Influence of larval traits on dispersal and connectivity patterns of two exploited marine invertebrates in central Chile

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Marine Ecology Progress Series 612: 43–64 (2019)

Supplement 1

Temperature dependent pelagic larval development: parameterization for *Fissurella latimarginata*

For *F. latimarginata*, the time to complete Planktonic Larval Duration (PLD) was reduced with increasing temperature, it was modeled according to the universal relationship proposed by O'Connor et al. (2007), but using their complete 72 species database published as supplemental information. O'Connor et al. (2007) seem to have used a database of only 69 species. Additionally, we include PLD observations for *F. latimarginata* under laboratory conditions (Chavez 2004) and our laboratory PLD observations for *Loxechinus albus* (see below) under three different experimental temperatures. In consequence, the resulting database that we used included 73 species in total.

We calculated the parameter β_0 for *F. latimarginata*

The general model has two constants (β_1 =-1.3637905 and β_2 =-0.3204597)

$$ln(PLD) = \beta_0 - 1.36 * ln (T/15) - 0.32 * ln((T/15)^2)$$

Equation S1

 β_1 and β_2 are constants described by O'Connor et al. (2007) and T is temperature in Celsius degrees and β_0 ($\beta_0 = 1.81$) is a species-specific parameter (see O'Connor et al., 2007 supplementary information).

We obtained β_0 considering the random and fixed effects in an linear mixed effects model, as proposed by O'Connor et al. (2007) in their supplemental information file (S1).

A developmental time of 5 days was reported for *F. latimarginata* at 17°C under laboratory conditions (Chavez 2004) and was used in equation S1 to obtain PLDs across a wide temperature range (from 9°C to 20°C), which rendered a PLD range between 4.0 and 11.3 days.

 $\beta_0 = 1.809649$

Linear Model

In order to model PLD_{temp} within ICHTHYOP we first transformed PLDs into daily growth rates (*GR*, um/day). We assumed linear growth from a hatching size of 190 microm to a settlement size of 210 microm (Chavez 2004), we named Ontogenetic Growth (OG),

$$GR(T) = OG / PLD(T)$$
,

Equation S2

and then calculated growth rate GR(T) considering the temperature experienced by the larvae at each time step (i.e. the growth function was updated at each time step), following the same method described in Garavelli et al. 2016. The temperature (T) experienced during each time

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step was obtained from the hydrodynamic model and larval size (L in mm) at each subsequent time step (t + dt) was calculated following equation S3.

$$L_{t+dt} = L_t + GR * (T) * dt$$
 Equation S3
 $GR = 0.00029073 * T - -0.00099052$ Equation S4

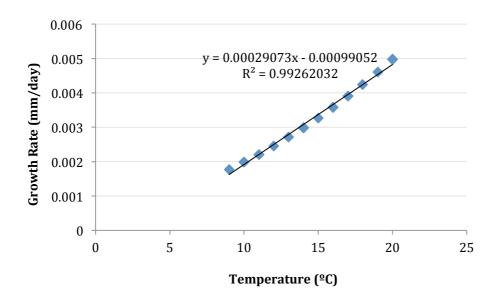
Table S1. Length of Fissurella latimarginata larvae, data obtained from Chavez (2004).

Length	microm	mm
Initial length	190	0.19
Recruitment length	210	0.21
Length variation	20	0.02

Table S2. Planktonic larval duration of *Fissurella latimarginata* at different temperatures.

Temperature	PLD (days)	Growth Rate	
		(mm/day)(GR)	
9	11.28	0.00177366	
10	10.07	0.00198536	
11	9.04	0.00221206	
12	8.15	0.002454	
13	7.38	0.00271146	
14	6.70	0.00298475	
15	6.11	0.00327423	
16	5.59	0.00358026	
17	5.12	0.00390321	
18	4.71	0.00424348	
19	4.35	0.00460147	
20	4.02	0.00497757	

Fig. S1. Relationship between temperature and growth rate of *Fissurella latimarginata* larvae.



Literature cited

Chavez LHP (2004) FONDEF DOOI1141d. Innovaciones tecnológicas para repoblamiento y producción de lapas chilenas de explotación (*Fissurella latimarginata* y *Fissurella cumingi*) en áreas de manejo y centros de cultivo. :255

Garavelli L, Colas F, Verley P, Yannicelli B, Lett C (2016) Influence of biological factors on connectivity patterns for *Concholepas concholepas* (loco) in Chile. PLoS One:209

O'Connor MI, Bruno JF, Gaines SD, Halpern BS, Lester SE, Kinlan BP, Weiss JM (2007) Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation. Proc Natl Acad Sci U S A 104:1266–71

Supplement 2

Temperature dependent pelagic larval development: parameterization for Loxechinus albus

In the case of *L. albus*, parameterization of temperature effects on larval development times was obtained through laboratory rearing experiments. To this end, we collected 33 mature urchin individuals (>7 cm) from subtidal areas around Las Cruces, central Chile and took them to the Estación Costera de Investigaciones Marinas where they were injected in the celomic cavity with 3 ml of 0.5M KCl to stimulate gamete release, following the protocol by Bustos et al. (1992). Eggs and sperm were washed with UV filtered seawater and sieved with 500 µm and 170 µm nylon mesh. Then, eggs from each female (n=4) were retained in 55 µm nylon mesh and divided into separate glass petri dishes, one for each female, where they were fertilized in an egg-sperm proportion of 1:100, from sperms of one male. The fertilized embryos were then divided in different batches, which were randomly assigned to experimental temperature treatments. Three temperature treatments were used: 10°C, 13°C and 17°C, encompassing the range observed in the study area (Thiel et al. 2007). The experiments started at the blastula stage and finished at the pre-metamorphic, competent larval stage. We recorded larval arm length under a microscope every 2 days until the 8-arms stage was reached. Thereafter, a reduction in arm length was observed until the premetamorphic stage was reached.

Considering the developmental characteristic of echinopluteus larvae, we used the proportion of time larvae remained in each developmental stage, with respect to total developmental time. Therefore, to model temperature effects on development we fitted the following linear function (equation S5) to experimental data:

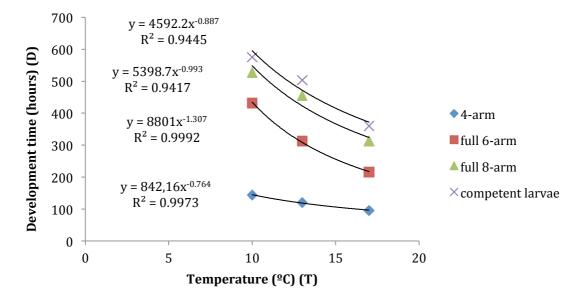
$$DP_{t+dt} = DP_t + K * (T) * dt$$
 Equation S5

where DP is Development Proportion, T is temperature in Celsius, dt is the time increment in days and K is a coefficient obtained from the relationship between growth rate and temperature (K= 0.38) through linear fitting. To incorporate the development proportion into the SEIBM, we followed the degree-day concept applied by Hinckley et al. (1996). At every time step, larvae advanced a fraction of the total development proportion depending on the temperature experienced during the time interval, until completing the entire PLD.

Table S3. Development proportion of each development larval stage of *Loxechinus albus* at three different temperatures.

Temperature (T)	Development time (days) (D)	Development time (hours) (D)	Development Stage	Development Proportion (DP)
17	4	96	4-arms	25%
17	9	216	6-arms	60%
17	13	312	8-arms	90%
17	15	360	Competent larvae	100%
13	5	120	4-arms	25%
13	13	312	6-arms	60%
13	19	456	8-arms	90%
13	21	504	Competent larvae	100%
10	6	144	4-arms	25%
10	18	432	6-arms	60%
10	22	528	8-arms	90%
10	24	576	Competent larvae	100%

Fig. S2. Relationship between development time and temperatures for each development stage of *Loxechinus albus* larvae.



Linear Model

We obtained a potential growth equation (D=a*T-b) for each development stage. From this equation we determined a development time (D) dependent on temperature (T).

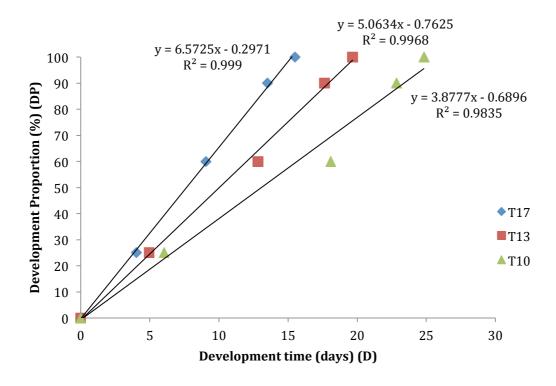
From data of development time for each development stage we obtained a temperature dependent continuous variable (Development Proportion, PD) for each development stage (e.g., DP (4-arms) = 4*100/15).

We correlate DP with days of development (DP = a*days - b), obtaining one equation for each temperature.

Table S4. Development time for each development proportion for *Loxechinus albus* larvae.

	$T^{o} = 17^{o}C$	$T^{o} = 13^{o}C$	$T^{o} = 10^{o}C$
Development Proportion (DP)	Development time (days) (D)	Development time (days) (D)	Development time (days) (D)
0	0	0	0
25	4	5	6
60	9	13	18
90	13	18	23
100	16	20	25

Fig. S3. Relationship between development proportion and development time in three different temperatures for *Loxechinus albus* larvae.

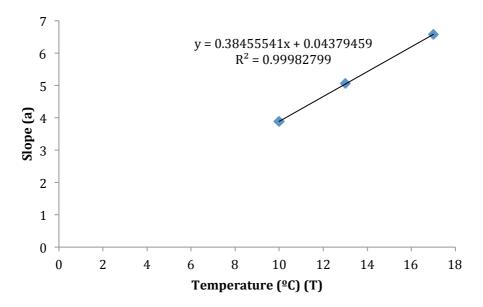


Finally, we estimated the slope of the equation of each experimental temperature, and plotted the slope versus temperature.

Table S5. Parameters of the equation of the relationship between development proportion and development time for *Loxechinus albus* larvae for three different temperatures.

Temperature (°C)	b	Slope (a)		
10	0.6896	3.8777		
13	0.7625	5.0634		
17	0.2971	6.5725		

Fig. S4. Relationship between slopes (showed in table S5) and temperature.



The slope of this linear model is the parameter K used in equation S5 $(DP_{t+dt} = DP_t + K * (T) * dt)$

Literature cited

Bustos E, Olave S, Troncoso R, Godoy C (1992) Investigación repoblamiento de recursos bentónicos Area Piloto IV Región. Etapa IV. 5. Investigaciones en erizo *Loxechinus albus* (Molina. 1782).

Hinckley S, Hermann AJ, Megrey BA (1996) Development of a spatially explicit, individual-based model of marine fish early life history. Mar Ecol Prog Ser 139:47–68

O'Connor MI, Bruno JF, Gaines SD, Halpern BS, Lester SE, Kinlan BP, Weiss JM (2007) Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation. Proc Natl Acad Sci U S A 104:1266–71

Thiel M, Macaya EC, Acuna E (2007) The Humboldt Current System of northern and central Chile: oceanographic processes, ecological interactions and socioeconomic feedback. Oceanogr Mar Biol 45:195–344

Supplement 3

Comparative results and discussion of model scenarios

Recruitment success

For *F. latimarginata* average PLD ranged between 5.83 and 5.70 days under fixed PLD scenarios (Table 2), and between 8.03 and 8.10 days under PLD_{Temp} scenarios (Table 2) showing an extension of precompetency time of 39% under PLD_{Temp} scenarios. Conversely for *L. albus* average PLD varied between 22.92 and 22.67 under fixed PLD scenarios (Table 2), and between 23.28 and 22.23 days under PLD_{Temp} scenarios (Table 2), not showing differences of precompetency time between PLD scenarios, even a reduction of 1% under PLD_{Temp} scenarios.

Significant among-year differences were observed in terms of recruitment success for both species ($X^2=20809.9$, df=3, p<0.01 for keyhole limpet and $X^2=5516.0$, df=3, p<0.01 for red sea urchin). The highest mean recruitment success in both species was observed in 2012 (Fig. S5A, B), while the lowest in 2011 for keyhole limpets (16.95%, Fig. S5A) and 2013 for red sea urchins (Fig. S1B). Larval DVM had significant effects on recruitment success in both species (behavior: $X^2 = 18609.9$, df= 1, p<0.01, for keyhole limpet and $X^2 = 9609.0$, df= 1, p<0.01 for red sea urchin), generally increasing onshore recruitment in both species (Fig. S5A, B). However, the effect of larval behavior on red sea urchin recruitment disappeared in 2011 (Fig. S5B). Consequently, the interaction term (year: behavior) was significant for red sea urchin ($X^2 = 1972.0$, df= 3, p< 0.01) and not significant for keyhole limpets ($X^2 = 153.8$, df= 3, p= ns), indicating that the effect of DVM depends on the year only for long PLD species (red sea urchin). Having a temperature dependent larval development time (PLD_{Temp}) significantly reduced recruitment success with respect to fixed development time in keyhole limpets and sea urchins ($X^2 = 29910.6$, df= 1, p<0.01, for keyhole limpet and $X^2 = 278.5$, df= 1, p<0.01 for red sea urchin), but the effect was much smaller and constant among years in red sea urchins (Fig. S5B). Therefore, the interaction term (year: PLD) was significant for keyhole limpet ($X^2 = 2874.9$, df= 3, p< 0.01) and not significant for red sea urchin ($X^2 = 95.0$, df= 3, p= ns), suggesting that temperature interactions with PLD vary more among years for short PLD species than long PLD species.

The interactive effects of larval traits on recruitment success was apparent for the short PLD species (keyhole limpet) (Fig S1A), which rendered significant the behavior: PLD interaction term (X^2 = 7026.2, df= 1, p< 0.01). For longer PLD species (red sea urchin) the interaction behavior: PLD was not significant (X^2 = 90.4, df= 1, p= ns), indicating that larval behavior had similar effects on recruitment in all years, regardless of the small fluctuations in time of PLD induced by temperature (Fig. S1B). Despite among year variation in average recruitment, the second order interaction term (year: behavior: PLD) was not significant in either species (X^2 = 207.2, df= 3, p= ns, for keyhole limpet and X^2 = 97.4, df= 3, p=ns for red sea urchin).

Some larval traits, but not all of them, had significant effects on connectivity patterns and, these changes affected some but not all indicators of retention recruitment in keyhole limpets and/or red sea urchins. A significant effect of temperature dependent PLD was observed on self-recruitment (SR) and LR in keyhole limpet (Table S5 and Fig. S6), which can be visually appreciated comparing panels C and D of Fig. 4. Higher larval LR and SR were observed under fixed PLD (Table 2) than when PLD was allowed to vary with temperature, probably due to increased dispersal distance (see below) and larval waste. No significant effect of behavior was detected on SR or LR in keyhole limpet (Fig. S6), nor did behavior modify the effect of type of PLD (interaction term behavior: PLD was not significant, Table S5). In

contrast, significant effects of larval behavior were observed on larval LR and SR in the case of the red sea urchin (Fig. S6), while the type of PLD and the interaction with behavior were not significant (Table S5). Interestingly, generally lower red sea urchin LR and SR were observed under DVM (Table 2). AR was not affected by larval PLD or behavior in both species (Table S5).

Dispersal distance

As expected, dispersal distances were generally longer for red sea urchins than keyhole limpets, but on some years (2013) such a pattern reversed, with red sea urchins mean dispersal distances being lower than those of keyhole limpets across all larval traits (Fig. S5C, D, average of 47.39 km for keyhole limpet and 39.52 km for red sea urchins). Consequently, we observed that release year had a significant effect on dispersal distance in both species ($X^2=26214.9$, df=3, p<0.01, for F. latimarginata and $X^2=42066$, df=3, p<0.01 for L. albus). Averaging across the four years of simulations showed increased mean dispersal distances in the much shorter PLD species, keyhole limpets, under some larval trait scenarios (Table 2). The year with highest mean dispersal distance was different between species; 2011 for keyhole limpet (79.85 km) and 2010 for red sea urchin (83.11 km) (Fig. S5C and D). Larval behavior had a significant effect on dispersal distance in both species $(X^2=463.3, df=1, p<0.01 \text{ for } F. \text{ latimarginata} \text{ and } X^2=6720, df=1, p<0.01 \text{ for } L. \text{ albus}), but in$ the opposite direction and generally larger effect on red sea urchins than keyhole limpets (Fig. 4C, D, Table 2). Consistently longer mean distances under DVM scenarios were observed for red sea urchin (Fig. S5D), increasing average dispersal distance across years from 49.41 to 76.98 under fixed PLD and from 56.96 to 70.29 km under PLD_{Temp} (Table 2). In the keyhole limpet, DVM generally and slightly decreased mean dispersal distance across vears (Fig. S5C, average 75.84 km in LAG and 64.09 km under DVM; Table 2).

When averaging across years, the type of PLD had significant main effect on dispersal distance only for keyhole limpet ($X^2=14901.7$, df=1, p<0.01, for F. latimarginata and $X^2=2$, df=1, p= ns for L. albus), increasing dispersal when PLD was temperature dependent (Fig. S5C, Table 2). In this short PLD species, an extension of two days of planktonic development increased dispersal distance from 57.10 to 75.84 km under LAG scenarios and from 54.92 to 64.09 km under DVM scenarios (Table 2). In contrast, the effect of PLD type on the red sea urchin was small and varied in direction depending on larval behavior: a slightly negative effect under DVM and slightly positive effect under LAG behaviors (Fig. S5D, Table 2). The interaction term (year: behavior) was statistically significant on dispersal distance for red sea urchin but not for keyhole limpet ($X^2=32.6$, df=3, p= ns, for F. latimarginata and $X^2=2523$, df=3, p< 0.01 for L. albus). The interaction term (year: PLD) was statistically significant on dispersal distance for both species (X²= 283.8, df=3, p-value<0.01, for F. latimarginata and X^2 = 49, df=3, p< 0.01 for L. albus). The behavior: PLD interaction term had a statistically significant influence on dispersal distance for red sea urchin and not for keyhole limpet (X^2 = 102.8, df=1, p= ns, for F. latimarginata and $X^2 = 530$, df=1, p< 0.01 for L. albus). The third level interaction term (year: behavior: PLD) was not significant in either species ($X^2 = 33.9$, df=3, p= ns, for F. latimarginata and X^2 = 15, df=3, p= ns for L. albus).

Fig. S5. Average recruitment success (A and B) and boxplots showing dispersal distance (C and D) for *Fissurella latimarginata* (A and C) and *Loxechinus albus* (B and D) in each year simulated under the four scenarios: Diel Vertical Migration behavior and fixed Planktonic Larval Duration (PLD) (DVM + PLD_{fixed}), DVM and PLD based on a species-specific temperature dependent PLD (DVM + PLD_{Temp}), passive Lagrangian transport (LAG) behavior and fixed PLD (LAG + PLD_{fixed}) and LAG and PLD based on temperature

dependent PLD (LAG + PLD $_{\text{Temp}}$). The black diamonds show the average across all four experiments in a given year.

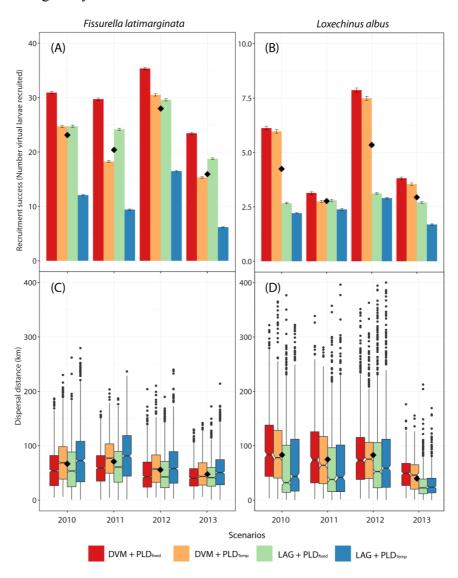
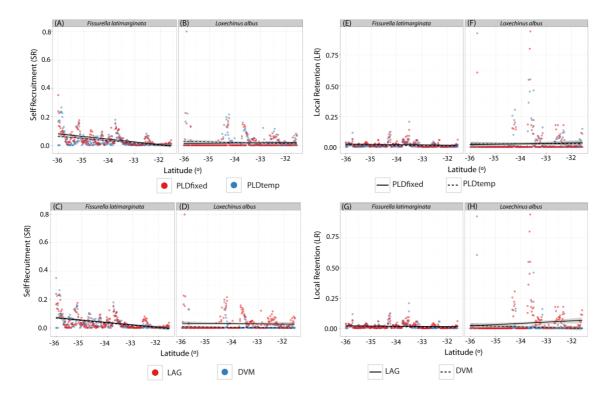


Table S5. Analysis of deviance for the Generalized Linear Models (GLMs) with quasipoisson error structure applied to the potential connectivity metrics calculated for self-recruitment, local retention, relative local retention and allochthonous recruitment for *Fissurella latimarginata* and *Loxechinus albus*.

	Fiss	urella latimarg	inata		
Self-recruitment ~ behavior * PLI					
Deviance explained: 1.82%					
•	Df	Deviance	Resid. Df	Resid. Dev.	Pr (>Chi)
NULL			555	26.34	`
Behavior	1	0.03	554	26.30	0.49
PLD	1	0.39	553	25.92	0.01
Behavior * PLD	1	0.06	552	25.86	0.33
Local retention ~ behavior * PLD	family= qua	asipoisson			
Deviance explained: 3.47%	, , 1	P			
NULL			555	11.42	
Behavior	1	$4.63*10^{-2}$	554	11.37	0.23
PLD	1	0.35	553	11.02	< 0.01
Behavior * PLD	1	$1.80*10^{-3}$	552	11.02	0.81
Relative local retention ~ behavio	r * PLD_fan				*****
Deviance explained: 1.52%	,	<i>j</i> 4.461p0100			
NULL			555	27.51	
Behavior	1	$4.28*10^{-3}$	554	27.50	0.86
PLD	1	0.41	553	27.09	0.08
Behavior * PLD	1	8.80*10 ⁻⁴	552	27.09	0.94
Allochthonous recruitment ~ beh	avior * PI D			27.07	0.51
Deviance explained: 0.00%	avioi i LD,	, raining quasip	0133011		
NULL			555	345.37	
Behavior	1	9.74*10 ⁻⁴	554	345.37	0.97
PLD	1	$7.28*10^{-3}$	553	345.36	0.93
Behavior * PLD	1	$0.03*10^{-4}$	552	345.36	0.99
Beliavioi TED	1	Loxechinus albi		343.30	0.99
Self-recruitment ~ Behavior * PL			13		
Deviance explained: 17.52%	D, family— q	uasipoisson			
NULL			555	33.15	
Behavior	1	5.63	554	27.51	< 0.01
PLD	1	0.16	553	27.35	0.23
	1	0.16 $0.97*10^{-3}$	552	27.34	0.23
Behavior * PLD			332	27.34	0.77
Local retention ~ Behavior * PLD	, ramny= qu	asipoisson			
Deviance explained: 8.85%			555	(0.47	
NULL Polyanian	1	<i>5</i> 10	555 554	60.47	< 0.01
Behavior	1	5.12 0.96*10 ⁻²	554 552	55.35	< 0.01
PLD	1		553	55.34	0.87
Behavior * PLD	1 * DLD. far	0.22	552	55.12	0.45
Relative local retention ~ Behavio	or " PLD, far	mny= quasipoiss	son		
Deviance explained: 2.63%			555	53.05	
NULL		0.00	555	53.85	0.00
Behavior	1	0.88	554	52.97	0.09
PLD	1	0.19	553	52.78	0.43
Behavior * PLD	1	0.34	552	52.43	0.29
Allochthonous recruitment ~ Beh Deviance explained: 0.00%	avior * PLD	, tamily= quasij	ooisson		
NULL			555	964.94	
Behavior	1	0.18	554	964.76	0.86
PLD	1	3.53*10 ⁻⁴	553	964.76	0.99
Behavior * PLD	1	$7.05*10^{-3}$	552	964.75	0.97
· ·			-		

Fig. S6. Relationship between self-recruitment (SR) and latitudes for *Fissurella latimarginata* (A and C) and *Loxechinus albus* (B and D), and between Local Retention (LR) and latitudes for *F. latimarginata* (E and G) and *L. albus* (F and H). The upper plots show the comparison between the two PLD scenarios, PLD fixed (red dots and solid line) and temperature-dependent PLD (blue dots and dashed line). The bottom plots show the comparison between behavior scenarios, passive Lagrangian transport (LAG) (red dots and solid line) and Dial Vertical Migration (DVM) (blue dots and dashed line).



Discussion

While location of origin and spawning date played major roles on dispersal distance and successful onshore recruitment, environmental conditions affecting larval development and larval behavior did have significant, albeit lower effects on these important population variables. Much has been speculated about the effect of increased sea surface temperature on larval dispersal and resulting recruitment and population connectivity, both in the context of latitudinal variation in mean temperatures (Thorson 1950, Bradbury et al. 2008, Ayata et al. 2010, Leis et al. 2013) and through climate change (O'Connor et al. 2007, 2012, Munday et al. 2009, Lacroix et al. 2018). Indeed, the dominant effect of temperature on metabolic and development rates (Gillooly et al. 2002, Brown et al. 2004) leads to highly predictable and universal reduction in larval development times (Connor et al. 2007), which is expected to generally reduce effective dispersal distances. However, the actual thermal regimes experienced by developing larvae in a complex realistic ocean might depart very significantly from laboratory controlled conditions. Therefore, it is critical to examine temperature effects under realistically variable thermal conditions and in different regions of the world. In our model, temperature dependent development had an important effect on recruitment success through changes in PLD, but surprisingly, the impact was greater on the short PLD species (keyhole limpets), than on longer PLD species (red sea urchin). For red sea urchin, the small effect of temperature on developmental time had marginal effects on recruitment success (Fig. S5B) and no consistent effect on dispersal distances (Fig. S5D). For F. latimarginata temperature dependent development increased the average time to reach the settlement size by two days, which represents 39% increase from the nominal development time. However, we used 5 days of precompetency period for both species although it might be extreme for F. latimarginata. Hence in this species we observed increased larval waste leading to lower recruitment (Fig. S5A) and slight but very consistent increase in average dispersal distances (Fig. S5C). It is remarkable that the relative impact of temperature dependent development is stronger on species exhibiting shorter larval developmental times. This is not because development in this species is more sensitive to temperature, but because of the differences in the actual thermal regimes and temperature ranges experienced in a realistic ocean, even when larvae are released at the same time. The longer the PLD, the more variable the thermal environment experienced through development. Long PLDs will necessarily extend beyond the warm water season and be exposed to colder waters that could have important effects on development times. Lacroix et al. (2018) predicts a PLD increase of 22% in a flatfish species in the North Sea in a climate change scenario, but our results suggest a complex interaction between the effect of temperature on developmental times and across regions since variability in temperature depends on the oceanographic conditions determining temperature (e.g., dominance of upwelling). Moreover, a rise in ocean temperature is expected to not only decrease larval duration, other consequences warrant consideration such as changes in spawning period (Fincham et al. 2013), changes in reproductive output (Shama 2015) and changes in larval mortality (Garavelli et al. 2016, Madeira et al. 2016). Thus, we submit that predicting consequences of increased ocean temperature on dispersal and recruitment can be counter intuitive and, is much more complex than simply projecting mean ocean temperature increases (Connor et al. 2007, Byrne & Selvakumaraswamy 2011, McLeod et al. 2015, Lacroix et al. 2018).

Laval behavior, especially the ability to perform diel vertical migration, has been pinpointed as the most important missing information in studies of larval dispersal (Levin 2006, Metaxas & Saunders 2009, Morgan 2014). Our results showed that DVM enhances recruitment success in both model species and across all years modeled. DVM increased recruitment success twice as much for red sea urchin than for the keyhole limpet, suggesting that DVM

seems to be more important in species exhibiting longer PLDs probably because larvae may experience baroclinic circulation patterns for longer periods of time. While the effect of DVM on spatial and temporal variability in recruitment was rather minor, it is remarkable that it was consistently positive across all conditions and for both species. In many modeling and observational studies conducted in upwelling regions DVM has been proposed as a mechanism promoting onshore larval retention (Marta-Almeida et al. 2006, Morgan et al. 2009, Aiken et al. 2011, Morgan 2014). Offshore currents at the surface and onshore currents at deeper depths during upwelling events (Strub et al. 1998, Kirincich et al. 2005, Morgan et al. 2009) allow organisms performing DVM to migrate below the Ekman layer, and reduce offshore transport (Marta-Almeida et al. 2006, Queiroga et al. 2007, Aiken et al. 2011). This general mechanism may play a role in the observed increased recruitment rates in our model. However, in contrast to the idea that DVM may enhance recruitment through reducing dispersal and increasing larval retention nearshore during development, DVM had positive effects on dispersal distance (see also Ospina-Alvarez et al. in press), negatively impacting local retention and self-recruitment, particularly of red sea urchins. In a previous study conducted in Monterey Bay, Carr et al. (2008) observed that DVM did not substantially lead to nearshore retention as the daytime return flow did not compensate offshore nighttime transport. In our study, for red sea urchin we also observed that allochthonous recruitment under DVM was mainly northward, compared to LAG where more than 20% was southward (Fig. 6). This result reinforces the idea that larvae that vertically migrate were advected northward and then a fraction returned to nearshore locations, possibly by the mechanisms described above. Thus, our results suggest that for species with moderate PLD (20 to 25 days), like the red sea urchins, in the upwelling ecosystem of central Chile, vertical migration is not a behavior promoting local retention, nor self-recruitment, but it increases the probability of successful onshore transport of competent larvae and, probably increases coastal alongshore dispersal distances in a coastal band across the region. Increased onshore recruitment and reduced dispersal have been suggested as one factor that may favour evolution of DVM in invertebrate and fish larvae (Batchelder et al. 2002, Marta-Almeida et al. 2006, Morgan 2014). DVM may provide an adaptive advantage as it leads to higher recruitment in our simulations for both species across all scenarios, but this comes at the expense of increased dispersal distances. Further studies are needed to determine if increased recruitment can be a sufficiently strong selective force leading to DVM in competent larvae.

Literature cited

- Aiken CM, Navarrete SA, Pelegrí JL (2011) Potential changes in larval dispersal and alongshore connectivity on the central Chilean coast due to an altered wind climate. J Geophys Res Biogeosciences 116:1–14
- Ayata S-D, Lazure P, Thiébaut É (2010) How does the connectivity between populations mediate range limits of marine invertebrates? A case study of larval dispersal between the Bay of Biscay and the English Channel (North-East Atlantic). Prog Oceanogr 87:18–36
- Batchelder HP, Edwards CA, Powell TM (2002) Individual-based models of copepod populations in coastal upwelling regions: Implications of physiologically and environmentally influenced diel vertical migration on demographic success and nearshore retention. Prog Oceanogr 53:307–333
- Bradbury IR, Laurel B, Snelgrove PV., Bentzen P, Campana SE (2008) Global patterns in marine dispersal estimates: the influence of geography, taxonomic category and life history. Proc R Soc B Biol Sci 275:1803–1809

- Brown CA, Holt SA, Jackson GA, Brooks DA, Holt GJ (2004) Simulating larval supply to estuarine nursery areas: How important are physical processes to the supply of larvae to the Aransas Pass Inlet? Fish Oceanogr 13:181–196
- Bustos E, Olave S, Troncoso R, Godoy C (1992) Investigación repoblamiento de recursos bentónicos Area Piloto IV Región. Etapa IV. 5. Investigaciones en erizo Loxechinus *albus* (Molina. 1782).
- Byrne M, Selvakumaraswamy P (2011) Sea urchin development in a global change hotspot, potential for southerly migration of thermotolerant propagules. Deep Res 58:712–719
- Carr SD, Capet XJ, McWilliams JC, Pennington JT, Chavez FP (2008) The influence of diel vertical migration on zooplankton transport and recruitment in an upwelling region: Estimates from a coupled behavioral-physical model. Fish Oceanogr 17:1–15
- Chavez LHP (2004) FONDEF DOOI1141d. Innovaciones tecnológicas para repoblamiento y producción de lapas chilenas de explotación (*Fissurella latimarginata* y *Fissurella cumingi*) en áreas de manejo y centros de cultivo. :255
- Connor MIO, Bruno JF, Gaines SD, Halpern BS, Lester SE, Kinlan BP, Weiss JM (2007) Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation. PNAS 104:1266–1271
- Fincham JI, Rijnsdorp AD, Engelhard GH (2013) Shifts in the timing of spawning in sole linked to warming sea temperatures. J Sea Res 75:69–76
- Garavelli L, Colas F, Verley P, Yannicelli B, Lett C (2016) Influence of biological factors on connectivity patterns for *Concholepas concholepas* (loco) in Chile. PLoS One:209
- Gillooly JF, Charnov EL, West GB, Savage VM, Brown JH (2002) Effects of size and temperature on developmental time. Nature 417:70–73
- Hinckley S, Hermann AJ, Megrey BA (1996) Development of a spatially explicit, individual-based model of marine fish early life history. Mar Ecol Prog Ser 139:47–68
- Kirincich AR, Barth JA, Grantham BA, Menge BA, Lubchenco J (2005) Wind-driven inner-shelf circulation off central Oregon during summer. J Geophys Res C Ocean 110:1–17
- Lacroix G, Barbut L, Volckaert FAM (2018) Complex effect of projected sea temperature and wind change on flatfish dispersal. Glob Chang Biol 24:85–100
- Leis JM, Caselle JE, Bradbury IR, Kristiansen T, Llopiz JK, Miller MJ, O'Connor MI, Paris CB, Shanks AL, Sogard SM, Swearer SE, Treml EA, Vetter RD, Warner RR (2013) Does fish larval dispersal differ between high and low latitudes? Proc Biol Sci 280:20130327
- Levin L a. (2006) Recent progress in understanding larval dispersal: New directions and digressions. Integr Comp Biol 46:282–297
- Madeira D, Costa PM, Vinagre C, Diniz MS (2016) When warming hits harder: survival, cellular stress and thermal limits of Sparus aurata larvae under global change. Mar Biol 163
- Marta-Almeida M, Dubert J, Peliz Á, Queiroga H (2006) Influence of vertical migration pattern on retention of crab larvae in a seasonal upwelling system. Mar Ecol Prog Ser 307:1–19
- McLeod I, McCormick M, Munday P, Clark T, Wenger A, Brooker R, Takahashi M, Jones G (2015) Latitudinal variation in larval development of coral reef fishes: implications of a

- warming ocean. Mar Ecol Prog Ser 521:129–141
- Metaxas A, Saunders M (2009) Quantifying the "bio-" components in biophysical models of larval transport in marine benthic invertebrates: advances and pitfalls. BiolBull 216:257–72
- Morgan SG (2014) Behaviorally Mediated Larval Transport in Upwelling Systems. Adv Oceanogr 2014:1–17
- Morgan SG, Fisher JL, Miller SH, McAfee ST, Largier JL (2009) Nearshore larval retention in a region of strong upwelling and recruitment limitation. Ecology 90:3489–3502
- Munday PL, Leis JM, Lough JM, Paris CB, Kingsford MJ, Berumen ML, Lambrechts J (2009) Climate change and coral reef connectivity. Coral Reefs 28:379–395
- O'Connor MI, Bruno JF, Gaines SD, Halpern BS, Lester SE, Kinlan BP, Weiss JM (2007) Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation. Proc Natl Acad Sci U S A 104:1266–71
- O'Connor MI, Selig ER, Pinsky ML, Altermatt F (2012) Toward a conceptual synthesis for climate change responses. Glob Ecol Biogeogr 21:693–703
- Ospina-Alvarez A, Weidberg N, Aiken C, Navarrete S (in Press) Larval transport in the upwelling ecosystem of central Chile: The effect of vertical migration for different larval development times and against the effect of environmental variability. Prog Oceanogr
- Queiroga H, Cruz T, Santos A dos, Dubert J, González-Gordillo JI, Paula J, Peliz Á, Santos a. MP (2007) Oceanographic and behavioural processes affecting invertebrate larval dispersal and supply in the western Iberia upwelling ecosystem. Prog Oceanogr 74:174–191
- Shama LNS (2015) Bet hedging in a warming ocean: Predictability of maternal environment shapes offspring size variation in marine sticklebacks. Glob Chang Biol 21:4387–4400
- Strub P, Mesías J, Montecino V, Rutlant J, Salinas S (1998) Coastal ocean circulation off western South America. In: In:, Robinson A, Brink K (eds) (eds) The sea, Vol 11. JWiley & Sons, New York, p 273–314
- Thiel M, Macaya EC, Acuna E (2007) The Humboldt Current System of northern and central Chile: oceanographic processes, ecological interactions and socioeconomic feedback. Oceanogr Mar Biol 45:195–344
- Thorson G (1950) Reproductive and larval ecology of marine bottom invertebrates. Biol Rev 25:1–45

Supplement 4

Fig. S7. Spatial variability on recruitment success and dispersal distance along the study region under different simulated scenarios. The map shows the study area where the recruitment (A to I) and release (H and J)- locations are represented by nearshore latitudinal bands of 2 km (location). Black bars show mean recruitment success (number of larvae that successfully reach the coastal zone) per latitudinal band and red lines indicate mean dispersal distance of successfully recruited larvae at a given latitudinal band. Recruitment success is shown for different simulation scenarios, and for Loxechinus albus and Fissurella latimarginata respectively, are: (A and F) passive Lagrangian transport and fixed Planktonic Larval Duration (PLD), (B and G) passive Lagrangian transport with a species-specific temperature-dependent PLD,, (C and H) particles with Diel Vertical Migration (DVM) behavior and fixed PLD, and (D and I) particles with DVM and PLD based on temperaturedependent PLD. The spatial distribution of larval released, measured as the contribution (percentage) of oocytes/m² (potential egg production) of each location to the regional (study area) production, is shown for L. albus (E) and F. latimarginata (J). Dispersal distance is orthodromic distance from the spawning (release) to the successful coastal recruitment location, in km.

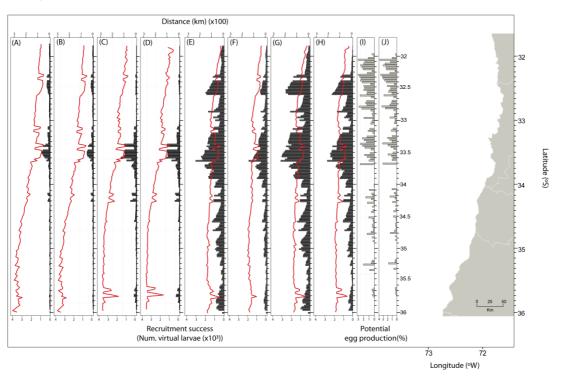
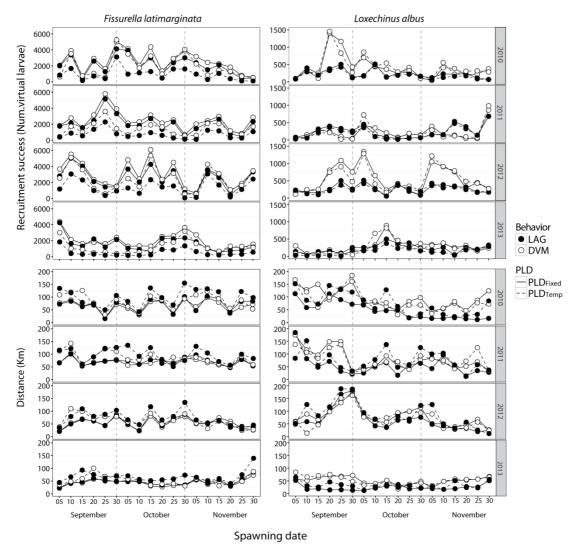


Fig S8. Temporal variability on the number of particles recruited (upper plot panel) and on dispersal distance traveled by recruited particles (lower plot panel) under different simulated scenarios. Black circles show passive Lagrangian transport (LAG) and white circles Diel Vertical Migration (DVM) behavior. Solid lines show fixed Planktonic Larval Duration (PLD_{fixed}), 5 days for F. latimarginata and 20 days for L. albus and dotted line)s temperature-dependent PLD (PLD_{Temp}).



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