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Effects of temperature and salinity on the survival and development of larval and juvenile *Palaemon serratus* (Decapoda: Palaemonidae) from Irish waters

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The combined effects of temperature and salinity on the survival and development of larval and juvenile Palaemon serratus *from the west coast of Ireland were investigated. Survival over time was measured at thirty combinations of temperature and salinity ranging from 10–19°C and 9–34‰ in a fully factorial design. Salinity had a stronger influence than temperature on survival at all larval stages except stage V. For juveniles the main effect changed from temperature between 100 and 200 degree days to salinity between 200 and 600 degree days and temperature between 600 and 800 degree days. Estimates of time taken to 50% mortality showed that juveniles tolerated lower salinities for longer periods and exhibited optimal salinity values which were 3‰ lower than larvae, at temperatures between 10 and 15°C. Larval stage durations were found to be influenced by temperature but not salinity. Comparison with published data suggests that populations of* P. serratus *have adapted to local conditions of temperature and salinity. The results presented here have practical implications for fisheries assessment and management, as the incorporation of environmental effects into stock–recruitment models can improve their predictive capacity.*

Keywords: *Palaemon serratus*, larvae, juveniles, temperature, salinity, development, survival

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INTRODUCTION

Decapod shrimps and prawns are an important component of coastal ecosystems as they provide a crucial link between the micro and macro trophic levels by feeding on algae, bryozoans, small crustaceans, molluscs and polychaetes and in turn are predated on by various species of fish and birds (Smaldon, 1993). *Palaemon serratus* (Pennant, 1777) is a coastal species of shrimp found in the Mediterranean, Black Sea and Atlantic Ocean from Mauritania to Denmark and is at the northern limit of its range around Ireland. It is harvested across this range and the commercial fishery in Irish coastal waters removed between 150 and 550 m per year between 1990 and 2006. This catch represented an annual removal of 29–66% of the spawning stock biomass between 2005 and 2006 depending on region (Kelly *et al.*, 2009). Irish landings of this species increased throughout the 1990s, although since 1999 the general trend has been downwards, with large inter-annual fluctuations in catch rates and landings (Fahy & Gleeson, 1996; Kelly *et al.*, 2009). The reasons for these fluctuations are not known, but may be due to inter-annual variability in recruitment either because of restricted spawning output, as a result of excessive fishing or natural mortality on mature adults, or due to variability around the stock–recruitment relationship caused by environmental effects acting on early life history stages.

The life cycle of *P. serratus* includes a planktonic larval phase and demersal juvenile and adult phases (Smaldon, 1993). Larvae hatch from May onwards and are common in inshore surface waters in July (Figueras, 1987). The number of larval stages is variable depending on environmental conditions but typically there are eight or nine (Fincham & Figueras, 1986). Late stage larvae settle into shallow sub tidal habitats in late July and August (Forster, 1951; De Bhaldraithe, 1971) and appear in the fishery in mid-October (Kelly *et al.*, 2009). Over this developmental period the larvae and juveniles are exposed to large variations in temperature and salinity due to the effects of solar heating, evaporation, rainfall and river flow (Figueras, 1987). These environmental variables have previously been shown to have significant effects on the survival, metabolism and growth of *P. serratus* larvae in the Mediterranean (Yagi & Ceccaldi, 1984, 1985; Yagi *et al.*, 1990).

Palaemonid shrimp have body fluids that are hypotonic to seawater and must hyporegulate in order to maintain the correct ionic balance (Panikkar, 1941; Parry, 1954; Spaargaren, 1972). When exposed to salinity outside of their optimum range they spend an increasing amount of energy on osmoregulation to maintain homeostasis. This energy demand is at the expense of other metabolic functions and if the environmental conditions deviate too far from the optimum, homeostasis cannot be maintained and the animal dies. In general, the palaemonid family of shrimp exhibits

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well developed hyper- and hypo-osmotic regulatory capabilities in mid-range salinities (Freire *et al.*, 2003). However, *P. serratus* is a marine species (Smaldon, 1993), which only enters estuaries temporarily prior to larval release. Consequently, it has a higher iso-osmotic point and a more restricted osmoregulatory range than the fully estuarine *Palaemon longirostris* and *Palaemon macrodactylus* (Gonzalez-Ortegon *et al.*, 2006). The influence of salinity on the rate of respiration in the larvae of *P. serratus* from the Mediterranean was found by Yagi *et al.* (1990) to have a quadratic shape with lower metabolic rates, as measured by oxygen consumption, occurring at both low (13‰) and high (43‰) salinities with the optimum between 25 and 31‰.

As with all ectotherms, the body temperature of *P. serratus*, and hence its metabolic rate, is dependent on ambient temperature. The relationship between metabolism and temperature is positive, but non-linear, with an upper and lower limit. In larval *P. serratus* the maximum metabolic rate of physiological processes, such as osmoregulation, was found by Yagi *et al.* (1990) to occur at 29°C. Combinations of low temperature and low salinity have a doubly negative effect on the growth and survival of *P. serratus* larvae (Yagi & Ceccaldi, 1985).

Off the south coast of Ireland, the average sub-surface water temperatures during the larval and post-larval period from May to July ranged from 12–15°C (Marine Institute data 2004–2006). In contrast the optimal temperature for rearing *P. serratus* in the UK was estimated by Reeve (1969b) to be in the range 22–26°C, and larval survival was reduced and development was prolonged at lower temperatures. Sub-surface salinity off the south coast of Ireland during April and May (Marine Institute data 2003–2007) was 26–35‰. In addition the annual rainfall data on the south coast (Met Eireann data 1998–2004) displayed 42% variation in annual precipitation which suggests that there is significant interannual variation in salinity in coastal and estuarine areas. It is therefore likely, given the published data, that temperature and salinity conditions in Irish waters are sub-optimal for development and survival of *P. serratus* unless these populations have specifically adapted to these conditions.

The purpose of the present work was to model the survival of larvae and juveniles of *P. serratus* hatched from mature berried females taken in Irish waters over a range of temperature and salinity conditions which reflect those in Irish coastal waters. Previous work on the related species *P. adspersus* and *P. squilla* (Berglund & Lagercrantz, 1983) showed adaptation of shrimp populations to local environmental conditions and significant genetic differences existed between populations along the European Atlantic coast. A comparison of the effects of temperature and salinity on larval development and survival in populations of *P. serratus* from Ireland and the Mediterranean might indicate if they have adapted to local conditions. Adaptive genotypic or phenotypic plasticity is an important feature of species physiology in coping with environmental change, at any given location, and in determining its overall geographical range (Gotthard & Nylin, 1995).

MATERIALS AND METHODS

Re-circulating aquaculture systems (RAS)

Adult shrimp were sourced from Rossaveel, County Galway on the mid-west coast of Ireland and were transferred directly to a laboratory at Carna, County Galway. Here the ovigerous females were removed and divided equally between 5 independent, 250 l, thermostatically controlled, re-circulating aquaculture systems (RAS). The water temperatures were set at 10°C, 12°C, 15°C, 17°C and 19°C and the brood-stock was fed to satiation with pelleted food (Frippak Ltd 'Breed Shrimp'). A light:dark cycle of 10:14 hours was maintained. Cannibalism and physical injury in the holding tanks due to aggressive behaviour (Reeve, 1969a) was minimized by the use of AquaMat^{TM} artificial seaweed. During the brood-stock holding period the temperature, dissolved oxygen (DO), salinity and ammonia levels were recorded on alternate days. Temperature, salinity and DO were monitored using a multi-probe (YSI 2500) while ammonia concentration was determined using a hand held colorimeter (Hach DR/850).

Embryo development was monitored by viewing egg samples under a binocular microscope (Philips, 1971). When well developed embryos were observed, a 70 l larval collection device was positioned underneath the outflow pipe from the main tank to collect larvae that were passively removed from the brood tank. To ensure that the larvae at the start of an experiment were at the same age, only larvae that hatched on the day prior to the beginning of the experiment were used.

Water quality parameters

Average water temperature over the brood stock holding period (17 February to 3 May 2005) for each RAS was 9.1°C, 11.6°C, 15.2°C, 16.7°C and 18.8°C. Dissolved oxygen values were higher at lower temperatures with an average of 7.6 mg.l^{-1} at 10°C and 6.1 mg.l^{-1} at 19°C. Levels of DO for the 12°C, 15°C and 17°C were in between these two extremes. In general it is recommended that DO levels in RAS be maintained at >5 mg.l^{-1} (Timmons *et al.*, 2002). Recorded values for salinity in the brood-stock holding systems showed a significant ($P < 0.01$) relationship with temperature which was possibly due to evaporation. Mean salinity at 10°C and 19°C was 34.8‰ and 36.6‰ respectively, with standard deviations across all RAS ranging from 0.42–0.86‰. The ammonia concentration showed no clear relationship with temperature and mean values ranged from 0.21 ± 0.17 mg.l^{-1} to 0.29 ± 0.26 mg.l^{-1}. A maximum of 1.05 mg.l^{-1} was recorded at 17°C. This value is a factor of 10 lower than the lethal limit for adult *P. serratus* of 10 mg.l^{-1} (Reeve, 1969a). Water temperatures recorded over the experimental period, 11April to 26 August 2005, fell within 0.2°C of the target with standard deviations of between 0.3°C and 0.6°C.

Larval experimental design

The temperature control systems for the larval experiments were set at 10°C, 12°C, 15°C, 17°C and 19°C. Each system contained six experimental vessels containing 1.5 l of diluted seawater at a salinity of 9‰, 14‰, 19‰, 24‰, 29‰ and 34‰. This resulted in a total of 30 temperature/salinity combinations in a fully factorial, non-replicated experimental design. This range of temperature and salinity was selected as it encompassed the environmental conditions likely to be experienced by larvae and juveniles in Irish waters during May and June. One hundred larvae at zoeal stage I were transferred into each of the 30 experimental vessels. To avoid temperature shock the larvae were sourced from the rearing

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systems at the same temperature as the experiments. Aeration was provided to each vessel and the rate of airflow was controlled to ensure a steady stream of bubbles. The shrimp larvae were supplied with live nauplius stage brine-shrimp (*Artemia salina*) at a density of ~10 ml^{-1}. To ensure maximum nutritional value and to reduce the risk of bacterial (e.g. *Vibrio* spp.) infection the *Artemia* cysts were decapsulated prior to incubation using sodium hypochlorite.

Numbers of viable larvae remaining in each experimental vessel were counted on alternate days. After counting, a subsample was viewed under a binocular microscope to determine the average larval stage (Fincham & Figueras, 1986). After counting and staging, the larvae were returned to the experimental vessel with water at the original temperature and salinity, and re-supplied with *Artemia* at the correct density.

Juvenile rearing

When larvae were to be on-grown to juveniles, they were removed from the larval collection system and transferred to a static 70-l vessel containing seawater at salinity of ~34‰. These rearing tanks were supplied with moderate aeration and immersion heaters which maintained the temperature at ~20°C. Brine-shrimp nauplii (*Artemia salina*) were prepared and added in the same manner as described for the larvae. In addition 3 l of mixed algal culture (*Tetraselmis* sp., *Isocrysis* sp. and *Nannochloropsis* sp.) was added to each rearing tank. These algal species have been shown to protect against disease, to enrich the nutritional content of the *Artemia* and to stimulate larval feeding (Duerr *et al.*, 1998; Soares *et al.*, 2006).

Previous work on the rearing of *P. serratus* larvae by Reeve (1969a) showed that the time taken from hatching to juvenile metamorphosis is a function of temperature and takes approximately 600 degree days. Degree days is the product of the number of days and temperature, and it is a necessary standardization because metabolism in exothermic animals, and hence the rate of development, is a function of temperature. Larvae at zoeal stage I were added to each rearing tank over a period of 6 days, after which a new tank was set up for subsequent batches of larvae. Separation of ages minimized the risk of cannibalism. Water quality was maintained by draining and refilling the rearing tanks on alternate days. *Artemia* nauplii and mixed algal culture were re-supplied as described above.

Juvenile experimental design

Before starting the juvenile experiments, a sub-sample was placed on a 1 mm Sedgewick–Rafter Counting Cell (Pyser SGI Ltd) and viewed under binocular microscope in order to determine the average size. Sixteen per cent of the juveniles used in the experiments (240/1500) were measured. The average total length ± standard deviation was 9.0 ± 0.7 mm with a range of 7–11 mm. Temperature and salinity conditions for the juvenile experiments were the same as those used in the larval experiments. The experimental vessels were modified by the addition of a single strip of AquaMat™ (~20 cm long by 1 cm wide). This provided the juveniles with a surface to settle on and was weighted at one end so that it floated vertically in the experimental vessel. *Artemia* feeding rates were the same as for larvae (~10 per ml), however, a small amount of prepared food (INVE Aquaculture Ltd Product: PL + 500) was also added. Fifty juveniles were introduced at the start of each experiment and the water was changed every other day at which time surviving juveniles were counted.

As age increased in the experiments, the variation in the moult-stage distribution also increased due to individual variation in the inter-moult period. In the larval experiments this developmental process was accounted for by following the numbers at each zoeal stage. However, juveniles do not exhibit discrete morphological changes as they grow. Consequently, selecting a point in time from the continuous time-series of juvenile data to draw samples was more subjective. Samples were extracted at 100, 200, 400, 600 and 800 degree days.

Modelling the experimental results

The numbers of larvae and juveniles surviving over time were plotted as wire-frame, three-dimensional charts: x (temperature), y (percentage surviving) and z (salinity). A temperature/salinity response surface model was then fitted to the x, y, z data so that larval and juvenile survival over time could be predicted over the range of temperature and salinity conditions covered in the experiments. In addition, the regression and analysis of variance (ANOVA) outputs of this analysis revealed which variable, or combination of variables, had the greatest effect on mortality. A quadratic model of the following form was fitted to the data:

$$y = a + (B_1x_1) + (B_2x_2) + (B_{11}x_1^2) + (B_{22}x_2^2) + (B_{12}x_1x_2) \quad (1)$$

where: y = larval/juvenile numbers, B_1 = factor 1 (i.e. temperature), B_2 = factor 2 (i.e. salinity), B_{11} and B_{22} = quadratic terms (i.e. 'temperature²' or 'salinity²'), B_{12} = interaction term (i.e. 'temperature by salinity') and a = constant.

The quadratic response surface model was fitted, in Minitab©, using a least squares loss function, as a multiple regression model with five explanatory variables (temperature, salinity, quadratic terms for each and interaction term). The statistical significance of each of the parameters in the quadratic model and their interactions can be interpreted as follows: if there is no relationship between the response variable and the explanatory variables then the response surface is flat with a slope of zero. If the linear term of one explanatory variable is significant then the surface is tilted along that axis. If the squared term of that same explanatory variable is also significant then the surface is both tilted and curved along that axis. If the linear and squared terms of both explanatory variables are both significant then the surface is tilted and curved along both axes thereby producing a dome shaped surface. If the interaction term is significant then the curvature of the dome surface will be asymmetrical.

Time taken to 50% mortality and estimation of optimal salinity

To compare the results of all the temperature/salinity experiments, a single numerical value, the time to 50% survival or LT_{50}, was calculated which described the larval and juvenile survival under each of the 30 temperature/salinity combinations. Linear regressions were constructed for each of the

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experiments using the natural log of the proportion alive against degree days. The point of intersection of the regression line and the x-axis provided the estimate of the time to 50% mortality. These LT_{50} values were then plotted against their respective salinities for each temperature tested, and a quadratic regression model was fitted. The asymptotic point on the model provided estimates of the optimal salinity for survival at each temperature while the intersection with the x-axis nearest the origin provided estimates of the 'critical salinity', i.e. the salinity that would 'instantaneously' reduce the number of larvae to 50%.

Larval development

The duration to each larval stage (in days) was taken as the median development point, or the point at which half of the larvae had moulted to the next stage. These values were then logged and plotted against temperature and salinity. Linear regression analyses were carried out to determine the effects of each experimental variable on the development rate. Declining numbers of larvae over time meant that the analyses were compromised for the later developmental stages.

RESULTS

Larval survival in relation to temperature and salinity

By larval stage II (Figure 1A) 100% mortality had occurred at 9‰ salinity, across all temperatures. A relatively flat-topped response was observed for all temperatures at salinities >19‰, however, numbers were also reduced for combinations of high salinity (29‰ and 34‰) and low temperature (10°C and 12°C). By larval stage III (Figure 1B) there was a decline in numbers alive at the lower temperatures (i.e. <15°C) which resulted in the formation of a slope from the lower left to the upper right hand side. This pattern continued to stage IV (Figure 1C) although by stage V there was an increased mortality at the higher temperature/salinity combinations, resulting in the formation of a single survival peak at 15°C and 29‰ (Figure 1D). Survival at stage VI (Figure 1E) was characterized by 2 peaks at 15°C and 24‰, and 19°C and 19‰. The survival peak at 15°C and 29‰ had weakened by stage VII (Figure 1F) and disappeared by larval stage VIII (Figure 1G) leaving a single maximum at 19°C and 19‰. By stage IX (Figure 1H) only 6 larvae out of the original 3000 were alive. No larvae achieved metamorphosis under the experimental conditions.

Juvenile survival in relation to temperature and salinity

After 100 degree days (Figure 2A) survival at the lowest temperature (10°C) and lowest salinity (9‰) was 42% while the average survival at 15 °C, 17 °C and 19 °C was >90%. Survival at 200 degree days at 10°C was <60% across all salinities and after 400 degree days it was <45% (Figure 2B, D). At the highest temperature of 19°C the survival at 34‰ salinity was 58% after 400 degree days. Highest survival (72–86%) occurred at 19–29‰ salinity and 15–17°C. After 600 degree days there were no juveniles alive at 10°C or 12°C, and the highest survival of 66% was at 17°C and 19‰ salinity (Figure 2F). This trend continued after 800 degree days with no survival across all salinities at 10°C, 12°C and 15°C and a single point of survival of 46% at 17°C and 19‰ salinity (Figure 2H).

A model of survival in relation to temperature and salinity

At zoeal stage II the fitted quadratic model accounted for 79% (adjusted R^2) of the variance in the survival in relation to temperature and salinity. Both salinity and salinity^2 terms were significant ($P < 0.01$). Thus the general shape of the quadratic model was tilted and curved along the salinity axis. At zoeal stage III both the linear salinity and salinity^2 variables remained significant ($P < 0.05$), however, by stage IV only the salinity^2 value was significant ($P < 0.05$). Temperature was the only significant variable at larval stage V ($P < 0.05$), although the goodness of fit of the model was just 48%. Salinity^2 was the most influential factor at larval stage VI ($P < 0.05$), VII ($P < 0.05$) and VIII ($P < 0.05$) and at the final larval stage, temperature ($P < 0.05$), temperature^2 ($P < 0.05$) and the interaction term ($P < 0.01$) were all significant. Thus salinity was the most influential variable in determining larval survival from stages I–IV, VI, VII and VIII, while temperature was most influential at stages V and IX. The ANOVA showed that the quadratic model was significant ($P < 0.01$) for larval stages II–V and IX and for stages VI and VIII ($P < 0.05$). The model was not significant for larval stage VII.

The fit of the quadratic model on the survival of the juveniles was more variable than for larvae with temperature, salinity and temperature^2 being significant ($P < 0.01$, adjusted R^2 64%) after 100 degree days. Temperature ($P < 0.05$) and salinity ($P < 0.01$) remained significant after 200 degree days, although the main response was related to salinity^2 ($P < 0.05$). After 400 degree days all variables, except the interaction term, were significant ($P < 0.01$, adjusted R^2 68%). Temperature and temperature^2 were the most influential variables after 600 degree days ($P < 0.01$). None of the variables were significant ($P > 0.05$, adjusted R^2 36%) after 800 degree days. The quadratic model was significant for the juvenile data ($P < 0.01$) for all of the time-points tested.

Time taken to 50% mortality and estimation of optimal salinity

The time taken to reduce the larval numbers to 50% (LT_{50}) (Table 1) was plotted against salinity and a quadratic model was fitted to estimate the optimal salinity for larval survival at each temperature (Table 2). The fit of the model was good for 10°C, 12°C and 15°C with $R^2 > 0.95$, however, it declined at 17°C ($R^2 = 0.58$) and 19°C ($R^2 = 0.10$). It was not possible to estimate the LT_{50} for the lowest salinity of 9‰ as the time-series for these experiments did not yield sufficient data. However, from the limited data it was evident that the LT_{50} at this salinity was 2–4 days at all temperatures. Optimal salinity at 10°C and 12°C was estimated to be 29‰ while at 15°C and 19°C it was 28‰. At 17°C the optimal salinity level was 21‰. In all cases the larvae preferred salinity of less than 34‰. The point where the quadratic curve

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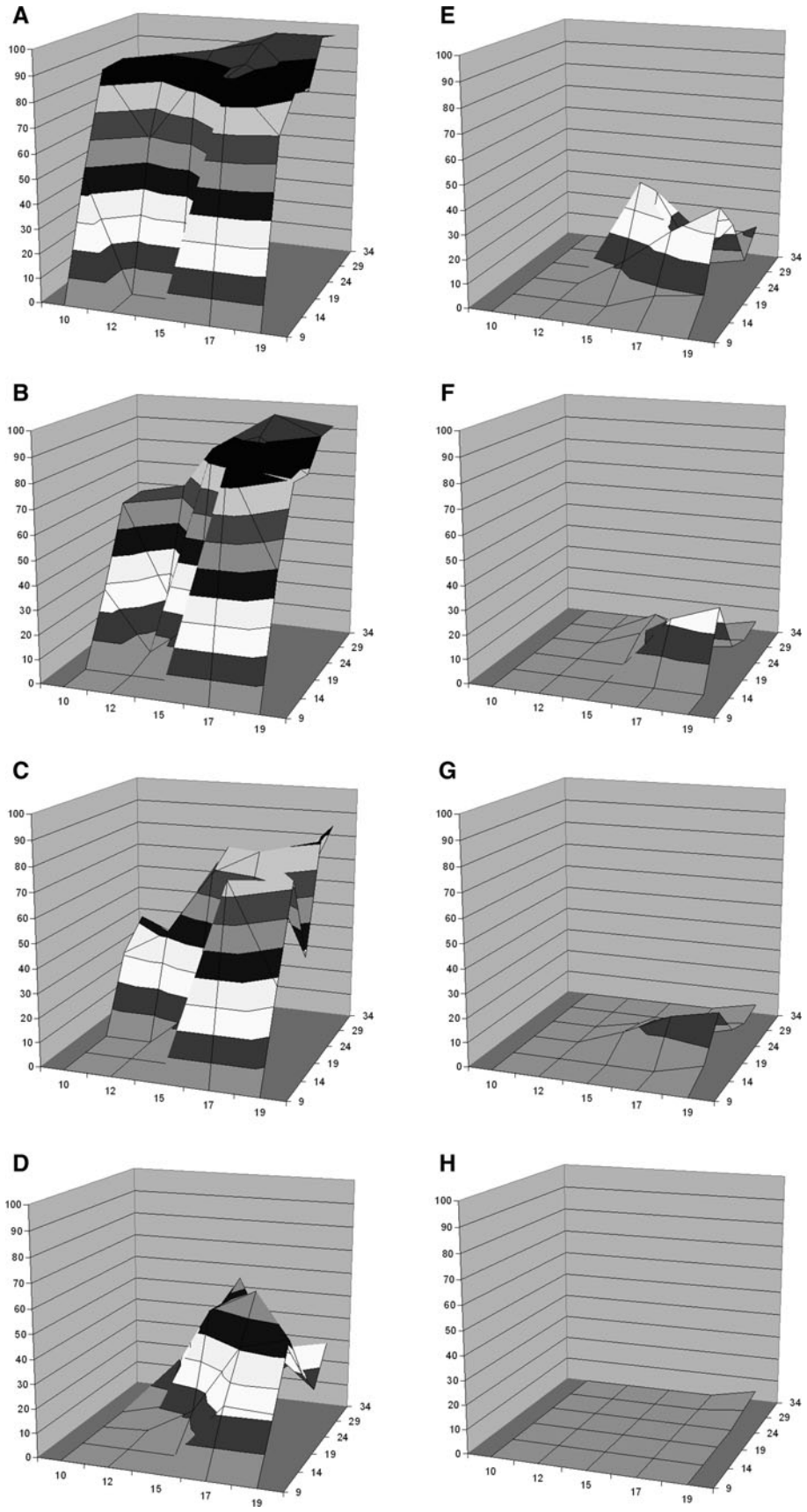

Fig. 1. Percentage survival (y-axis) of *Palaemon serratus* larvae in relation to temperature (x-axis) and salinity (z-axis) at zoeal stages II–IX (charts A–H).

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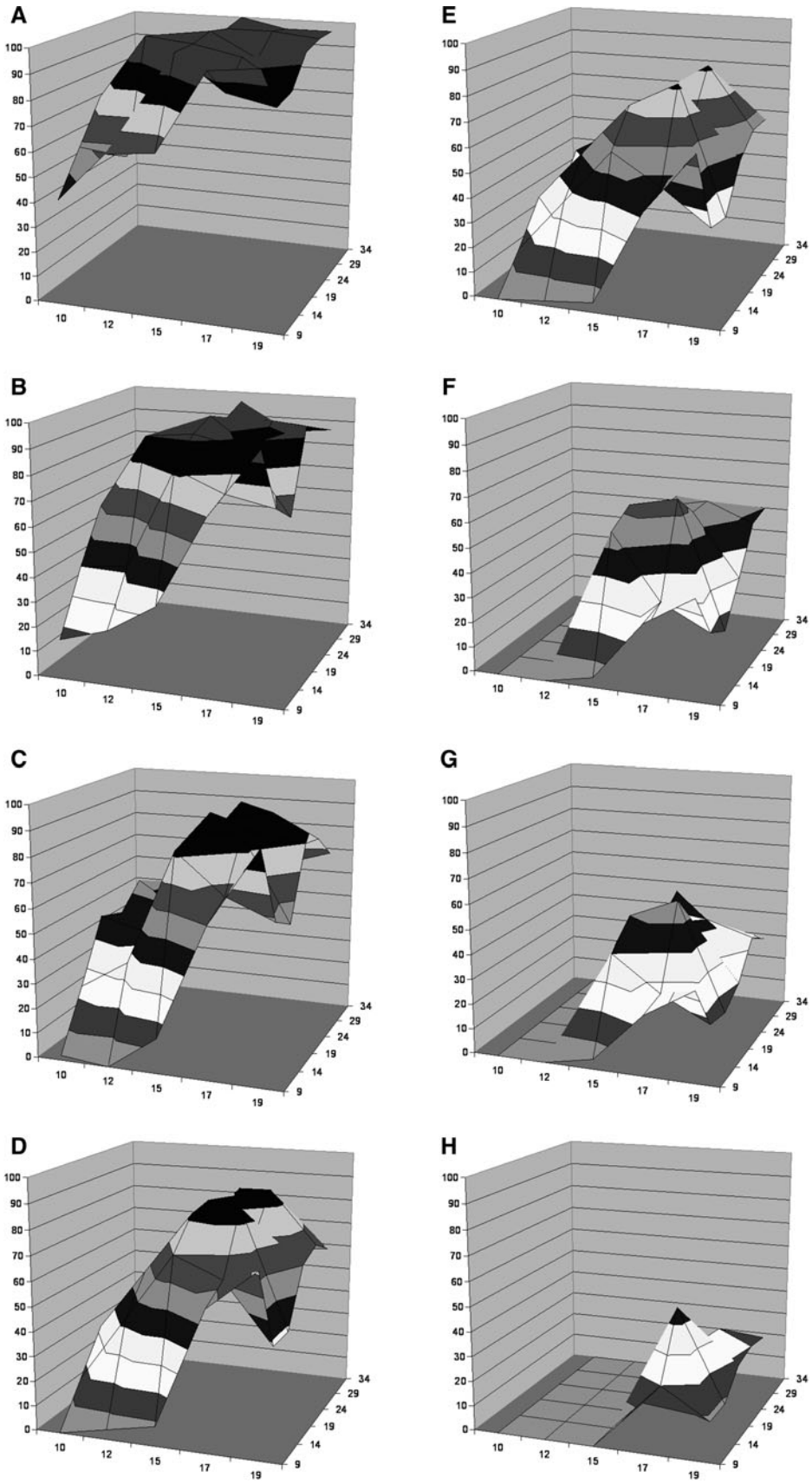

Fig. 2. Percentage survival (y-axis) of *Palaemon serratus* juveniles in relation to temperature (x-axis) and salinity (z-axis) at 100, 200, 300, 400, 500, 600, 700 and 800 degree days (charts A–H).

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Table 1. Linear regression coefficients for natural log of proportion of *Palaemon serratus* larvae alive (y-axis) against time (x-axis) and time required to reduce initial numbers to 50%.

Temperature (°C)	Salinity (‰)	Slope	Constant	R^2	N	Days to 50%	Degree days to 50%
10	9	–	–	–	1	–	–
10	14	0.2634	−4.6108	0.90	12	17.5	175.0
10	19	0.1776	−5.0022	0.90	21	28.2	281.7
10	24	0.1066	−3.8686	0.93	29	36.3	362.9
10	29	0.0788	−3.3775	0.88	29	42.9	428.6
10	34	0.0781	−2.7614	0.84	28	35.4	353.6
12	9	–	–	–	1	–	–
12	14	0.8448	−6.1332	0.99	4	7.3	87.1
12	19	0.3523	−4.9765	0.90	14	14.1	169.5
12	24	0.1917	−4.6177	0.98	20	24.1	289.1
12	29	0.1163	−3.1675	0.93	20	27.2	326.8
12	34	0.1261	−2.8951	0.89	20	23.0	275.5
15	9	–	–	–	1	–	–
15	14	0.6852	−6.3455	0.91	5	9.3	138.9
15	19	0.1570	−2.5924	0.85	19	16.5	247.7
15	24	0.1675	−4.0540	0.94	19	24.2	363.0
15	29	0.1749	−4.1410	0.91	19	23.7	355.1
15	34	0.1755	−3.7118	0.87	15	21.1	317.2
17	9	–	–	–	1	–	–
17	14	0.2196	−4.1683	0.89	15	19.0	322.7
17	19	0.1734	−3.1603	0.85	15	18.2	309.8
17	24	0.3280	−6.0763	0.91	13	18.5	314.9
17	29	0.3403	−6.7046	0.88	11	19.7	334.9
17	34	0.3195	−4.8069	0.90	11	15.0	255.8
19	9	–	–	–	1	–	–
19	14	0.2095	−2.6623	0.94	15	12.7	241.4
19	19	0.1613	−3.0648	0.96	15	19.0	361.0
19	24	0.2235	−3.0377	0.92	14	13.6	258.2
19	29	0.3346	−5.1921	0.95	14	15.5	294.8
19	34	0.2771	−4.5359	0.95	15	16.4	311.0

intersected the x-axis represented the salinity level that would 'instantaneously' reduce the number of larvae to 50%. At 10°C this critical salinity was ~9.5‰ while at 12°C and 15°C it was estimated to be 12.0‰ and 10.5‰ respectively. Values for LT_{50} at 17°C and 19°C were similar across all salinities, implying that the larvae tolerated salinities as low as 14‰ for extended periods at temperatures ≥17°C.

Juveniles had a greater tolerance of low salinity than larvae (Table 3). At 9‰ salinity and 10°C the LT_{50} was 111 degree days, while at 12°C and 15°C the LT_{50} was 139 degree days and 158 degree days respectively. LT_{50} values at 9‰ salinity and 17°C and 19°C were 499 degree days and 621 degree days respectively. At 10°C, salinity of ~5.5‰ was required to 'instantaneously' reduce the number of juveniles to 50% (Table 4). The optimal salinity for juvenile survival at 10°C was 26‰ while at 12°C and 15°C it was 27‰ and 25‰. The optimal salinity at 17°C was 23‰, although the survival at this temperature was similar across all salinities. At 19°C it was 29‰. The optimal salinity of 26‰ for juvenile survival at temperatures of 10°C, 12°C and 15°C was, on average, 3‰ lower than that for larvae.

Larval development

Multiple linear regression of the log development rate on temperature and salinity showed that the time to each larval stage was significantly ($P < 0.01$) influenced by temperature but not salinity. The various salinity treatments were consequently used as pseudo replicates to calculate the average developmental durations at each temperature (Table 5). The relationship between temperature (T) and development rate (D) to larval stage IV (Figure 3) was described by a negative power function ($D = 2874.9 \times T^{-1.7978}$) and was significantly

Table 2. Quadratic regression coefficients for LT_{50} in degree days against salinity to estimate optimal and critical values for *Palaemon serratus* larval survival.

Temperature (°C)	N	Squared term	Linear term	Constant	R^2	Critical salinity (‰)	Optimal salinity (‰)
10	5	−1.08	62.04	−490.91	0.96	9.5	29
12	5	−1.00	58.57	−551.56	0.96	12.0	29
15	5	−1.19	66.42	−564.46	0.98	10.5	28
17	5	−0.34	13.97	182.89	0.58	–	21
19	5	−0.19	10.70	157.02	0.10	–	28

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Table 3. Linear regression coefficients for natural log of proportion of *Palaemon serratus* juveniles alive (y-axis) against time (x-axis) and time required to reduce initial numbers to 50%.

Temperature (°C)	Salinity (‰)	Slope	Constant	R^2	N	Days to 50%	Degree days to 50%
10	9.0	0.1985	−2.2087	0.93	15	11.1	111.3
10	14.0	0.0706	−1.2545	0.81	25	17.8	177.7
10	19.0	0.0580	−1.7625	0.92	24	30.4	303.9
10	24.0	0.0664	−1.8329	0.77	25	27.6	276.0
10	29.0	0.0504	−1.7859	0.73	25	35.4	354.3
10	34.0	0.0630	−1.5937	0.78	25	25.3	253.0
12	9.0	0.2720	−3.1466	0.94	12	11.6	138.8
12	14.0	0.1040	−1.6413	0.76	13	15.8	189.4
12	19.0	0.2450	−5.6522	0.90	6	23.1	276.8
12	24.0	0.1267	−2.7149	0.77	13	21.4	257.1
12	29.0	0.1460	−2.8018	0.80	13	19.2	230.3
12	34.0	0.1171	−2.5218	0.70	13	21.5	258.4
15	9.0	0.1158	−1.2204	0.79	23	10.5	158.1
15	14.0	0.0705	−2.8499	0.82	21	40.4	606.4
15	19.0	0.0890	−3.9883	0.90	21	44.8	672.2
15	24.0	0.0917	−3.9892	0.97	19	43.5	652.5
15	29.0	0.0965	−3.8746	0.94	21	40.2	602.3
15	34.0	0.1073	−4.4550	0.93	20	41.5	622.8
17	9.0	0.0722	−2.1185	0.88	30	29.3	498.8
17	14.0	0.0794	−2.5569	0.91	32	32.2	547.4
17	19.0	0.0664	−3.1859	0.98	32	48.0	815.7
17	24.0	0.0737	−2.8402	0.98	32	38.5	655.1
17	29.0	0.1009	−4.0969	0.98	32	40.6	690.3
17	34.0	0.0921	−2.9454	0.93	32	32.0	543.7
19	9.0	0.1295	−4.2295	0.97	26	32.7	620.5
19	14.0	0.1105	−2.2221	0.96	22	20.1	382.1
19	19.0	0.1039	−1.8848	0.94	22	18.1	344.7
19	24.0	0.1162	−3.2704	0.97	28	28.1	534.7
19	29.0	0.1008	−3.1710	0.97	27	31.5	597.7
19	34.0	0.1057	−3.0960	0.95	28	29.3	556.5

different for Irish and Mediterranean (Yagi & Ceccaldi, 1985) populations (analysis of covariance, $P < 0.05$).

DISCUSSION

The results presented show that larvae and juveniles of *Palaemon serratus* survive and develop over a broad range of salinity and temperature. Nevertheless, increased mortality rates were observed at combinations of low temperature and low salinity. Larval survival increased with increasing salinity at temperatures between 10 and 19°C although survival at 34‰ was also sub-optimal. At low salinity the survival of juveniles was higher than that of larvae and they also had lower salinity optima. The tolerance of larval *P. serratus* to a broad range of salinities is not unusual among the Palaemonidae and has been demonstrated in the early life stages of *Palaemon xiphas* and *Palaemon adspersus* (Guerao *et al.*, 1993). Such euryhaline physiology is evidence of adaptation by these shrimp to the low salinity conditions which they encounter in coastal and estuarine habitats during their early life history (Smaldon, 1993).

It is generally recognized that temperature, acting either independently or in conjunction with other environmental factors, is one of the major factors affecting the survival of decapod larvae (Costlow, 1967; Hicks, 1973; Rochanaburanon & Williamson, 1976; Rothlisberg, 1979; Cockroft & Emmerson, 1984; Preston, 1985; Anger, 1991; Brown *et al.*, 1992; Kumlu *et al.*, 2000; Lárez *et al.*, 2000; Zacharia & Kakati, 2004; Li & Hong, 2007). However, in the present study the quadratic response model showed that salinity was more important than temperature in determining survival at all larval stages except stage V. In the case of juveniles the main curvature of the model changed from temperature after 100 degree

Table 4. Quadratic regression coefficients for LT_{50} in degree days against salinity to estimate optimal and critical values for *Palaemon serratus* juvenile survival.

Temperature(°C)	N	Squared term	Linear term	Constant	R^2	Critical salinity (‰)	Optimal salinity (‰)
10	5	−0.74	38.57	−189.28	0.86	5.5	26
12	5	−0.41	21.49	−19.31	0.82	–	27
15	5	−1.86	93.05	−453.10	0.82	–	25
17	5	−1.36	61.43	−33.96	0.67	–	23
19	4	−2.31	136.54	−1413.60	0.99	–	29

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Table 5. Average cumulative duration (days) of *Palaemon serratus* to each larval stage in relation to temperature (number of experimental observations, standard deviation).

Temperature (°C)	ZI–ZII	ZI–ZIII	ZI–ZIV	ZI–ZV	ZI–ZVI	ZI–ZVII	ZI–ZVIII	ZI–ZIX
10	17.4 (5, 1.7)	35.5 (4, 2.5)	49.3 (3, 1.2)	–	–	–	–	–
12	14.0 (4, 0.0)	25.5 (4, 4.7)	32.7 (3, 4.2)	37.3 (3, 2.3)	–	–	–	–
15	8.8 (5, 1.8)	15.5 (4, 1.9)	19.5 (4, 1.0)	27.0 (4, 2.0)	30.0 (3, 0.0)	35.0 (2, 1.4)	38.0 (1, -)	–
17	6.0 (5, 0.0)	10.8 (5, 1.1)	17.6 (5, 0.9)	20.8 (5, 1.8)	26.7 (3, 1.2)	27.0 (2, 1.4)	29.0 (2, 1.4)	–
19	4.8 (5, 1.1)	8.4 (5, 2.2)	15.6 (5, 2.2)	20.0 (5, 0.0)	21.6 (5, 0.9)	24.0 (5, 0.0)	26.0 (5, 1.4)	28.0 (2, -)

days to salinity after 200 degree days and back to temperature after 600 and 800 degree days.

The increase in larval mortality rates after ~300 degree days may have been unrelated to temperature and salinity and may instead have been due to changes in the physiology of the larvae at this point in their development. Yagi *et al.* (1990) noted that a maximum respiration rate was observed in zoeal stage IV which corresponded with a shift towards a more carnivorous diet. A sudden increase in proteasic activity had previously been noted at this stage by Van Wormhoudt (1973) suggesting an increase in dietary protein. In the present study 49%, 62% and 81% of the larvae at 15°C, 17°C and 19°C respectively were at zoeal stage IV when the mortality rates increased. It seems likely that the additional metabolic demand of making the developmental transition from zoeal stage IV resulted in the increased mortality rates observed at this time.

Genetic studies of *P. adspersus* and *P. squilla* show that gene flow is restricted between neighbouring populations (Berglund & Lagercrantz, 1983). This restricted gene flow may be the result of the estuarine distribution limiting offshore and alongshore dispersal of the early life stages and may lead to adaptation to local environmental conditions and to different physiological preferences at different latitudes (Bilton *et al.*, 2002; Freire *et al.*, 2003). Experiments by Yagi & Ceccaldi (1985), on a Mediterranean population, found that survival was highest at high temperature (21–25°C) and high salinity (25–37‰). This contrasts with the present work where larval survival was highest between 15–17°C and optimal salinity was ≤29‰.

While larval survival rates in the present study were more influenced by salinity, larval development rates were determined solely by temperature. Comparison with data from Yagi & Ceccaldi (1985) showed that at a given temperature the development rate was slower for the Irish than the Mediterranean population. The Irish larvae also went through nine zoeal stages whereas the Mediterranean larvae metamorphosed after six. Additional larval stages can occur as a result of stressful environmental conditions but typically there are 8–9 (Fincham & Figueras, 1986).

Different temperature and salinity optima for survival and development rate between Irish and Mediterranean populations of *P. serratus* suggest that populations are adapted to local environmental conditions. However, direct experimental comparisons between the two populations would be necessary to discount the role of experimental variation in relation to this hypothesis. Irish populations appear to have lower temperature and salinity optima for survival although their development rate, at a given temperature, was slightly slower. Tolerance to lower temperatures and salinities in the Irish

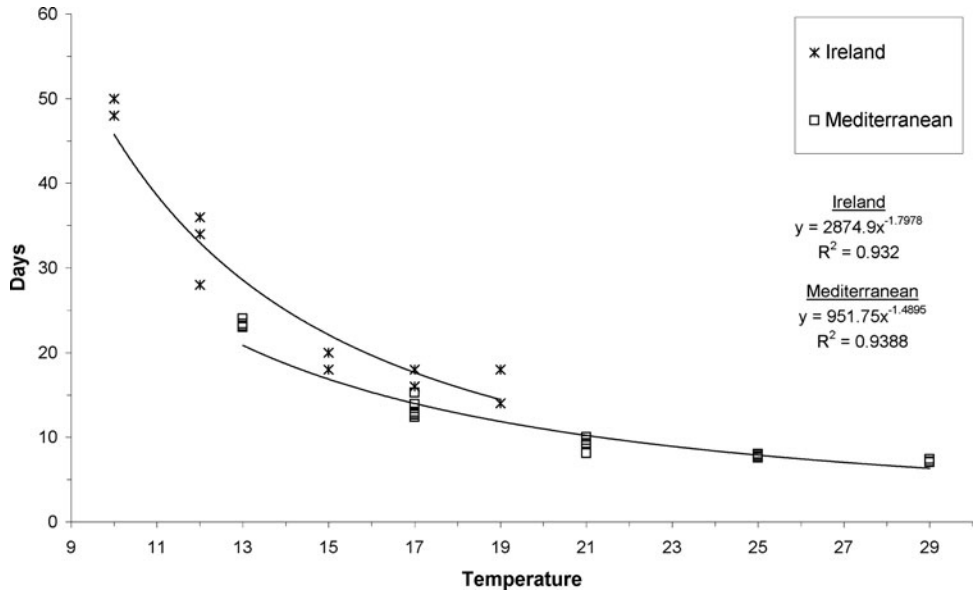

Fig. 3. Development rate of Irish and Mediterranean *Palaemon serratus* larvae to zoeal stage IV at various temperatures.

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population suggests a capacity to adapt to conditions at higher latitudes. Together with rising ocean temperatures, due to global warming, this capacity may lead to a northward expansion of *P. serratus* in European waters. In fact since the 1990s, Irish shrimp fisheries have extended from the south to the north of the country suggesting that this expansion may have already begun (Kelly *et al.*, 2009). The results also suggest that Mediterranean and Irish populations may have different spawner recruit relationships. The larval development rate at a given temperature is shorter in the Mediterranean population. Because larval mortality rates are very high even small reductions in the duration of the larval phase can significantly increase the proportion of the larval population recruiting to the juvenile phase. The efficiency of recruitment, for a given spawning output, may therefore be lower at higher latitudes because temperatures are lower. Recruitment may also be more variable at higher latitudes, where there is likely to be a higher frequency of low salinity and low temperature events, which reduce larval survival.

The results presented here have practical implications for fisheries assessment as the incorporation of environmental effects into stock–recruitment models can improve their predictive capacity. Such models have been used in the management of many shrimp fisheries around the world, e.g. the tiger shrimp (*Penaeus esculentus*) in Western Australia (Penn & Caputi, 1986), the ocean shrimp (*Pandalus jordani*) in the Canadian Pacific (Hannah, 1993) and the white shrimp (*Litopenaeus setiferus*) in coastal waters off Georgia, USA (Belcher & Jennings, 2004). Reducing the unexplained variation in the stock–recruitment relationship will enable reference points for recruitment over-fishing to be identified and increase the certainty in recruitment prediction. The laboratory model described here could also be used to hindcast the likely effects of variability in local temperature and salinity on shrimp recruitment. Given that the Irish shrimp fishery primarily exploits the 1+ year-class there is scope to include environmental effects on likely recruitment success in the previous year for the management of mortality on the exploited year class. These data, together with information on the relationship between development time and temperature, also informs bio-physical modelling of dispersal capacity of larval populations of *P. serratus*.

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