Dispersal of *Munida gregaria* (Decapoda: Galatheidae) larvae in Patagonian channels of southern Chile

Roxana León, Leonardo R. Castro, and Mario Cáceres


The dispersal of *Munida gregaria* larvae in Chilean Patagonian channels was assessed in spring 2002 and 2003, and winter 2003. In winter 2003, zoea I was the most abundant stage in all channels and there were no larval stages older than zoea IV. In spring 2002 and 2003, there were six larval stages in all channels, and the greater abundance of older larvae suggested that reproduction takes place in winter and larval development in spring. Further, analysis of spatial distribution by stage revealed that early zoeae moved seawards. Generalized Additive Models analyses showed that most larval stages were temperature-dependent, and that the salinity range of the youngest zoea was wider than that of older larvae and post-larvae, coinciding with an ontogenetic distribution change from estuary to shelf. Residual flows determined with an acoustic Doppler current profiler revealed two layers of opposite flow: the shallowest layer moved seawards and the deeper layer onshore. The surface layer was wider in spring than in winter because of seasonal increase in fresh-water input. The dispersal pattern of *M. gregaria* consisted of an inner channel larval release in winter, followed by an along-channel larval drift and subsequent export to the shelf in spring. The mechanism by which juveniles return to the channels seemed to be associated with the onshore subsurface flow.

**Keywords:** export strategy, larval distribution, Magellan Province, Patagonian fjords, squat lobster.

Introduction

At least two main strategies of larvae associated with hydrodynamics have been proposed to explain the persistence of invertebrate populations with planktonic larval stages within estuaries (Sandifer, 1975; Strathmann, 1982; Epifanio, 1988a, b; Bilton et al., 2002): (i) the retention of larval stages within an estuary through behaviour (i.e. vertical migrations) associated with estuarine circulation, tides, or other processes, and (ii) the export of newly hatched stages from the estuary onto the shelf and a subsequent return migration by late larvae or early post-larvae. There is no clear distinction between these two strategies, though, and species may adopt an intermediate approach, with larvae developing either in neritic or in lower estuarine areas, depending on the characteristics of a particular estuary (including outflow rates) and its adjacent coast (Bilton et al., 2002). These strategies, although observed in many types of estuary, remain to be investigated in areas of the world where different types of retention and export mechanisms co-occur, given complex topography such as fjords, channels, basins of different size, and embayments.

The Magellan Zoogeographic Province in southern Chile is an extensive estuarine system stretching from Puerto Montt (42°30′S) to Cabo de Hornos (55°58′S), 780 nautical miles in length and including many islands with innumerable channels and fjords. This complex system resulted from continental glacial erosion attributable to the advance and retreat of ice during the Quaternary. In addition to the tectonic collapse of the longitudinal valley south of Puerto Montt, ice melted and the sea level rose to fill the basins after the glaciation and during the warmer interglacial period. Fresh-water inputs from river run-off, glacial meltwater, and heavy rains in the channels and fjords currently generate a positive estuarine circulation there (Silva et al., 1998; Antezana, 1999a; Silva and Ortiz, 2002; Palma and Silva, 2004). This geographical complexity produces a diversity of bathymetries and coastline landforms, which are responsible for the region’s complex hydrodynamics. Channels with strong tidal currents combine and alternate with systems driven by density gradients and wind; in turn, the latter drive the different environmental conditions encountered there by the fauna and flora.

In all, 17 species of galatheid have been identified along Chile’s coast. In the northern and central part of the country, *Pleuroncodes monodon* and *Cervimunida johni* are the most studied because of their economic value and heavy exploitation (Longhurst, 1968; Gallardo et al., 1994, 2004). Both species inhabit shallow and abyssal waters associated with anoxic or biogenic substrata (Retamal, 1994). Later larval stages of *P. monodon* have been associated with the oxygen minimum layers in the water column (Yannicelli et al., 2006b). Southern Chile has six species of squat lobster. The most abundant are *Munida subrugosa* (sensu White,
1847) and *Munida gregaria* (*sensu* Fabricius, 1793), and both species represent an important part of the benthic community, constituting approximately half the invertebrate biomass in the Magellan region (Arntz and Gorny, 1996).

In the southern Atlantic Ocean, *M. subrugosa* extends from Uruguay’s continental shelf waters (35°S) to Cabo de Hornos (55°S), including the Falkland Islands; in the Pacific, it is found from Chiloé (41°S) to Cabo de Hornos (55°S). Its bathymetric distribution extends from the sublittoral to 1137 m (Retamal, 1994; Arntz et al., 1999). *Munida gregaria* is found from Chiloé (41°S) to Cabo de Hornos (55°S), and its vertical distribution extends from 0 to 60 m (Retamal, 1994). Based on their geographic distributions, Viruesa (1977) and Tapella et al. (2002) proposed that *M. subrugosa* and *M. gregaria* are sympatric species in the Beagle Channel. Morphologically, Williams (1973, 1980) and Zeldis (1985) proposed that *M. subrugosa* and *M. gregaria* are a single species exhibiting two morphs: the former pelagic and the latter benthic. In the Beagle Channel, both species are benthic and similar in size. Recently, Pérez-Barros et al. (2008) used molecular data to argue against their current separate taxonomic status, and considered both species to be *Munida* sp. Following the International Code of Zoological Nomenclature (ICZN) and the evidence provided here, we validate Williams’ (1980) initial proposal, and consider the two to be the same species, namely *M. gregaria*.

In the Beagle Channel system, *Munida* shows a winter-based seasonal reproductive cycle associated with the spring–summer primary production peak (Tapella et al., 2002). Females brood their eggs for 3–4 months (June–September) until the larvae hatch (Lovrich, 1999). The species produces a large number of small eggs (~4300, average size 0.10 mm³; Tapella et al., 2002), and larval development includes five zoeal stages following a planktotrophic development period (Roberts, 1973; Williams, 1980; Vera and Bacardit, 1986; Lovrich, 1999; Thatje et al., 2003). Farther north in the Magellan Province, such in the fjords and channels of the Aysén Region, there is a seasonal pattern of localized dense larval abundance in spring. Mujica and Medina (1997) proposed that greater concentrations of early larval stages were to be found in the Lemuy and Darwin channels and that, concurrently, post-larval stages were to be found at much lower densities (maximum 38 larvae 1000 m⁻³) in Seno de Beloncavi, Seno de Aysén, and the Moraleda, King, Darwin, and Pulluche channels.

The extensive latitudinal distribution in the Magellan Province and the wide bathymetry occupied by *M. gregaria* suggest that the species might be adapted to survive in diverse environmental conditions throughout its life cycle. Adults live inside the channels, associated with areas of detritus accumulation, whereas the larvae reside in the water column, where environmental conditions (temperature, salinity, oxygen concentration) frequently vary. Here, we assessed the dispersal strategy of *M. gregaria* larvae in channels of the Aysén Region (northern Magellan Province) by investigating ontogenetic changes in distribution throughout the area in association with seasonal and spatial hydrographic variability. Our approach included estimating (i) the larval hatching period, (ii) the temporal and spatial distributions of different larval stages in the channels, (iii) larval depth variations in the water column, and (iv) the association of larval stages with environmental characteristics in the channels using Generalized Additive Models (GAMs).

### Methods

#### Study area and fieldwork

Our study was conducted in the channels and fjords of Aysén (northern Magellan Province, Chile) and included the Moraleda (45°S), Ninualac (45°05'S), Darwin (45°30'S), and Pulluche (45°50'S) channels (Figure 1). Oceanographic cruises were carried out on board the RV “Vidal Gormaz” in spring 2002 (17–23 November), winter 2003 (9–21 August), and spring 2003 (7–18 November). All channels were sampled during each cruise (except the Darwin Channel in spring 2002). The hydrographic characteristics of the water column (temperature, salinity, and dissolved oxygen) were obtained from CTD casts (SeaBird-25, equipped with an oxygen sensor). Velocity measurements were obtained at three stations located in the middle of the Ninualac, Darwin, and Pulluche channels in winter and spring 2003 (depicted by stars in Figure 1) over a 24-h period. Measurements were made with an RD Instruments 307 kHz Workhorse Acoustic Doppler Current Profiler (ADCP), which was mounted, facing down, on a 3-m long catamaran attached to the starboard side of the “Vidal Gormaz”. Good quality data were obtained through the first 100-m depth, and data ensembles were averaged every 30 s. Water velocity was decomposed into east (u) and north (v) flow components at each station. Poor data were removed following Vallee-Levinson and Atkinson (1999). The semi-diurnal tidal signal, represented by the M₂ constituent, with a period of 12.42 h, and the diurnal signal, represented by the K₁ constituent, with a period of 23.93 h, were separated from the subtidal signal of flow components using a least-squares sinusoidal regression analysis (Itzawa et al., 1991) to obtain the corresponding amplitudes and phases. The residual flow remaining after this sinusoidal analysis approximated the mean flow during the observation period.

Stratified zooplankton samples were obtained at all oceanographic stations from oblique plankton tows carried out with a Tucker trawl, with 1-m² frame and 300-μm mesh, equipped with a General Oceanic flowmeter, from 4 or 5 depths (0–20, 20–50, 50–75, 75–100, 100–150 m), depending on the station’s maximum depth. Samples were preserved in buffered 5% formaldehyde. Once in the laboratory, *M. gregaria* larvae were sorted, quantified, and identified by developmental stage following Roberts (1973): zoea I (ZI), zoea II (ZII), zoea III (ZIII), zoea IV (ZIV), zoea V (ZV), and post-larvae (P).

#### Data analysis

The density of each larval stage at each sampling depth and time was expressed as number m⁻³, Dᵢ, and larval abundance (N, individuals m⁻²) throughout the water column at each station was estimated as:

\[
N = \sum_{i=1}^{n} D_i a_i
\]

where \(D_i\) is the larval density at each depth stratum \(z_i\), and \(a_i\) the amplitude of stratum \(z_i\). Because of the large numbers and wide differences (three orders of magnitude) in larval concentration, larval abundance was transformed to (log (x+1)).

Analyses to summarize and compare larval distributions by stage in each channel and their relationships with hydrographic characteristics included weighted mean distance (km) offshore...
where \( i \) is the station in the channel, \( d \) the distance (km) of station \( i \) from the innermost station in each channel, \( N_i \) the larval abundance in the water column at the station, and \( NT \) the sum of abundances from all stations in the channel.

GAMs are used widely in marine science to predict abundance, to identify important habitats (Swartzman et al., 1992, 1995; Maravelias et al., 2000; Jensen et al., 2005), and to model stock–recruitment relationships (Cardinale and Arrhenius, 2000). We used GAMs to examine the significance of environmental characteristics such as temperature, salinity, dissolved oxygen, and geographic location (latitude, longitude) on the relative density of *M. gregaria* larval stages. Such an approach has been particularly useful in modelling the distribution of aquatic organisms, because the patchy distributions produce survey catches that are often zero-inflated (Maravelias, 1999). Here, we used GAMs with a Poisson error distribution, as considered appropriate for random count data (Begg and Marteinsdottir, 2002; Castillo-Jordán et al., 2007). We also used a log link by running the ‘mgcv’ library (v.1.1-8), following Wood (2000, 2003), under the software environment (Rv.2.0.2; Ihaka and Gentleman, 1996; http://www.r-project.org). The general model form is:

\[
D = \alpha + s(\text{Lon}, \text{Lat}) + s(T) + s(S) + s(O),
\]

where \( D \) is larval density (individuals \( 1000 \text{ m}^{-2} \)), \( \text{Lon} \) and \( \text{Lat} \) are geographic longitude and latitude, \( T \) the temperature (°C), \( S \) the salinity (psu), and \( O \) the concentration of dissolved oxygen (ml l\(^{-1}\)).

**Results**

Vertical distributions of salinity and temperature in the four channels studied are shown in Figures 2–5. Water column temperature
was almost vertically homogeneous, varying within ranges no wider than 2.5°C in all channels. There was evidence of the typical seasonal surface heating during spring in most of the temperature distributions. Salinity also showed evidence of surface increases in fresh-water input during spring from the south (Moraleda Channel; Figure 2) and from the east (Ninualac, Darwin, and Pulluche channels; Figures 3–5), as suggested by the deepening of the 30 psu isohaline on the southern and eastern sides, respectively, during spring. Fresh-water input was also accompanied by increases in dissolved oxygen on the southern and eastern sides of the channels, at the surface during spring. The channels studied therefore seem to receive most of their fresh water from continental drainage input located at ~45.5ºS.

Residual-current velocities of the z-flow (along-channel) component in winter and spring 2003 are shown in Figure 6. Except for the Pulluche Channel (right panel), profiles in the Ninualac and Darwin channels showed evidence of a typical two-layer estuarine circulation pattern. The flow was seawards (negative values) in the first 20–40 m and onshore (positive values) in the layer below. The Ninualac Channel surface layer was thicker in spring than in winter, suggesting a seasonal increase in fresh-water discharge. That channel also had the largest residual velocities of the second layer of the three studied sites, reaching 10 cm s⁻¹ at a depth of 60 m. The Darwin Channel showed no significant differences between winter and spring profiles, and the velocities in the lower layer there were weaker than in the Ninualac Channel. In the Pulluche Channel, both profiles suggested weak seaward flow in the top 70 m and no evidence of an onshore flow deeper. There, a transient wind event during winter produced a negative (landward) flow in the top 10 m.

Figure 2. Moraleda Channel temperature and salinity vertical sections during (a) spring 2002, (b) winter 2003, and (c) spring 2003. Numbers in parenthesis at the top right of each panel are maximum and minimum values of the variables. The northern side is on the left and the southern on the right.
Seasonal and interannual variability in larval abundance

Trends in the abundance of the different zoeal stages varied among seasons and years. In spring 2002, all larval stages were found, but ZV was most common. In winter 2003, only four larval stages were found, with ZI the most abundant. In spring 2003, again all larval stages were found, but ZII was the most abundant.

In the Moraleda Channel (Figure 7a) in spring 2002, all stages were found (zoeae and post-larvae). ZIV was the most abundant and P the least abundant. In winter 2003, early stages were more common, with ZI the most abundant and ZII the least. By spring 2003, all larval stages were found, but ZII was the most abundant.

In the Ninualac Channel in winter 2003 (Figure 7c), ZI were the most abundant and ZIV the least. In spring, ZII dominated and P were least abundant. Finally, in the Pulluche Channel in spring 2002 (Figure 7d), post-larvae dominated, and ZI were rarest. In winter 2003, ZI were many and ZIV rare. In spring 2003, both P and ZI abundances were low.

Spatial distribution of larvae in the channels

A mosaic plot of larval distributions by stage (Figure 8) and the weighted mean offshore distance index (OD in km) from the inner stations in each channel (Figure 9) reveals that early stages moved from the inner zone (inshore) to mid-channel and that the later stages in the outer channels moved offshore as they developed.
Moraleda Channel
The singular spatial distribution and OD index values for larvae cover the whole range from the inner (south) to the outer (north) areas (Figures 8a and 9a). By spring 2002, ZI and ZII were mainly in the inner channel, and ZIII and ZIV were better represented in the middle sector and offshore. Conversely, ZV and P were outside the channel. In winter 2003, ZI and ZII were in mid-channel. ZI and ZII were distributed seawards in the previous spring, whereas ZIII was only found outside the channel. ZIV and ZV were outside and also seawards, and post-larvae were in the middle and inshore channel.

Ninualac Channel
The distributions of larval stages and OD indices covered the whole area from inside (east) to outside (west) of the channel (Figures 8b and 9b), with a pattern similar to those of the other channels. In spring 2002, ZI and ZII were inside the channel, ZIII better represented in mid-channel and offshore, ZIV throughout and outside the channel, ZV in mid-channel, and P throughout the channel but mainly in the middle and outside. In winter 2003, ZI were mainly in the middle and ZII outside the channel. In spring 2003, ZI was found in the middle and outside the channel, whereas ZII, ZIII, ZIV, and ZV were outside; P was found mainly outside, ZIII mainly in the middle, ZIV and ZV principally in the middle and seawards, and P outside the channel and seawards.

Pulluche Channel
In spring 2002, ZI, ZII, and P were mainly in mid-channel, and ZIII, ZIV, and ZV mainly outside (Figures 8d and 9d). In winter 2003, all stages from ZI to ZIV were mainly in mid-channel, but by spring 2003, ZI was mainly inside, ZII–ZV in mid-channel, and P principally outside the channel.

Environmental variables and GAM analysis
Generally, all the main covariables (temperature, salinity, oxygen, latitude, and longitude) had significant effects on the relative abundance of larval stages (Table 1). Latitude and longitude significantly \((p < 0.005)\) influenced all stages. All larval stages except ZII were affected by temperature, and salinity influenced ZIII, ZV, and P. Late stages (ZV, and P) were also affected by dissolved oxygen. However, depth and time had no significant effect on the distributions of the larval stages.

GAM analysis demonstrated that the spatial distribution of larvae was associated with the environmental characteristics we studied (Table 2). Early stages (ZI–ZIII) were well distributed by latitude, whereas later stages (ZIV–P) tended to be in the south. In terms of longitude, ZI were distributed within the channels and the more advanced stages were more dispersed outside. Although early stages seemingly had limited temperature-dependence, later stages were more associated with higher
temperatures. ZIII, ZV, and P followed an euryhaline distribution, and late stages were more associated with high concentrations of dissolved oxygen.

Discussion
Most benthic estuarine macro-invertebrates use a planktonic larval stage to aid dispersal, unlike the juvenile and adult populations, which rarely disperse and tend to be restricted in their distributions (Bilton et al., 2002). Information on dispersal strategies of such taxa is scarce, so we lack a complete understanding of the sequence of larval developmental events. Owing to the complexity of the Patagonian Channel system and the wide latitudinal and depth distribution of *M. gregaria* reported there, we assessed the dispersal of the larval stages to determine the mechanisms that allow the species to persist in the region, with its highly contrasting seasonal environment.

Seasonal and interannual changes in larval abundance
The abundances of ZI and ZII in August (winter) and the greater abundance of ZV and P in November suggest that *M. gregaria* reproduce in winter and that larvae develop mainly in spring. These results support the observations of Tapella et al. (2002) farther south that the species releases larvae in winter in the Beagle Channel, and that the seasonal abundance of *M. gregaria* larvae in different systems is associated with peak spring phytoplankton production (Zeldis, 1985; Antezana, 1999b; Lovrich, 1999; Thatje et al., 2003). In our study, differences in total larval abundance and also in the frequency of stages were recorded.

Figure 5. Pulluche Channel temperature and salinity vertical sections during (a) spring 2002, (b) winter 2003, and (c) spring 2003. Numbers in parenthesis at the top right of each panel are maximum and minimum values of the variables. The eastern side is on the right and the western on the left.
between spring of 2002 and 2003, with fewer larvae in 2003 than in 2002, but similar abundance of all zoeae stages in 2003 in contrast to the greater abundances of older stages in 2002 (Figure 7). The causes of these differences are not known. However, lower concentrations of chlorophyll a (V. Montecino, pers. comm.) were also observed in spring 2003, as well as lower temperatures; these factors may have resulted in less reproductive output or lowered the development times of the zoeal stages. Decreased recruitment after cold springs has been reported for some crustacean populations (Lindley, 1988; Lindley et al., 1993; Sulkin et al., 1996; Anger, 2001).

We found a similar trend in frequency distribution by stage among the channels during each season (Figure 7). In spring 2002, we found all developmental stages in all channels, and their larval frequency distributions followed the same trend (more later stages), particularly in the Pulluche and Ninualac channels. In winter, ZI was the most abundant in all channels. However, whereas the first four stages were present in the Pulluche and Darwin channels, only the first two stages of zoea were present in the Moraleda and Ninualac channels. The differences in zoeal stage frequency distributions between these two pairs of channels in winter may be attributed to the effect of stratification, because the main sources of fresh-water inputs are located at ~45.5°S, as mentioned above. During winter, there is a decrease in fresh-water input that reduces stratification, affecting mostly those channels located far to the north of the region. In addition, the lack of light during winter, together with a reduction in stratification, result in a decrease in primary production, which affects the whole system trophically.

**Ontogenetic along-channel changes in larval distribution**

Spatial distribution analyses by larval stage [mosaic diagrams, weighted mean offshore distance index (OD), latitude–longitude GAM analysis] revealed that early zoeal stages tended to move from the inner part of the Moraleda Channel (south) to the outer stations along that channel (from south to north). Post-larval stages, on the other hand, returned to the inner channel (Figures 8 and 9a, Table 2). The Ninualac, Darwin, and Pulluche channels (from east to west) displayed a similar pattern; early stages were inside the channels (east), whereas advanced stages tended to be seawards (west). The one exception was the Darwin Channel in spring 2003, where early zoeae were found at the outer stations. The GAM analyses also showed a close relationship between hydrographic characteristics (temperature, salinity, and dissolved oxygen) and the different larval stages (Tables 1 and 2). Interestingly, the relationships were more evident for the older larval stages than for the earlier ones, suggesting that
the earlier stages are more tolerant of wide environmental conditions than older stages.

All larval stages (except the infrequent ZII) were significantly temperature-dependent ($p < 0.005$, Table 1). Temperature is a key factor determining larval duration because different developmental stages are strongly temperature-dependent (Gillooly et al., 2002). The temperature dependence of larval development is an important component of many ecological processes, including larval mortality, dispersal, population connectivity, and recruitment dynamics (Levin, 2006; O’Connor et al., 2007).

The dependence of ZIII, ZV, and P distribution on salinity was statistically significant, although the salinity range dependence decreased as the ontogeny advanced (Tables 1 and 2). Therefore, salinity effects on the larval physiology of decapod crustaceans can trigger observable adaptive responses in their life history. Salinity fluctuations, in turn, can modify the early morphology (changes in ontogeny), the physiological adaptation that is stress-osmotic dependent, and the selection of the larval export strategy (Giménez and Anger, 2001, 2003; Charmantier et al., 2002; Giménez and Torres, 2002; Anger, 2003). Later larval stages, in particular, are more salinity-dependent during moulting, because changes in the salinity regime may alter the normal process of ecdysis (Charmantier et al., 2002). In fact, changes in the life-history patterns of polyhaline crab larvae (i.e. Carcinus maenas) have been reported as a result of physiological processes associated with salinity (Queiroga et al., 1994). The dependence of ZV and P on oxygen was significant too, suggesting that, as larval development advances, the larvae become more dependent on greater concentrations of oxygen (Bishop et al., 2004). Whether this trend is maintained in older juvenile stages is not known. However, the life history of other species suggests that adults are more tolerant of low oxygen because they settle in detritus-rich environments where oxygen concentrations can be as low as 0.15 ml $l^{-1}$ (Burd and Brinkhurst, 1984). A pattern of ontogenetic change in residence depth associated with changes in oxygen concentration has also been observed for other galatheids from the Humboldt Current, such as P. monodon (Yannicelli et al., 2006b). Larvae of that species are released in low-oxygen waters, intermediate zoal stages drift in more oxygenated waters, and ZV and P commence vertical migration to oxygen-deficient layers, where they settle and grow until reproduction.

**Dispersal strategy of larval stages of M. gregaria**

We have proposed a conceptual model for *M. gregaria* larval dispersal in which the water circulation pattern in the channels plays a major role in determining the direction of transport. Our results show that early larval stages are released inside the channels and, as the larvae develop, they are exported towards the shelf, either along the short transverse channels or the wide south–north Moraleda Channel (Cáceres et al., 2007). There is indeed
a clear relationship between larval distribution and water column characteristics in the channels, younger larvae occurring in a wider salinity range (inshore) and older larvae tending to be in a narrower salinity range (offshore).

Ontogenetic changes in distribution, in which larvae move away from the release area as they develop and post-larvae return to the channels to support the known adult distribution patterns have been reported for other decapods (Epifanio, 1988b; McConnaugha, 1988, 1992; DiBacco et al., 2001). The dispersal pattern adopted by *M. gregaria* in the Patagonian channels follows a strategy similar to that observed in other estuaries for the similar species in New Zealand (Zeldis, 1985), but also for fish larvae in the Patagonian fjords (Landaeta and Castro, 2006). Larval dispersal depends not only on the complex physical processes that occur on spatial and temporal scales, but is also closely related to behaviour of the organisms (Morgan, 1995), the intrinsic morphological and functional group-specific characteristics of the larvae (Young, 1995), and other higher frequency oceanographic processes (e.g. tides). Here, we assessed processes on the scale of days to a few weeks and, in spatial terms from kilometres to a few weeks, and in spatial terms from kilometres. The scales of time and space to which we refer in our model provide understandable mechanisms for dispersal of the early larvae and juveniles. The mechanisms we describe need to be coupled to subsequent return mechanisms that, although not yet clear, are expected to be found nearshore, so allowing larval retention between the shelf and channels and avoiding an offshore loss of larvae from the channels where the youngest larval stages were released initially.

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**Figure 8.** Mosaic plot showing a representation of the spatial distribution by larval stage of *Munida gregaria* in the channels during each cruise. Numbers on the top of each plot are station numbers from the innermost station (1). N, northward (offshore); S, southward (inshore); E, eastward (inshore); W, westward (offshore). The darkness of the shading corresponds to number of individuals 100 m$^{-2}$, expressed as log $x+1$ (ZI, zoea I; ZII, zoea II; ZIII, zoea III; ZIV, zoea IV; ZV, zoea V; P, post-larvae).
Figure 9. Mean weighted distance of the different larval stages of *Munida gregaria* from the innermost station in each channel and cruise (ZI, zoea I; ZII, zoea II; ZIII, zoea III; ZIV, zoea IV; ZV, zoea V; P, post-larvae).

Table 1. Summary of GAM analyses used on spatial distributions of *Munida gregaria* larvae.

<table>
<thead>
<tr>
<th>Stage</th>
<th>s (Longitude, latitude)</th>
<th>s (Temperature)</th>
<th>s (Salinity)</th>
<th>s (Oxygen)</th>
<th>Deviance explained (%)</th>
<th>Adjusted $r^2$</th>
<th>GCV score</th>
</tr>
</thead>
<tbody>
<tr>
<td>ZI</td>
<td>$39.182 (&lt;0.001)$</td>
<td>$33.758 (&lt;0.001)$</td>
<td>n.s.</td>
<td>n.s.</td>
<td>48.8</td>
<td>0.577</td>
<td>0.144</td>
</tr>
<tr>
<td>ZII</td>
<td>$39.082 (&lt;0.001)$</td>
<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
<td>42.4</td>
<td>0.391</td>
<td>0.224</td>
</tr>
<tr>
<td>ZIII</td>
<td>$26.725 (&lt;0.001)$</td>
<td>$16.339 (0.003)$</td>
<td>$9.946 (0.009)$</td>
<td>n.s.</td>
<td>43.3</td>
<td>0.389</td>
<td>0.131</td>
</tr>
<tr>
<td>ZIV</td>
<td>$24.232 (0.002)$</td>
<td>$31.254 (&lt;0.001)$</td>
<td>n.s.</td>
<td>n.s.</td>
<td>56.3</td>
<td>0.565</td>
<td>0.120</td>
</tr>
<tr>
<td>ZV</td>
<td>$13.557 (0.022)$</td>
<td>$31.239 (&lt;0.001)$</td>
<td>$6.585 (0.044)$</td>
<td>$12.755 (&lt;0.001)$</td>
<td>66.4</td>
<td>0.642</td>
<td>0.205</td>
</tr>
<tr>
<td>P</td>
<td>$21.517 (&lt;0.001)$</td>
<td>$21.115 (&lt;0.001)$</td>
<td>$9.874 (0.013)$</td>
<td>$9.877 (0.020)$</td>
<td>68.0</td>
<td>0.644</td>
<td>0.382</td>
</tr>
</tbody>
</table>

ZI, zoea I; ZII, zoea II; ZIII, zoea III; ZIV, zoea IV; ZV, zoea V; P, post-larvae; n.s., not significant. The $\chi^2$ values approximate significance smooth terms associated with (longitude, latitude), (temperature), (salinity), and (oxygen), respectively. Significance values ($p$-levels) are shown in parenthesis. GCV score is the general cross-validation score for each analyse ($n = 169, p < 0.05$).
Table 2. Range dependence of Munida gregaria larvae on environmental variables.

<table>
<thead>
<tr>
<th>Stage</th>
<th>Latitude (°S)</th>
<th>Longitude (°W)</th>
<th>Temperature (°C)</th>
<th>Salinity (psu)</th>
<th>Oxygen (ml l⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>ZI</td>
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</tr>
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<td>6.0–6.5</td>
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<td>P</td>
<td>44.8–45.9</td>
<td>73.8–74.3</td>
<td>10.0–11.2</td>
<td>28.0–31.8</td>
<td>5.5–6.5</td>
</tr>
</tbody>
</table>

ZI, zoea I; ZII, zoea II; ZIII, zoea III; ZIV, zoea IV; ZV, zoea V; P, post-larvae.

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