t = -1.01$, $P = 0.335$). There was no correlation between PPD and temperature ($P = 0.526$) or latitude ($P = 0.197$), nor between egg size and time to gastrula ($P = 0.276$). However, there was a significant negative relationship between egg size and PPD ($r_s = 0.70$, $P = 0.005$). Egg size ($P = 0.002$) but not temperature ($P = 0.204$) was a predictor of PPD in a multiple linear regression analysis ($F_{2,10} = 10.63$, $r^2 = 0.68$). Sample size in LP was too low to examine within-mode results.

In pooled classes (52 PP; 35 LP) PPDs were significantly longer in PP than in LP (mean of 37 vs. 25 days; $t = -3.64$, d.f. = 85, $P < 0.001$). Time to gastrula (obligate non-feeding phase) was significantly longer in LP than PP (87.3 vs. 27.2 h; $U = 551$, $P = 0.002$), as was the ratio of time to gastrula to PPD (15.8 vs. 3.6%; $t = 7.83$, $P < 0.001$). Furthermore, rearing temperatures in LP were significantly lower than in PP (mean of 15.0 vs. 21.0 °C;
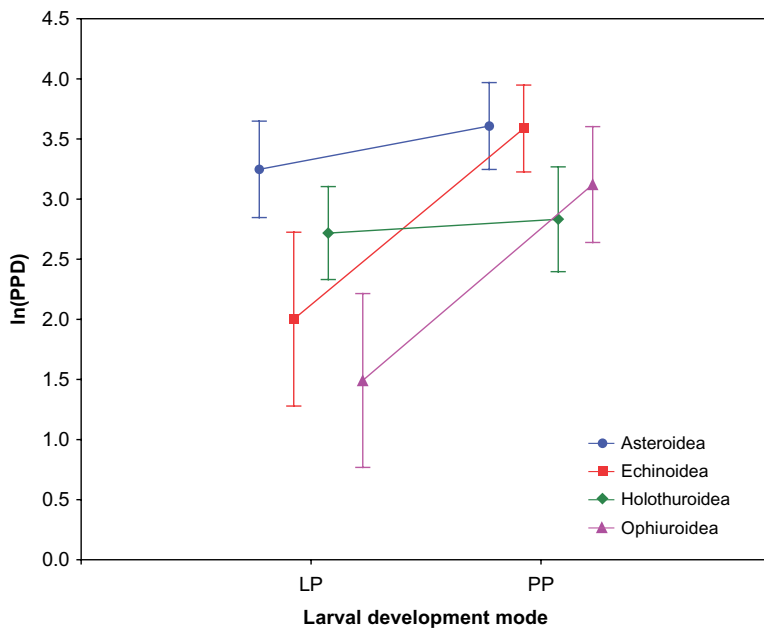
Figure 4 Results of a two-way ANOVA showing significant interaction between class and larval mode ($F_{3,79} = 4.94$, $P = 0.003$) on pelagic propagule duration (PPD) for the two pelagic larval modes (LP, lecithotrophic pelagic; PP, planktotrophic pelagic) within four echinoderm classes. Data are shown as Least Square Mean ± 95% confidence interval. Data points are offset for clarity.

Table 1 Summary of per class analyses on echinoderm species for which pelagic propagule duration (PPD) and time to gastrula were available (*n* = 87). Comparison between planktotrophic pelagic (PP) and lecithotrophic pelagic (LP) larval modes on the basis of PPD, time to gastrula stage, time to gastrula relative to PPD, and temperature at which the PPD was measured. Correlations (positive, negative, absent) between PPD and temperature or latitude and between egg size and time to gastrula or PPD are also shown (see also Figs S1 and S2**).

Class	Comparisons between larval modes				Correlations			
	PPD	Time to gastrula	Time to gastrula relative to PPD	Temperature	PPD versus temperature	PPD versus latitude	Egg size versus time to gastrula	PPD versus egg size
Asteroidea	PP = LP	PP = LP	PP < LP	PP = LP	Negative	Positive	Absent	Absent
Echinoidea	PP > LP	PP = LP	PP < LP	PP = LP	Negative	Positive	Absent	Absent
Holothuroidea	PP = LP	PP < LP	PP < LP	PP > LP	Absent	Absent	Positive	Absent
Ophiuroidea	PP > LP	PP = LP	PP < LP	PP = LP	Absent	Absent	Absent	Negative
Pooled	PP > LP	PP < LP	PP < LP	PP > LP	Negative	Positive	Positive	Absent

= denotes no significant difference; < or > indicate a significant difference and direction of largest mean value.

$U = 473.5$, $P = 0.005$). There was a significant negative correlation between PPD and temperature ($r_s = 0.42$, $P < 0.001$) and a positive correlation with latitude ($r_s = 0.30$, $P < 0.006$). The overall relationship between egg size and time to gastrula was significant and positive ($r_s = 0.32$, $P = 0.003$), but the relationship between egg size and PPD was not ($P = 0.064$). Within larval modes, a significant positive relationship was found between egg size and PPD in LP ($r_s = 0.531$, $P = 0.001$), but not in PP ($P = 0.818$). Both egg size ($F_{2,74} = 16.37$, $P = 0.016$) and temperature ($P < 0.001$) were significant predictors of PPD in a multiple linear regression analysis ($r^2 = 0.31$).

On the whole, patterns associated with larval mode in the Echinodermata do not clearly follow any phylogenetic trend (Table 1). Asteroidea and Holothuroidea showed no correlation between PPD and larval mode, while Echinoidea and Ophiuroidea did. The classes in which differences emerged each had data

sets skewed towards planktotrophs (71% in Ophiuroidea and 80% in Echinoidea), whereas the classes in which no difference in PPD was found had nearly equal representatives of the two modes. Apart from the consistently greater egg size and ratio of time to gastrula to PPD in lecithotrophs than in planktotrophs, the various effects and correlations were often skewed by only one or two classes, and not always the same ones (Table 1).

Analysis by geographic region

The full subset for analysis of PPD among geographic regions (defined in Table S2) comprised 135 entries (84 PP; 51 LP) distributed as shown in Fig. 5(a) and (b). PPD was found to vary significantly amongst the 14 regions ($F_{13,121} = 4.72$, $P < 0.001$). Two-way ANOVAs were conducted on a condensed subset that included only the regions with at least five species and repre-
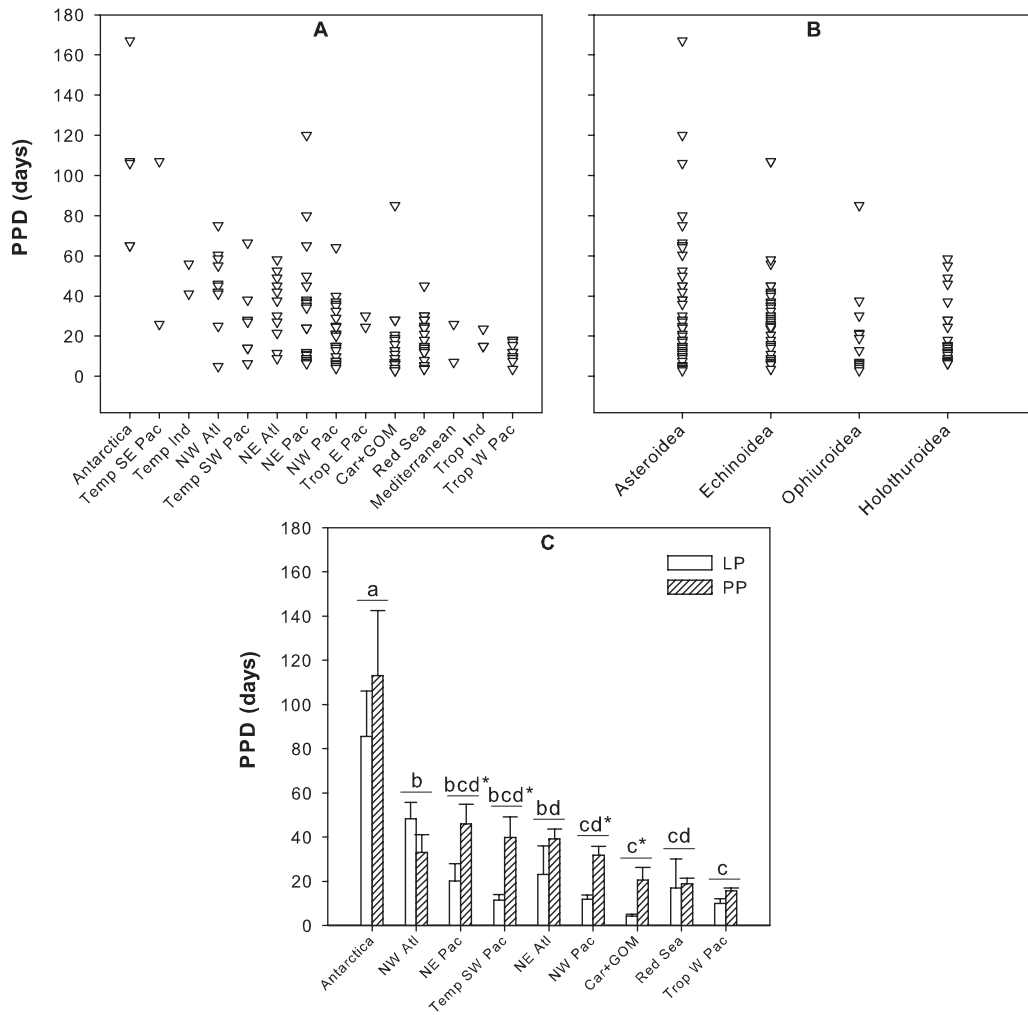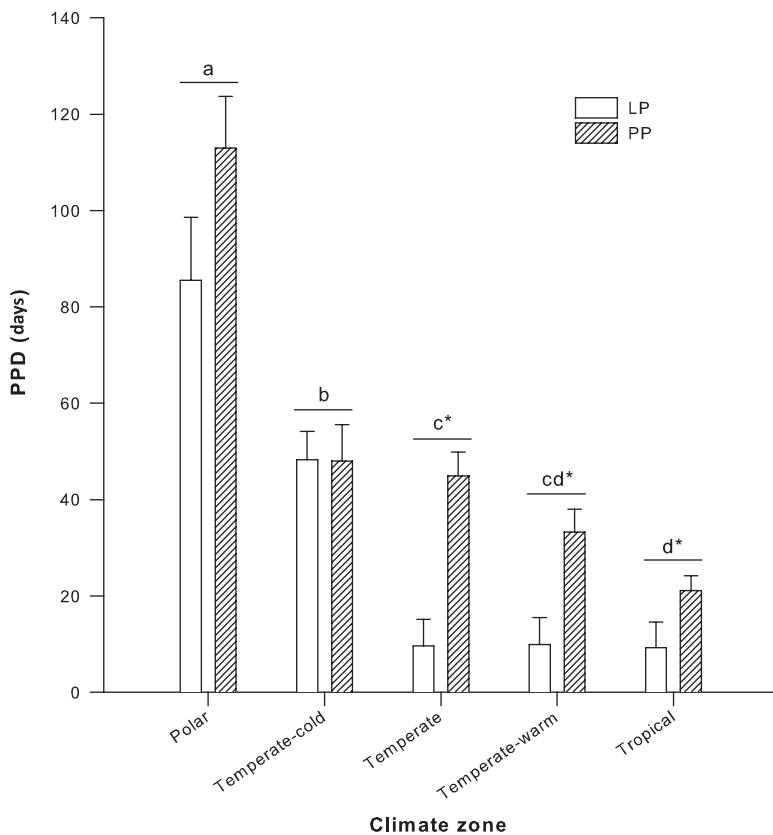
Figure 5 Ranges of pelagic propagule duration (PPD) according to (a) geographic regions and (b) classes of echinoderms. (c) Comparison of PPD in regions with five or more species and representatives of both larval modes (LP, lecithotrophic pelagic; PP, planktotrophic pelagic); data presented as mean ± SE where different letters indicate significant differences in mean PPD among regions [two-way ANOVA, $F_{8,106} = 9.24$, $P < 0.001$; Student–Newman–Keuls (SNK), $P < 0.05$], and asterisks identify regions in which mean PPD differs significantly between the two larval modes ($F_{1,106} = 25.47$, $P < 0.001$; SNK, $P < 0.05$). Statistical analysis was performed on ln-transformed data. Abbreviations for oceanic regions in (a): north-west Atlantic, NW Atl; north-east Atlantic, NE Atl; north-east Pacific, NE Pac; temperate south-east Pacific, Temp SE Pac; temperate Indian, Temp Ind; temperate south-west Pacific, Temp SW Pac; north-west Pacific, NW Pac; tropical east Pacific, Trop E Pac; Caribbean and Gulf of Mexico, Car + GOM; tropical Indian, Trop Ind; tropical west Pacific, Trop W Pac.

sentatives of both larval modes (73 PP and 51 LP distributed in nine regions; Fig. 5c). There were significant differences in PPD between modes ($F_{1,106} = 25.47$, $P < 0.001$) and across regions ($F_{8,106} = 9.24$, $P < 0.001$), with Antarctica showing consistently longer PPDs in pairwise comparisons ($P < 0.001$). No significant interaction was found between region and larval mode ($F_{8,106} = 1.43$, $P = 0.191$). A significant difference in PPD between larval mode was observed in four regions (north-east Pacific, north-west Pacific, temperate south-west Pacific, Caribbean–Gulf of Mexico; Fig. 5c; SNK, $P < 0.05$) but not in the five others (Antarctica, $P = 0.682$; north-west Atlantic, $P = 0.661$; north-east Atlantic, $P = 0.072$; Red Sea, $P = 0.419$; tropical west Pacific,

$P = 0.181$). Significant egg size differences between PP and LP occurred in all regions ($F_{8,99} = 130.02$, $P < 0.001$; SNK, $P < 0.036$), except the Red Sea ($P = 0.113$).

Analysis by climate zone

The subset for this analysis contained 120 entries (74 PP; 46 LP) for which the precise sampling latitude and experimental seawater temperature were known, allowing us to separate them into climate zones (tropical, temperate-warm, temperate, temperate-cold, polar; defined in Fig. 6). A significant interaction occurred between larval mode and climate zone ($F_{4,110} =$

Figure 6 Differences in pelagic propagule duration (PPD) based on climate for two larval modes (PP, planktotrophic pelagic; LP, lecithotrophic pelagic). Climate zones were determined based on latitude of origin and rearing temperature, where polar is > 60° N/S and 0–5 °C; temperate-cold is 40–60° N/S and ≤ 10 °C; temperate is 30–55° N/S and 11–19 °C, temperate-warm is 30–55° N/S and 20–28 °C; and tropical is 0–30° N/S and ≥ 22 °C. Data shown as mean ± SE, with significant differences among climes identified by different letters [two-way ANOVA, $F_{4,110} = 21.92$, $P < 0.001$; Student–Newman–Keuls (SNK), $P < 0.05$], and significant differences between larval modes within each clime identified with an asterisk ($F_{1,110} = 29.09$, $P < 0.001$; SNK, $P < 0.05$). Statistical analysis was performed on ln-transformed data.

4.27, $P = 0.003$; Fig. 6). In separate *t*-tests, species from tropical, temperate-warm and temperate climes exhibited distinct PPDs on the basis of larval mode ($P < 0.001$) but species from temperate-cold ($P = 0.921$) and polar climes ($P = 0.593$) did not. There was a smoother more continuous decline in PPD across climes in PP than in LP (Fig. 6). When focusing on the echinoderm class with representatives of both larval modes in all climate zones (Asteroidea: 23 PP; 22 LP), we found a similar pattern except there was no significant interaction between the factors ($F_{4,35} = 1.29$, $P = 0.292$). Only temperate and temperate-warm species displayed a significant difference in PPD between PP and LP modes (SNK, $P = 0.020$ and 0.001, respectively) while tropical species joined polar and temperate-cold species in not exhibiting any significant difference ($P > 0.194$).

Analysis of range size

In a subset of species from all classes (29 PP; 13 LP) that exhibited relatively long PPDs (≥ 30 days; Table S5), PPD was not significantly different between LP and PP ($t = 0.52$, d.f. = 40, $P = 0.607$). The range size based on surface area was on average larger in LP (1847×10^4 km^2) than in PP (1501×10^4 km^2), but not statistically so ($t = 1.61$, d.f. = 40, $P = 0.114$), whereas the greater species range based on maximal linear distance in LP (10,835 km) than in PP (6815 km) was statistically supported ($t = 2.11$, d.f. = 40, $P = 0.041$; Fig. 7). There was no correlation between PPD and either measure of distribution range

($P = 0.854$ and 0.932 for area and distance, respectively). Two-way ANOVAs could not be performed on this subset because there were no LP modes in Echinoidea and Ophiuroidea. There was no significant correlation between egg size and PPD ($P = 0.235$) or egg size and range size, whether measured as surface area ($P = 0.420$) or linear distance ($P = 0.162$). Temperature was inversely related to PPD ($r_s = 0.362$, $P = 0.026$) but not to either measure of range size ($P > 0.05$).

In species with short PPDs (< 30 days; Table S6) from all classes (24 LP; 47 PP), PPD was significantly influenced by larval mode ($F_{1,63} = 31.56$, $P < 0.001$), with post hoc tests showing significance in echinoids ($P = 0.003$) and ophiuroids ($P = 0.001$) but not in asteroids ($P = 0.461$) or holothuroids ($P = 0.557$). Species range was on average significantly greater in PP than in LP, both based on surface area (2726×10^4 vs. 794×10^4 km^2; $t = -2.80$, $P = 0.007$) and maximum distance (9467 vs. 4828 km; $t = -3.53$, $P < 0.001$; Fig. 7). Still, there was no correlation between PPD and range size ($P = 0.985$ and 0.432 for area and distance, respectively). Relationships with temperature and egg size contrasted those for PPD > 30 days. Significant negative relationships occurred between egg size and PPD ($r_s = 0.495$, $P < 0.001$), and between egg size and range based on area ($r_s = 0.241$, $P = 0.0495$) and distance ($r_s = 0.311$, $P = 0.010$); but temperature was not correlated to PPD or any measure of range size ($P > 0.203$). Two-way ANOVAs (class × larval mode) showed that geographic range based on area was not significantly different between larval modes ($F_{1,63} = 3.40$, $P = 0.070$), whereas range based on maximum distance was ($F_{1,63} = 5.90$, $P = 0.018$); post hoc tests
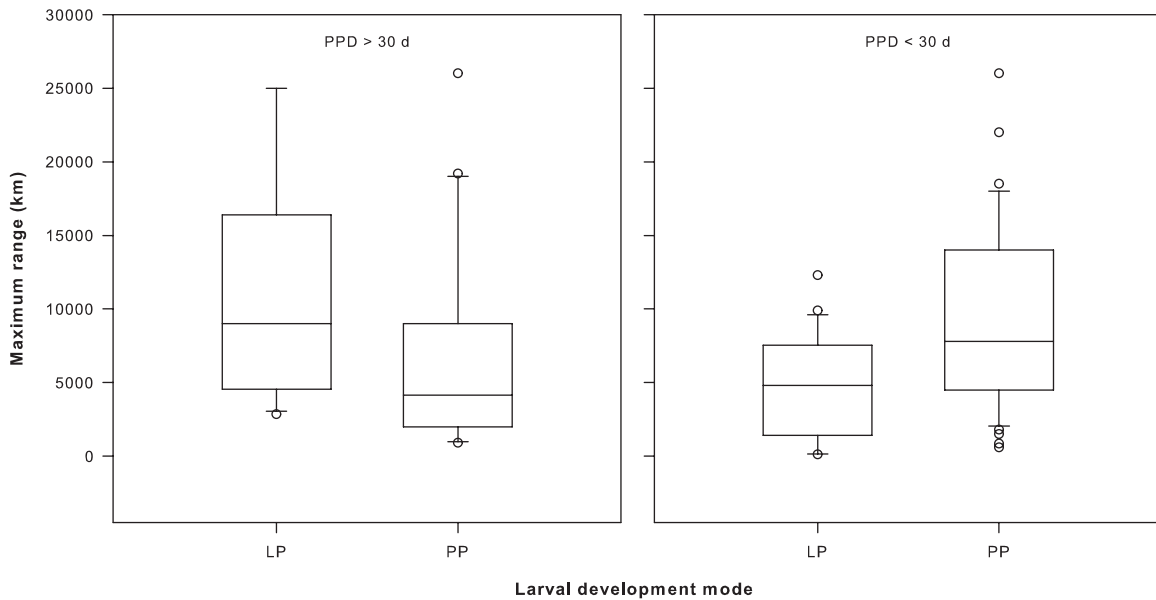
Figure 7 Distribution range size (as maximum linear distance between the outermost limits of occurrence) recorded in a subset of representatives from the four echinoderm classes (Tables S5 and S6) on the basis of larval mode (PP, planktotrophic pelagic; LP, lecithotrophic pelagic). The left panel represents species with pelagic propagule duration (PPD) of 30 days or more and the right panel shows species with PPD shorter than 30 days. The upper and lower boundaries of the boxes denote lower and upper quartiles, respectively; the line across the box indicates the median; whiskers show 5th/95th percentiles; open circles are outliers.

did not reveal any significant differences in PPD between LP and PP within any of the classes ($P > 0.05$).

While lecithotrophs exhibited greater geographic ranges at PPDs $\geq$ 30 days and planktotrophs exhibited greater ranges at PPDs < 30 days, PPDs did not directly explain the greater geographic range within either group. Temperature differed significantly among short and long PPDs (mean of 23.6 vs. 12.0 °C; $U = 351$, $P < 0.001$) but was unrelated to range size within the groups and related to PPD only in species with long PPDs. Egg size was not significantly different between the two groups ($t = 1.37$, $P = 0.173$); it had an influence on both PPD and range within short PPDs and no effect on any variable within long PPDs. Species pooled regardless of PPD length showed no significant difference in range size between PP and LP, whether based on maximum area ($U = 1265$, $P = 0.390$, $n = 113$) or distance ($U = 1205.5$, $P = 0.221$). Two-way ANOVAs did not reveal any interactions, or any differences in range among classes or larval modes. Finally, a three-way ANOVA (class × larval mode × PPD category), restricted to Asteroidea and Holothuroidea to ensure non-empty cells, confirmed the interacting effects of PPD category (short versus long) and larval mode (PP versus LP) on the range area ($F_{1,57} = 5.45$, $P = 0.023$) and distance ($F_{1,57} = 13.55$, $P < 0.001$). Pairwise analyses mirrored the inverse trends shown in Fig. 7.

DISCUSSION

PPD and dispersal: a fading paradigm

Dispersal is the usual suspect when trying to explain the occurrence of planktotrophic larvae with longer pelagic durations, although the notion is still vigorously debated and has been the subject of several recent reviews (e.g. Cowen & Sponaugle, 2009; Weersing & Toonen, 2009; Zimmer et al., 2009; Selkoe & Toonen, 2011). Here we limit our discussion to material that is directly relevant both to PPD and larval mode.

For many scientists, dispersal cannot explain the origin or maintenance of feeding larvae (Palmer & Strathmann, 1981) in spite of its reputed macroevolutionary importance (e.g. Jeffery & Emlet, 2003). In some of the earliest discussions on this topic, Thorson (1950) did not propose a strict dichotomy in dispersal distances between larval modes. Emlet (1995) later examined dispersal distance based on larval mode (determined by egg size) in 215 regular echinoids and showed that at depths above 100 m species with pelagic feeding larvae had larger distribution ranges than species with non-feeding larvae, either pelagic or brooded. Below 100 m, however, there was no relationship between geographic range size and larval mode (Emlet, 1995). In contrast, Young et al. (1997) found greater bathymetric and geographic ranges in lecithotrophic bathyal and abyssal echinoids and asteroids. They proposed that lecithotrophic development does not necessarily constrain dispersal in the deep sea, and that low metabolic rates characteristic of cold environments (Shilling & Manahan, 1994) might result in deep-sea planktotrophs spending no more time in the plankton than pelagic lecithotrophs (Young et al., 1997).

Recent reviews of studies on genetic structure in various benthic species have also shown that intuitively predicting dispersal based on larval mode and PPD would not provide an accurate picture (Levin, 2006; Weersing & Toonen, 2009). When PLD is used as a proxy of dispersal, it is not a global determinant of range size (Levin, 2006; Lester et al., 2007). We found

evidence that a combination of PPD and larval mode is probably at play: while PPDs were not good predictors of species range sizes, equally long PPDs (30–85 days) yielded consistently larger range sizes in lecithotrophs than in planktotrophs. Lester *et al.* (2007) reported larger ranges in planktotrophs ($n = 22$) but in comparison to mixed pelagic and non-pelagic lecithotrophs ($n = 13$), thus not restricting their assessment to pelagic developers.

There is also a greater recognition that behaviour has the potential to affect dispersal (Metaxas & Saunders, 2009), emphasizing the distinction between the pelagic embryonic phase, where dispersal is passive, and the pelagic larval phase, where behavioural components emerge. The impact of larval behaviour on dispersal distance was recently shown: organisms with short dispersal distances either had brief PPD or, if their PPD was long, tended to remain very close to the bottom during the pelagic phase (Shanks, 2009). The end of the dispersal phase may also depend on substrate/habitat selectivity at settlement, with opportunistic larvae potentially dispersing further than selective larvae, as shown in studies on coral reef fish (Levin, 2006; Cowen & Sponaugle, 2009).

Overall, there is increasing evidence that neither larval mode nor PPD/PLD can be used as accurate proxies for dispersal, which is increasingly viewed as a by-product of pelagic development (Palmer & Strathmann, 1981; Giangrande *et al.*, 1994; Strathmann, 2007). Growing support is driven by recent synthesis work. Shanks & Eckert (2005) presented evidence that PLD may favour settlement into parental habitats rather than dispersal. Weersing & Toonen (2009) showed that PLD was a poor predictor of connectivity (< 10%) and that the weak relationship between PLD and genetic structure (F_{ST}) was driven by species that do not disperse at all. A follow-up analysis concluded that approximately a quarter to a third of the variance in F_{ST} or IBD slope was explained by PLD, depending on whether non-pelagic developers were included or not (Selkoe & Toonen, 2011). Currents that concentrate larvae (Selkoe & Toonen, 2011), environmental features (seascape genetics; Selkoe *et al.*, 2010), and selection against exogenously-derived recruits (phenotype–environment mismatch; Marshall *et al.*, 2010) may also explain why levels of connectivity are often lower than that predicted based on PLD alone.

PPD in response to the environment

Rather than a means of dispersal, we can view PPD as a component of life history, which is responding to a variety of biotic (e.g. food supply, predation pressure) and abiotic (e.g. temperature, substratum) factors. When considering a data set such as we have compiled here, with PPDs from a variety of locations and habitats, it is important to acknowledge our limited ability to consider synergistic effects. For example, PPD co-evolved with various other traits (e.g. fecundity, longevity) whereas temperature reflects changes in latitude linked to regional specificities (e.g. currents, productivity, habitat complexity, predation pressure).

Based on data compiled mainly from echinoderms, Thorson (1950) observed that within restricted areas, temperature was 'of the greatest influence upon the duration of the pelagic life'. Hoegh-Guldberg & Pearse (1995) proposed that, for asteroids, temperature, rather than egg size, food or other variables, could best explain latitudinal differences in developmental rates. Here we found different correlations between rearing temperature and PPD in the various classes (i.e. absent in ophiuroids and holothuroids, negative in asteroids and echinoids; Table 1) yielding a negative correlation in the pooled Echinodermata. Similar mixed patterns were observed in correlations between latitude and PPD (i.e. absent in ophiuroids and holothuroids, positive in asteroids and echinoids) yielding an overall positive relationship in Echinodermata. The combination of egg size and temperature did not accurately or consistently predict PPD across all classes. This indicates that the influence of temperature may be taxonomically and/or geographically constrained.

A unified, parameterized model for the temperature dependence of larval development in 72 species of marine invertebrates (including four echinoderms) revealed that planktonic larval duration (PLD, in this paper termed PPD) was significantly linked to temperature (O'Connor *et al.*, 2007). However, the investigators found that cold-temperate species had shorter PPDs than would be predicted by temperature alone. Their model was also consistent with the prediction of shorter PPDs in lecithotrophic than planktotrophic species (O'Connor *et al.*, 2007). However, the data set was strongly biased towards planktotrophs with only 16 lecithotrophs examined, 88% of them from temperate or cold areas. Furthermore, many lecithotrophs were of the demersal/brooding mode (mostly Arthropoda) rather than the pelagic mode. Overall, the link between egg size and development time may be more important/relevant within larval modes than among them (i.e. we found a significant relationship within lecithotrophs but not within planktotrophs or overall). Also, temperature may have an indirect effect given the reasonable relationship between egg size and biochemical composition: lipids get used more slowly at low temperatures leading to the assumption that PPD may extend for > 6 months in some Antarctic species (Shilling & Manahan, 1994; M.A.S., unpublished data).

The strong regional patterns seen in the present study may therefore reflect selective pressures at the habitat level. Small-scale shifts in larval modes have been documented, e.g. roughly equal proportions of feeding and non-feeding pelagic larvae in rocky habitats and a dominance of pelagic planktotrophs in soft-bottom subtidal habitats (Grantham *et al.*, 2003). Recently, PPD was proposed to be one of many life-history traits shaped to exploit local oceanographic conditions for the maintenance of adult populations (Shanks & Eckert, 2005). Furthermore, Havenhand (1993) proposed that in species with short life cycles (nudibranchs), variation in PPD could directly affect growth and reproductive output and consequently influence fitness. The optimal time to metamorphose was suggested to illustrate a trade-off between mortality and growth rates (Werner, 1988): higher mortality and/or slower growth in the pre-metamorphic habitat will favour early settlement in the post-metamorphic habitat (where mortality is lower and/or growth optimized). It is

generally presumed that prolonged pelagic life leads to larval loss (Thorson, 1950) and that the lecithotrophic larva (pelagic or not) is an evolutionary derivative of the planktotrophic larva (e.g. Strathmann, 1985). Thus Havenhand (1993) suggested that lecithotrophic species would have evolved an abbreviated PPD to favour transition to the less threatening post-metamorphic habitat. However, recent experimental studies have shown that larval mortality in the plankton is lower than traditionally expected (Johnson & Shanks, 2003) and that predation rates on marine propagules are higher in the benthos than in the plankton (Allen & McAlister, 2007).

The predation pressure hypothesis can further be examined from an evolutionary perspective. In echinoderms, it is largely agreed that feeding larvae evolved from a planktotrophic dipleurula larva (Byrne *et al.*, 2007; Raff, 2008; Nielsen, 2009). However, it has recently been argued, based on the fossil record and phylogenetic studies, that pelagic lecithotrophy and planktotrophy both correlate in time with a dramatic rise in the number and type of epibenthic suspension feeders in the Early Ordovician (Peterson, 2005). Hence, benthic rather than planktic predation would have driven the evolution of planktotrophy. The same increase in benthic predation was also proposed to have driven the multiple reversals back to lecithotrophy as the increase in egg size would reduce mortality of early embryos due to positive buoyancy and other defence mechanisms. Overall, predation pressure could be the determinant of long pelagic phases (spending more time in the low-predation planktonic habitat away from epibenthic suspension feeders), rather than PPD being a consequence of feeding versus non-feeding larval mode.

A closer look at shifts in life-history traits among phylogenetically related species might offer interesting insights. Our findings show that not all classes of echinoderms have developed the same combinations of larval modes and PPDs. In part this may be the result of differences in evolutionary history, as previously shown in the Asterinidae, where lecithotrophy is more prevalent than in other asteroid families (Byrne, 2006). Furthermore, the release of pelagic and non-pelagic larvae by the same parent asteroid has been documented (Mercier & Hamel, 2008), presumably illustrating an on-going evolution in response to shifting environmental conditions.

Emerging hypotheses

Strathmann (2007) proposed an interesting list of explanatory hypotheses for long PLDs (= PPDs) in benthic marine animals: (1) pelagic embryos or larvae are released when the cost of protection becomes too high in regards to its effectiveness; (2) feeding larvae are pelagic to favour growth and minimize predation, and their dispersal is incidental; and (3) only larvae released close to competence (short PLDs) use the pelagic stage as a means of dispersal and habitat selection.

One of the assumptions made by Strathmann (2007) is that 'the longest PLDs are for obligately feeding larvae'. Consequently, the adaptive advantages of long PLDs in non-feeding

larvae are largely overlooked in his assessments. The same author also states that 'protected benthic embryos develop more slowly than pelagic solitary embryos', and suggests that this reflects their respective risks of predation. Evidence of this remains rather slim in echinoderms, with north-west Pacific asteroids showing no effect of egg size on the duration of early embryonic cell cycles (Strathmann *et al.*, 2002). In contrast, we have shown that the obligate non-feeding period (to gastrula) is comparable between planktotrophs and lecithotrophs in all classes except in holothuroids where it is significantly longer in lecithotrophs (Table 1). However, the proportion represented by this obligate non-feeding period relative to overall PPD is consistently greater in lecithotrophs, both within and across classes. Furthermore, the present review of Echinodermata does not support the presumed occurrence of a dichotomy in development rates between protected and non-protected propagules (whether feeding or non-feeding) based on time to gastrula ($U = 362.5$, $P = 0.193$, $n = 11$ and 87) or time to metamorphosis ($U = 756.0$, $P = 0.130$, $n = 22$ and 87).

The assumption that the dichotomy in egg sizes seen between planktotrophs and lecithotrophs is accompanied by parallel changes in energetic/biochemical composition is increasingly being questioned. Sewell & Young (1997), for example, hypothesized that the eggs of ophiuroids and holothuroids might differ in terms of biochemistry from the other echinoderm classes; a contention supported by Falkner *et al.* (2006) where lecithotrophic ophiuroids fell in the 'wrong' part of the standard echinoderm egg size versus lipid/protein content curve. Interestingly, ophiuroids and holothuroids sometimes clustered in our analyses, and ophiuroids stood out in being the only class to exhibit a (negative) correlation between egg size and PPD (Table 1). Eventually, deeper knowledge of how the biochemical composition of eggs is altered between planktotrophs and lecithotrophs will clarify our understanding of the selective forces that have shaped the evolution of these strategies (Moran & McAlister, 2009) and of the role of dispersal and PPD in echinoderm life histories.

CONCLUSIONS

Two primary findings are evident from this study of PPD in echinoderms. Firstly, we have highlighted the synergistic influence of phylogeny and climate on the occurrence of differences in PPDs between planktotrophs and lecithotrophs. In contrast to the 'widely accepted assertion' that planktotrophs have smaller eggs and longer PPDs than lecithotrophs, we have shown that, while planktotrophs do have smaller eggs, a significant difference in PPD with larval mode is seen only in Echinoidea and Ophiuroidea (with few LP), not in Asteroidea and Holothuroidea (with roughly equal representatives of both larval modes). Species from colder climes (temperate-cold, polar) tend to display relatively constant PPDs regardless of larval mode, whereas species from temperate and warm regions display a more marked dichotomy. Regional patterns also emerge, with Antarctic species exhibiting significantly longer

PPDs irrespective of larval mode, and only four basins containing species with significantly different PPDs on the basis of larval mode (north-east Pacific, north-west Pacific, temperate south-west Pacific, Caribbean–Gulf of Mexico). Together these findings indicate that the duration of the pelagic phase, whether measured as mean PPD, shortest PPD or PLD, is not tied to the larval mode (planktotroph versus lecithotroph), but rather that the latter may instigate shorter or longer PPDs according to a scheme that varies under different evolutionary and environmental pressures.

Our second important finding is that PPD in Echinodermata does not correlate with geographic range size. In addition, planktotrophs and lecithotrophs do not exhibit significantly different range sizes, although differences are observed when short and long PPDs are examined separately. For PPDs < 30 days, planktotrophs display greater ranges than lecithotrophs, whereas for PPDs ≥ 30 days, lecithotrophs are more widely distributed.

We conclude that, for echinoderms, the general acceptance of (1) larval mode as a reliable predictor of PPD and (2) PPD as a predictor of distribution range size is unfounded when considered across broad geographic and taxonomic scales. Current views on PPD and derived biological traits may have been influenced by the use of a potentially biased subset of species (e.g. echinoids in which lecithotrophs are rare), and geographic locations (e.g. north-west Pacific, Caribbean–Gulf of Mexico). Using taxonomically and regionally specific data sets, we have shown that the simplified assertion that planktotrophs disperse more widely than lecithotrophs cannot be broadly applied. More balanced data sets for other classes/phyla and regions are needed to investigate the universality of our conclusions.

In support of taxonomic and regional specificities, there was no consistent continuous predictor of PPD (egg size, temperature, latitude); instead, each of them interacted significantly with class and larval mode. Egg size was not clearly correlated to PPD in most data sets and showed no significant relationship with geographic range; thus it should not be used as a simplistic proxy of dispersal potential. Furthermore, the influence of temperature on PPD appears to be more complex than a simple inverse relationship (not seen in two of the classes). While obtaining more (and more reliable) empirical data on PPD and dispersal is commonly viewed as a priority, developmental and behavioural factors should also be given more attention to avoid laboratory artefacts (Metaxas & Saunders, 2009). Although static conditions are currently the norm (Table S1) we advocate the use of flow-through conditions (Mercier & Hamel, 2010) for future determination of PPDs, which allows for the incorporation of environmental variability.

Oversimplification of the planktotrophic–lecithotrophic dichotomy with respect to PPD should be made cautiously to avoid biasing our understanding of the complex and varied evolutionary mechanisms operating in marine systems. The dispersal biology of echinoderms is likely to be far more complex than their comparative embryology might suggest (Hart, 2002) and the same may be true of other widely distributed marine phyla with diverse larval modes.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Figure S1 Relationship between egg size and pelagic propagule duration.

Figure S2 Relationship between temperature and pelagic propagule duration.

Table S1 Complete data set, including selection criteria, notes and sources.

Table S2 Geographic regions and corresponding climate zones used in the study.

Table S3 Data set used for ANCOVAs and per class analyses.

Table S4 ANCOVA results.

Table S5 Data set used for range size analysis with pelagic propagule duration $\geq$ 30 days.

Table S6 Data set used for range size analysis with pelagic propagule duration < 30 days.

BIOSKETCHES

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