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Effects of climate change on fish reproduction and early life history stages

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Abstract. Seasonal change in temperature has a profound effect on reproduction in fish. Increasing temperatures cue reproductive development in spring-spawning species, and falling temperatures stimulate reproduction in autumn-spawners. Elevated temperatures truncate spring spawning, and delay autumn spawning. Temperature increases will affect reproduction, but the nature of these effects will depend on the period and amplitude of the increase and range from phase-shifting of spawning to complete inhibition of reproduction. This latter effect will be most marked in species that are constrained in their capacity to shift geographic range. Studies from a range of taxa, habitats and temperature ranges all show inhibitory effects of elevated temperature albeit about different environmental set points. The effects are generated through the endocrine system, particularly through the inhibition of ovarian oestrogen production. Larval fishes are usually more sensitive than adults to environmental fluctuations, and might be especially vulnerable to climate change. In addition to direct effects on embryonic duration and egg survival, temperature also influences size at hatching, developmental rate, pelagic larval duration and survival. A companion effect of marine climate change is ocean acidification, which may pose a significant threat through its capacity to alter larval behaviour and impair sensory capabilities. This in turn impacts on population replenishment and connectivity patterns of marine fishes.

Additional keywords: acidification, estrogens, larval behaviour, spawning, temperature.

Introduction

Temperature is a fundamental physical regulatory factor in the lives of fishes and this effect is expressed particularly strongly in the control of all reproductive processes from gamete development and maturation, ovulation and spermiation, spawning, embryogenesis and hatching, to larval and juvenile development and survival. In reproductively mature adults, temperature is generally considered to be a secondary cue to photoperiod in phasing reproductive seasonality but it has a major role in synchronising the final stages of reproductive maturity, and also in truncating reproductive episodes (reviewed in Pankhurst and Porter 2003). The effects of temperature can be differentially expressed depending on when in the annual thermal cycle spawning normally occurs, with increasing spring temperatures being required to cue maturation in spring and early summer spawners (e.g. Stacey 1984; Scott and Pankhurst 1992; Shimizu 2003), but elevated temperatures delaying the onset of maturation and ovulation in autumn-spawning species (reviewed in Pankhurst and King 2010). Temperature has a similarly important role in the modulation of post-fertilisation processes both through its rate-determining effects on embryogenesis and hatching (Pauly and Pullin 1988) and subsequent larval development (Howell *et al*. 1998), growth (Jobling 1997) and survival (Sponaugle and Cowen 1996).

Complications in the assessment of the effects of temperature in the natural environment arise from the fact that much of our current understanding is generated from controlled laboratory experiments that typically test thermal tolerances rather than behavioural preferences. For example, studies on salmonids show that there is often a wide gap between tolerance and preference profiles. Atlantic salmon *Salmo salar* have upper thermal tolerances in the 22–24°C range (Barton 1996) but ocean-range preferences for temperatures at 4–10°C (Reddin *et al*. 2000) and similar effects are reported for other salmonids (reviewed in Pankhurst and King 2010). This means that temperatures that might not be high enough to elicit tolerance-related responses in captivity can induce significant preference-related effects in the natural environment. Single-domain temperature experiments also generally ignore the synergistic interaction of temperature with other physical and biotic variables. Temperature effects on reproduction can be differentially expressed under different photoperiod regimes (Pankhurst and Porter 2003) and recent experiments on tropical damselfish show that temperature effects are modulated by nutritional status (Donelson *et al*. 2010). Finally, some species exhibit variation in thermal reaction norms across their geographic range that indicates some capacity for acclimation and adaptation to temperature gradients (Angilletta 2009; Gardiner *et al*. 2010), and potentially to a changing climate.

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The effects of climate change on aquatic species will vary with latitude, habitat, water column characteristics, and in riverine systems, flow regimes. However, some general expectations of climatic change are for possible phase-shifting of seasonal temperature profiles, elevated seasonal maxima and minima, and as a consequence of increases in atmospheric CO_2, increasing ocean acidification. Riverine habitats are likely to experience elevated temperatures in association with decreased flow rates and increasing incidence of hypoxic conditions, but with quite marked regional differences in effect. For example, parts of tropical Australia are predicted to experience increased rainfall and flow regimes whereas both are likely to be markedly reduced in south-western Australia (Lough *et al*. 2011). A reasonable prediction is that the effects of temperature change on reproduction will be most widespread in marine systems, but probably most extreme in riverine systems. Lacustrine habitats will experience a range of effects depending on lake inflows, water column structure and lake basin topography (Wahl and Löffler 2009). In addition to increases in temperature, elevations in atmospheric CO_2 mean that marine systems will also be affected by ocean acidification, which has the potential to directly influence reproduction and early life stages of marine species (Ishimatsu *et al*. 2008), and to interact with the effects of temperature (Pörtner and Farrell 2008).

With the caveats noted above, the implication is that any changes in thermal regime occasioned by climate change will have major consequences for fish reproduction, and that these effects will be exercised across all stages of the reproductive process (Graham and Harrod 2009; Jonsson and Jonsson 2009; Pankhurst and King 2010). The extent of these effects will be determined by a range of factors including specific physiological tolerances, capacity for acclimation and adaptation, scope for behavioural avoidance, capacity to extend or shift ranges, and the timing of thermal challenges with respect to the reproductive cycle. The possible outcomes range from extremes of complete reproductive and recruitment failure to changes in seasonal phasing of reproduction and possible increases in species range (Munday *et al*. 2008*a*). This review examines the basis for some of these effects at the level of the individual and the possible consequences for population-level events in terms of adult reproduction, and subsequent egg, larval and juvenile development and survival.

Reproduction

Endocrine control of reproduction

Changes in environmental variables are transduced into effects on reproductive processes through the hypothalamo–pituitary–gonadal (HPG) axis. This begins with hypothalamic synthesis and synaptic release of peptide gonadotropin-releasing hormones (GnRH) onto the gonadotropic cells of the pituitary gland, where they stimulate the synthesis and release of the protein hormones, follicle-stimulating hormone (FSH) and luteinising hormone (LH) (reviewed in Planas and Swanson 2008; Levavi-Sivan *et al*. 2010; Zohar *et al*. 2010). In many species, there is also inhibitory tone imposed by the action of dopamine (DA)-secreting neurones, with the release of FSH and LH being dependent on the balance between GnRH stimulation and DA inhibition (reviewed in Dufour *et al*. 2010). The GnRH–pituitary interaction is further modulated by melatonin produced by the light-sensitive pineal gland by as-yet poorly understood mechanisms (reviewed in Migaud *et al*. 2010), by the kisspeptin system through direct effects on the activity of GnRH-producing neurones (reviewed in Akazome *et al*. 2010) and by the feedback effects of gonadal steroids (reviewed in Pankhurst 2008).

FSH is involved in stimulating the early stages of gamete development and LH in the control of maturational events, with both exercising their effects at the gonadal level through binding with G protein-coupled membrane-bound receptors in the ovary and the testis, giving rise to an increase in intracellular cAMP levels (Planas and Swanson 2008). This in turn results in the activation of protein kinases and the susbesequent *de novo* synthesis and releases of gonadal steroids through the sequential cleavage of the base molecule cholesterol. In males, the predominant steroids produced are the androgens, testosterone (T) and its more biologically active metabolite 11-ketotestosterone (11KT); females also produce T but this is further metabolised to the oestrogen 17β-oestradiol (E_2). Both sexes also produce a progesterone-like maturational steroid (typically 17,20β-dihydroxy-4-pregnen-3-one, 17,20βP or 17,20β,21-trihydroxy-4-pregnen-3-one, 20β-S) in response to gonadal stimulation by LH (Pankhurst 2008). The actions of gonadal steroids include the stimulation of gametogenesis in both sexes, spermiation in males and vitellogenesis (yolk accumulation) and oocyte maturation in females, as well as regulating secondary sexual characters and a suite of sexual behaviours (Pankhurst 1998, 2008). A key step in the reproductive development of females is the stimulation by E_2 of hepatic synthesis of the egg yolk precursor vitellogenin (Vtg) which is released into the plasma from where it is taken up by the developing oocytes. E_2 also stimulates the ovarian and hepatic synthesis of zona pellucida proteins (ZP) that will ultimately form the chorion (egg shell) of the ovulated ovum (Tyler *et al*. 2000; Babin *et al*. 2007; Modig *et al*. 2007).

Temperature and the HPG axis

Temperature change has the capacity to affect the HPG axis at multiple sites through its reaction-rate-determining effects on hormone synthesis and action, and its effects on hormone structure. This is reflected in a minimum temperature threshold for most endocrine events, increasing hormone synthesis, activity and metabolism across the physiological tolerance range and decreasing activity at the top end of that range (Pankhurst and King 2010). Inhibitory effects at higher temperature may arise from conformational changes in proteins (e.g. FSH, LH and their receptors, steroid-synthesising enzymes), and also the increasing tendency for steroid hormones to form water-soluble conjugates at high temperatures (reviewed in Van Der Kraak and Pankhurst 1997). Steroid conjugates (usually sulfates or glucuronides) suffer the dual fate of no longer being soluble in (and able to pass through) cell membranes to gain access to their intracellular receptors, and of being more available for kidney filtration and excretion in the urine, significantly reducing their plasma residence times.

Irrespective of the mechanisms involved, it is clear that thermal inhibition of reproduction is present across a wide spread of taxa, habitats and temperature ranges with the main difference between species being the absolute temperature at

which the suppressive effects occur (Table 1). In cold temperate and sub-Arctic species, the inhibitory effects typically appear at temperatures of 11–12°C, among cold-temperate species at around 18°C, temperate species at ~24°C and tropical species at 30°C and above (Table 1). This supports the view that all species are likely to show similar responses to rising temperatures, but that the thresholds for these effects will vary in relation to specific thermal tolerance ranges. There is also some evidence that the ranges over which normal function can be maintained may be broader in cool-water and temperate species than among tropical species (Nilsson *et al*. 2009; Donelson *et al*. 2010).

More detailed understanding of the mechanisms involved in the thermal inhibition of reproductive processes is derived mainly from studies on temperate species, with most evidence from studies on salmonids. Arctic charr, *Salvelinus alpinus*, held at 10°C (a temperature that suppresses normal ovulation) show greater responsiveness (LH secretion and subsequent ovulation) to synthetic analogues of GnRH (GnRHa) combined with the dopamine antagonist pimozide than GnRHa alone, suggesting that part of the inhibitory mechanism involves increases in dopamine inhibition at the level of the pituitary (Gillet and Breton 2009). In Atlantic salmon, *Salmo salar*, elevated summer and autumn temperatures inhibit the activity of the steroid-converting enzyme P_{450} aromatase (arom) and the subsequent ovarian synthesis of E_2 from androgen precursors. This in turn results in reductions in the hepatic synthesis of Vtg and subsequent reductions in final egg size, fertility and survival. Exposure to elevated temperature during vitellogenesis also results in reduced affinity of hepatic E_2-receptors. Exposure to elevated temperatures at the completion of vitellogenesis (late autumn) inhibits the synthesis of the maturational steroid 17,20βP and subsequent progression of oocytes through final oocyte maturation (the resumption of meiosis) and ovulation (reviewed in Pankhurst and King 2010).

Similar effects are seen in non-salmonids, with wolffish, *Anarhichas lupus*, showing reduced plasma levels of T and E_2, retarded ovulation, and reduced fertility and survival (Tveiten and Johnsen 2001; Tveiten *et al*. 2001), red seabream, *Pagrus major*, showing inhibition of expression of genes coding for arom and 11β-hydroxylase (which mediates the conversion of T to 11KT) (Lim *et al*. 2003), and freshwater pejerrey, *Odontesthes bonariensis*, showing reduced plasma levels of E_2 in females and T in males (Soria *et al*. 2008). At higher levels in the HPG axis, red seabream exposed to typical summer temperatures (that truncate normal spawning) showed reduced central expression of genes for GnRH and its pituitary receptor, and reduced pituitary expression of the β-subunit gene for LH (LHβ) (Okuzawa *et al*. 2003). Similarly, pejerrey displayed reduced expression of LHβ and the receptor for FSH in females exposed to moderate elevations in temperature (Soria *et al*. 2008). There is also some evidence that high temperature may interfere with the transduction of photoperiod signals to the reproductive axis, although as noted earlier, the mechanism in fish is still not well understood. The amplitude of the nocturnal surge in melatonin in fish is greater at higher temperature and if, as in some birds, melatonin exerts its role through stimulation of factors that inhibit GnRH synthesis (reviewed in Migaud *et al*. 2010), then temperature-regulated increases in melatonin secretion could

Table 1. Summary of inhibitory effects of elevated temperature on reproduction across a range of species, habitats and thermal ranges
Temperatures above which effects occur (where known)

Species	Habitat	Effects	Authors
Arctic charr *Salvelinus alpinus*	Cold temperate/sub-Arctic freshwater	Inhibition of LH secretion, ovulation (10–11°C)	Gillet 1991; Jobling *et al*. 1995; Gillet and Breton 2009
Wolffish *Anarhichus lupus*	Cold temperate/sub-Arctic marine	Reduced steroid (T and E_2) production, ovulation, fertility and survival (12°C)	Tveiten and Johnsen 2001; Tveiten *et al*. 2001
Lake whitefish *Coregonus lavaretus*	Cold temperate lacustrine	Delayed ovulation and spawning	Wahl and Löffler 2009
Atlantic salmon *Salmo salar*	Cold temperate anadromous	Reduced Vtg and ZP gene expression, steroid (T, E_2 and 17,20βP) production, aromatase activity, ovulatory frequency, fertility, egg survival (18°C)	Pankhurst and King 2010
Rainbow trout *Oncorhynchus mykiss*	Temperate freshwater	Reduced steroid production (T, E_2, 17,20βP), fertility and survival (18–21°C)	Pankhurst *et al*. 1996; Pankhurst and Thomas 1998
Red seabream *Pagrus major*	Temperate marine	Aromatase and 11β-hydroxylase inhibition(24°C)	Lim *et al*. 2003
Pejerrey *Odontesthes bonariensis*	Warm temperate freshwater	Reduced LH β-subunit and FSH-receptor gene expression, T and E_2 levels, fertility (24°C)	Soria *et al*. 2008
Spiny damselfish *Acanthochromis polyacanthus*	Tropical marine	Reduced reproductive output, aromatase activity, E_2 production (30°C)	Donelson *et al*. 2010; N. W. Pankhurst, P. M. Pankhurst and L. Gonzalez-Reynoso, unpubl. data
Humbug dascyllus *Dascyllus aruanus*	Tropical marine	Reduced E_2 production (33°C)	N. W. Pankhurst, P. M. Pankhurst and L. Gonzalez-Reynoso, unpubl. data

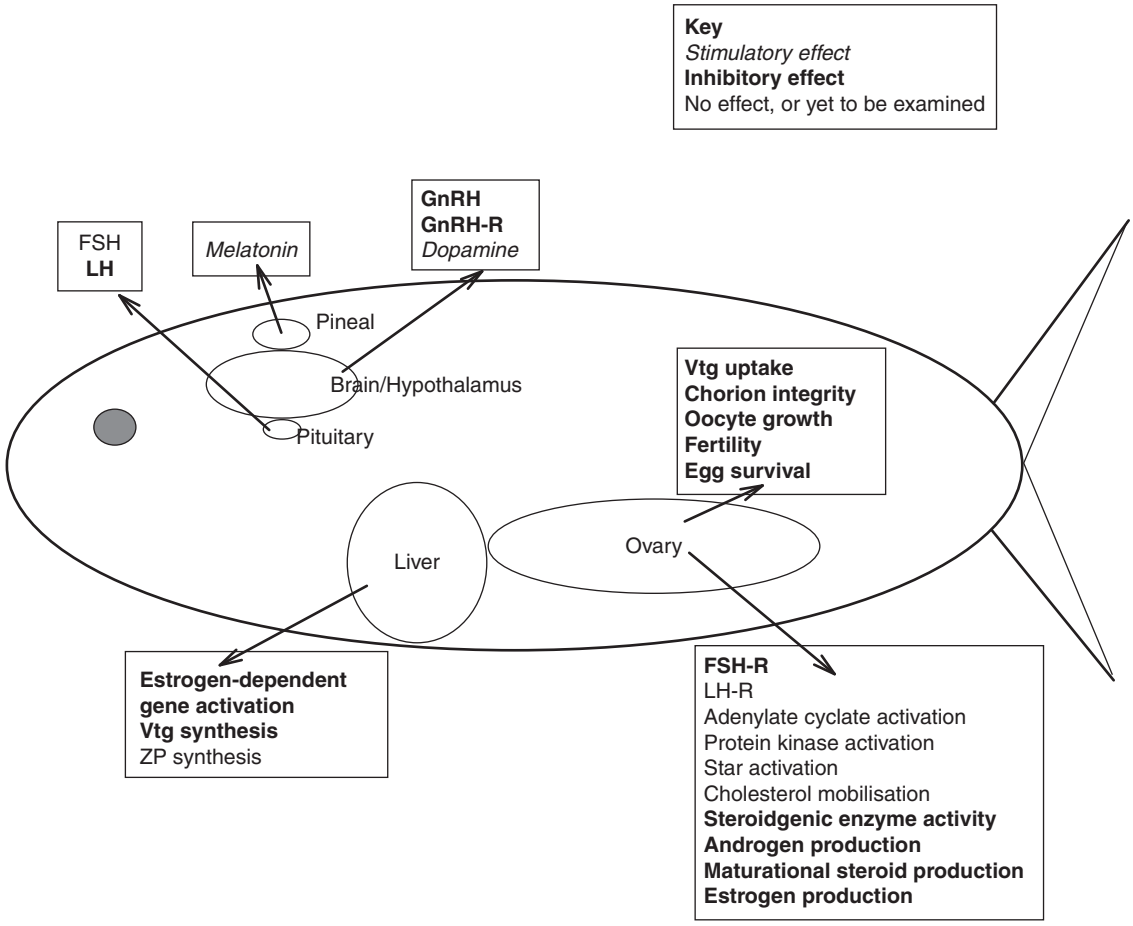

Fig. 1. Schematic summary of the effects of above-normal temperature on reproductive processes in teleost fish. Components in bold are inhibited by high temperature, items in italics are stimulated at high temperature, normal text means no measurable effect or yet to be investigated. Abbreviations are defined in the text.

also result in an inhibitory effect at the pituitary level. With the caveat that the understanding of all of the possible effects of temperature on reproductive physiology is not complete, it is clear that temperature regulates reproduction at multiple sites in the reproductive pathway (Fig. 1).

Stress and reproduction

An alternative, non-exclusive explanation for the inhibitory effects of elevated temperature is the possibility that thermal inhibition occurs through activation of the hormonally-mediated stress response. In turn, stress is known to have marked inhibitory effects on reproduction in fish (Pankhurst and Van Der Kraak 1997; Leatherland *et al*. 2010; Schreck 2010). Stress stimulates activation of an acute catecholamine-mediated response that has the primary effect of rapidly increasing energy availability and the delivery of O_2 to the tissues, followed by a longer and more sustained activation of the hypothalamic–pituitary–interrenal (HPI) axis, resulting in plasma elevations of the steroid cortisol in teleosts and chondrosteans, and 1α-hydroxycorticosterone in elasmobranchs (reviewed in Pankhurst 2011). Short-term increases in corticosteroids increase the availability of a variety of energy substrates, but longer-term exposure to elevated cortisol results in suppressive effects on a range of functions including reproduction, growth and immune function (Pankhurst 2011). Some of the longer-term effects can be explained by the largely catabolic effects of cortisol, but stress is also capable of suppressing plasma levels of T and E_2 in as little as 15–30 min after the imposition of stress (Haddy and Pankhurst 1999), and there is equivocal evidence that this rapid effect is the direct result of cortisol action (Pankhurst *et al*. 1995).

A consideration for the role of stress in temperature-mediated suppression of reproduction is whether environmental temperature change actually stimulates a stress response. Increases in temperature can be an effective stressor in the laboratory context (Pankhurst 2011) but elevations in temperature that inhibit reproduction in broodstock Atlantic salmon do not result in significant elevations of plasma cortisol (Pankhurst *et al*. 2011), strongly suggesting that the marked inhibitory effects observed in salmonids are not being exercised through the HPI axis. There is also the consideration as to whether environmental conditions are routinely stressful for fish in the natural environment, and the conclusion is that there is not strong evidence for initiation of stress responses under quite wide ranges of environmental conditions (Schreck 2010; Pankhurst 2011). The

caveat here is that events that do stimulate stress responses in free-ranging vertebrates from other classes are typically associated with extreme weather events. For fish populations, this is likely to coincide with storms and floods, when sampling from wild populations is generally precluded (Pankhurst 2011). However, environmental changes predicted for riverine environments such as increasing temperatures, decreased flow rates and O_2 saturation (Morrongiello *et al*. in press) may well generate conditions that do stimulate activation of the HPI axis. A reasonable prediction is that this will contribute to reproductive suppression in these environments, separately or additively to direct thermal effects on reproductive endocrine processes.

Additional considerations

Despite the general consistency of the effects of elevated temperature on reproduction described above, data from an increasing number of studies suggest that there will be subtleties in the way that these effects are likely to be expressed. This in turn is going to make the precise nature of effects arising from climate change harder to predict. A first consideration will be when in the reproductive cycle thermal challenge occurs. Studies on austral stocks of Atlantic salmon have shown that females are reasonably robust in terms of their response to elevated temperature for much of the summer and autumn, but highly sensitive to thermal disruption in February during a period of substantial oocyte growth and gonadal reorganisation (King *et al*. 2007). The implication is that elevated temperature may have more, or less, benign effects depending on whether or not it consistently occurs across this period of heightened sensitivity.

Temperature change may also have differential impacts on sympatric species with different seasonal spawning patterns. For example, spiny damselfish, *Acanthochromis polyacanthus*, spawn in spring and early summer on Australia's Great Barrier Reef, and show temperature inhibition of ovarian steroidogenesis above 30°C (Donelson *et al*. 2010; N. W. Pankhurst, P. M. Pankhurst and L. Gonzalez-Reynoso, unpubl. data). In the same regions, humbug dascyllus, *Dascyllus aruanus*, spawn later in the summer when temperatures are typically higher, and do not show evidence of inhibition of steroidogenesis until temperatures reach 33°C (N. W. Pankhurst, P. M. Pankhurst and L. Gonzalez-Reynoso, unpubl. data). This suggests that as in temperate species (Pankhurst and Porter 2003), increasing temperature plays a normal role in truncating spawning episodes in spring spawners, and cueing the onset of spawning in summer spawners. Under this scenario, the effects of any increase in temperature will depend on the timing of this increase with respect to the reproductive cycle and the natural seasonal timing of spawning. For example, a higher summer maximum may have negligible effects on spiny damselfish reproduction if it occurs during a period when spawning is normally suppressed, but might reduce a spring-spawning window if the rate of the spring increase in temperature became steeper, (i.e. the effects will be strongly dependent not only on the absolute temperature but also the annual pattern of thermal change).

The response to thermal stress may also be variable within the same population. Recent work with Atlantic salmon shows that the effect of summer and autumn exposure to high temperature (22°C) is partially determined by the age class of broodstock. Both first-spawning-season (maiden) and second-spawning-season (repeat) females show depression of plasma E_2 and Vtg levels, reduced expression of Vtg and ZP genes, delay in maturation and ovulation and reduced fertility and egg survival (Pankhurst *et al*. 2011). However, repeat females show higher fertility and survival than maidens for reasons that are not clear but may relate to overall larger egg size and maternal endowment with vitellogenin. A similar effect operating in natural populations would generate differential impacts depending on the age structure of the population, and one prediction may be that heavily fished populations dominated by younger fish might have heightened susceptibility to thermal disruption of reproduction.

Within-population variability is also likely to occur as a function of individual nutritional status. It is well known that there is a tightly coupled relationship between nutritional status and reproductive output (Lambert *et al*. 2000); however, experiments with spiny damselfish have shown that high nutritional status confers some protection from the inhibitory effects of exposure to high temperature (Donelson *et al*. 2010). The basis for the effect is not known but may be related to the permissive effects that several nutritionally regulated endocrine factors (e.g. thyroid hormones, insulin-like growth factor I) exert on the HPG axis (reviewed in Pankhurst *et al*. 2008). On this basis, another prediction may be that temperature effects on reproduction of natural populations will be exacerbated if there is a concurrent negative impact on food availability.

An observation based on the consistent effect of increasing temperature in inhibiting gonadal arom activity in fishes is that arom suppression will have at least two additional potential effects on reproduction based on the roles of arom in sex determination, and sex inversion, respectively. Phenotypic sex in fish can be quite labile during the period of primary sex determination, such that female phenotypes emerge in the presence of brain arom-dependent oestrogen synthesis, and males in the absence of arom activity (reviewed in Devlin and Nagahama 2002). Higher temperatures inhibit arom activity and drive sex determination towards the male phenotype (reviewed by Guiguen *et al*. 2010). A prediction here is that increasing sea temperatures will increase the proportion of fish developing as male, even within the thermal range over which reproductive performance can be maintained. The possible impacts of this on population resilience are not known. Similarly, many teleost species undergo sex inversion (Frisch 2004), with the presence of gonadal arom activity maintaining the ovarian condition in protogynous species, and being requisite for the transition from male to female in protandrous species. The primary control mechanism appears to be mainly exercised by social context (e.g. Munday *et al*. 2006) but the underlying physiological mechanism is strongly dependent on the subsequent activation or inhibition of arom activity. Thermal inhibition of arom activity may generate premature transition from female to male in protogynous species and inhibition of transition to female in protandrous species, even in the presence of the appropriate social context. Here also, the possible impacts at population level are not known.

Ocean acidification and reproduction

Uptake of additional CO_2 at the ocean surface, owing to increasing concentrations of CO_2 in the atmosphere, is causing ocean pH to decline and reducing the carbonate ion concentration of the shallow ocean. This process, known as ocean acidification, is considered to be a serious threat to marine species, especially for calcifying species that require carbonate ions to form their shells and skeletons (Hoegh-Guldberg *et al*. 2007; Fabry *et al*. 2008; Smith 2009). Elevated pCO_2 can also have a direct physiological effect on aquatic species through disruption of acid–base balance and limiting oxygen supply (Pörtner *et al*. 2004; Pörtner and Farrell 2008). The effects of increasing pCO_2 in water is probably of greater concern than reducing pH *per se*, because of the high permeability to biological tissue of gaseous CO_2 relative to hydrogen ions (Brauner 2009). Experiments with red seabream (*Pagrus major*) demonstrate that larval fish are more sensitive to the effects of acidification with CO_2 than to the same pH achieved with mineral acids (Kikkawa *et al*. 2004). Increased pCO_2 in tissue causes acidosis (lowering of pH and accumulation of bicarbonate), which can be detrimental to many cellular processes, including protein synthesis, enzymatic function and oxygen transport (Pörtner *et al*. 2004). Fish compensate for acidosis by acid–base equivalent ion transport from the body to the environment, mostly across the branchial epithelium, and to a lesser extent, via the kidneys and intestine (Claiborne *et al*. 2002).

In general, fishes appear to be more tolerant to increases in ambient CO_2 than many invertebrates (Ishimatsu *et al*. 2008; Widdicombe and Spicer 2008), possibly because of their well-developed mechanisms for acid–base regulation (Pörtner *et al*. 2004; Melzner *et al*. 2009). However, very little is known about the effects that chronic exposure to levels of pCO_2 predicted to occur over the next 50–100 years (up to ~1000 ppm CO_2) might have on fish reproduction. The few preliminary studies available suggest the impacts might not be substantial. Sperm motility of the flounder, *Limanda yokohamae*, is arrested by mild increases in pCO_2 (Inaba *et al*. 2003), but similar effects were not observed in 10 other species from a range of families (Inaba *et al*. 2003) or in the Baltic cod, *Gadus morhua* (Frommel *et al*. 2010). Sensitivity of fish eggs to elevated CO_2 varies markedly between species, but species tested to date typically have 24-h LC50 (lethal concentration resulting in 50% mortality) values well above 10 000 ppm CO_2 (Ishimatsu *et al*. 2008). Furthermore, Munday *et al*. (2009*a*) did not detect any effect of exposure to 1000 ppm CO_2 on the embryonic duration or survival of clownfish (*Amphiprion percula*) eggs. Eggs of pelagic spawners might be more sensitive to CO_2 stress than the eggs of benthic spawners such as clownfishes, because pelagic eggs probably experience less fluctuation in environmental pCO_2 than benthic eggs, but this hypothesis has not been adequately tested.

One potential concern is that higher pCO_2 may limit the scope for aerobic performance in adults (Pörtner and Farrell 2008), which could affect reproductive output. Aerobic scope of two tropical cardinalfishes, *Ostorhinchus doederleini* and *O. cyanosoma*, declined by 33% and 47%, respectively, when they were exposed to ~1000 ppm CO_2 at the average summer temperature (29°C) for the study population and at temperatures up to 3°C above average (Munday *et al*. 2009*b*). Whether such a loss in aerobic capacity has an effect on reproduction is unknown, but it is reasonable to suspect that it will. For example, collapse of aerobic scope in association with anomalously high water temperature has been linked to failed migration (and thus spawning) in sockeye salmon, *Oncorhynchus nerka* (Farrell *et al*. 2008). The possible effects of elevated CO_2 on endocrine pathways that mediate reproduction in fishes are currently unknown.

Early life history stages

Effects on egg incubation

Eggs are one of the most thermally sensitive life stages in fishes and tolerance limits appear to be within ± 6°C of the spawning temperature for many species (Rombough 1997). Small increases in temperature can dramatically increase egg mortality, especially in tropical species (Gagliano *et al*. 2007). Consequently, survivorship to hatching could decline as oceans and rivers warm, unless species adjust the timing of spawning to suit the optimal temperature for embryo development. Such shifts appear likely because gametogenesis is highly temperature-sensitive in many fish species (discussed above) and breeding may cease before critical thermal limits for egg survival are reached. For example, the critical temperature for gametogenesis of brook trout, *Salvelinus fontinalis*, is ~2°C lower that the thermal limit for normal development of fertilised eggs (Rombough 1997). Nevertheless, some species spawn at sub-optimal temperatures and may suffer reduced embryonic survival as a result, both because increased temperature during ovulation can reduce gamete viability (Van Der Kraak and Pankhurst 1997) and because increased temperature during embryogenesis increases mortality (Gillet *et al*. 1996; Pankhurst and Thomas 1998; Janhunen *et al*. 2010).

Temperature also has a highly significant effect on the rate of embryonic development. For many species, the rate of embryonic development more than triples for each 10°C increase in temperature (i.e. $Q_{10} > 3$) (Rombough 1997). An increased developmental rate means that the incubation period declines as average water temperature increases. Incubation period is also dependent on egg size, with larger eggs taking longer to develop than small eggs (Pauly and Pullin 1988). Consequently, increased temperature may advance hatching by minutes to hours in small eggs, and by hours to days in large eggs, with the effects being most marked in cold-water species with long incubation periods (Rombough 1997). Whether shorter incubation periods affect individual fitness may depend on the potential for a mismatch between the timing of hatching and favourable conditions for larval survival. For example, hatching of benthic eggs often occurs at night when larvae are less susceptible to visual predators (Robertson 1991; Michael 2008). At least in some species, hatching can be cued by environmental factors that are not temperature-dependent, such a diurnal light cycles, which may help ensure larvae hatch at the appropriate time even if they are competent to hatch earlier.

Effects on larvae

Temperature affects metabolism, growth, developmental rate and stage duration of larval fishes (reviewed by Houde 1989;

Blaxter 1991; Benoît *et al*. 2000). Metabolic rate, measured as mass-specific oxygen consumption, increases sharply with increasing temperature in larval fishes, although responses vary considerably among species (Houde 1989; Rombough 1997). Higher metabolic rates mean that fish have higher basal energy demands at higher temperatures. Larval growth rates also increase with temperature for both temperate (Blaxter 1991; Benoît *et al*. 2000) and tropical species (McCormick and Molony 1995; Meekan *et al*. 2003; Green and Fisher 2004), with temperature explaining up to 89% of variation in growth rates among cohorts of some species (Sponaugle and Cowen 1996). Thermal reaction norms of growth in larval fish tend to be approximately linear until the lethal upper thermal limit is reached, at least in the majority of species studied to date (Sponaugle and Cowen 1996; Rombough 1997). This contrasts with thermal reaction norms of growth in juveniles and adults, which usually decline well before the lethal thermal limit is reached (e.g. Munday *et al*. 2008*b*). As a result, we might expect that larval growth rates will tend to be maintained as water temperatures increase as a result of global warming, even if temperatures exceed optimum conditions for some other life processes.

In warmer water, developmental rates increase and therefore stage durations are shorter. The time until yolk absorption, metamorphosis and pelagic larval duration (PLD) are all negatively correlated with temperature, both within species (Rombough 1997; Fuiman *et al*. 1998; Green and Fisher 2004) and among species (Houde 1989; Benoît *et al*. 2000). In one of the clearest examples of this effect, PLD of reef fishes is closely correlated with temperature in a range of species (McCormick and Molony 1995; Sponaugle and Cowen 1996; Green and Fisher 2004). There are also strong correlations between PLD and growth rates, with fast-growing larvae often exhibiting shorter larval durations (Houde 1989; McCormick and Molony 1995; Sponaugle and Cowen 1996; Benoît *et al*. 2000; Green and Fisher 2004). The relationship between growth rate and PLD will influence size at settlement, which is often variable between cohorts (Sponaugle and Cowen 1996; Fuiman *et al*. 1998) because these rates are not perfectly reciprocal and because growth also depends on a range of other factors such as food supply. Larger size at settlement may offer some survival advantages (Sogard 1997); however, small individuals settling in warmer conditions may grow faster after settlement and quickly reach equivalent sizes to fish that settle in cooler conditions (Sponaugle and Cowen 1996).

As mortality rates are usually very high during the larval phase, faster growth and reduced PLD at higher temperatures might increase larval survivorship (Houde 1989; Bergenius *et al*. 2002; O'Connor *et al*. 2007). Across a broad range of species, the slope of the relationship between PLD and temperature is steepest in cool-water species (O'Connor *et al*. 2007), and small increases in water temperature might be expected to have the greatest effect on high-latitude species. However, even among tropical fishes, PLD can decline by 4–8% per °C (Munday *et al*. 2009*c*), which could have a significant effect on survivorship. Within the temperature range currently experienced by reef fishes, warmer years generally appear to favour good recruitment events for a variety of species (Meekan *et al*. 2001; Wilson and Meekan 2002; Cheal *et al*. 2007), which is consistent with the hypothesis that reduced PLD tends to increase larval survivorship. Recruitment of the bluehead wrasse, *Thalassoma bifasciatum*, in the Florida Keys increases with temperature, but also becomes more variable at high temperatures (Sponaugle and Cowen 1996), possibly because of the increased risk of starvation in warm-water cohorts. Although the growth rate of marine fish larvae increases with temperature, growth efficiency does not (Houde 1989; Rombough 1997). Furthermore, larvae require more food at higher temperatures to sustain higher metabolic rates. As a result, larvae are more susceptible to starvation at higher temperatures and this may explain observations of more variable recruitment and episodes of recruitment failure during periods of anomalously high water temperature. For example, recruitment of most reef fish species failed in French Polynesia during a warm El Niño period (Lo-Yat *et al*. 2011), suggesting that either reproduction or larval survival of a broad range of species was dramatically reduced at high summer temperatures.

Together, these observations demonstrate that increased temperatures will affect the life history and demography of larval fish, possibly affecting recruitment success and population dynamics. Small increases in temperature might tend to favour recruitment in some species, especially at higher latitudes. Larger temperature increases could lead to recruitment failures, especially at low latitudes, and at times or places where food supply is limited (Munday *et al*. 2008*a*). Larval success and patterns of recruitment will also be strongly affected by the effects of temperature on reproduction, which is likely to be one of the first processes impacted by increasing water temperature. A summary of the demonstrated and possible effects of increased temperature and pCO_2 on early life history traits is shown in Fig. 2.

Ocean acidification and early life history stages

Larval stages are predicted to be more sensitive to elevated pCO_2 than adults because they have a larger surface area-to-volume ratio, and thus are more susceptible to changes in ambient conditions, and because they might have less-developed mechanisms for acid–base balance compensation (Fabry *et al*. 2008; Ishimatsu *et al*. 2008; Melzner *et al*. 2009). Acid–base balance in adult fish is mostly maintained by ion transport across the gills (Claiborne *et al*. 2002). Although very little is known about the mechanisms and pathways of acid–base regulation in larval fishes, it is clear that they must be capable of acid–base homeostasis (Brauner 2009). Indeed, the early ontogenetic development of gills in larval fish may be more important in ionoregulation and maintaining acid–base balance than for oxygen delivery (Fu *et al*. 2010). Similar to the egg stage, the 24-h LC50 for larval fish is generally above 10 000 ppm CO_2 for the few species tested to date (Kikkawa *et al*. 2003; Ishimatsu *et al*. 2008). Furthermore, two recent studies have not detected significant negative effects on life history traits of larval reef fishes reared in conditions simulating near-future CO_2 in the ocean. Munday *et al*. (2009*a*) did not detect negative effects on the size at hatching, growth rate, size at settlement, or critical swimming speed of clownfish, *Amphiprion percula*, larvae reared from hatching in seawater aerated with up to 1000 ppm CO_2. Similarly, juvenile spiny damselfish, *Acanthochromis polyacanthus*, reared for 3 weeks at up to 850 ppm CO_2 were the same size as fish reared in

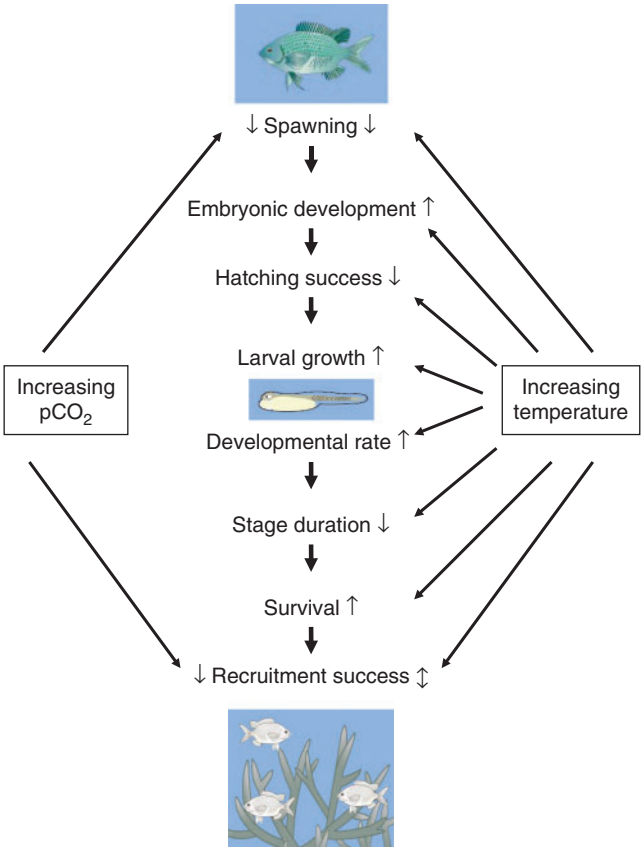

Fig. 2. Physiological and ecological responses to increased water temperature and elevated pCO_2 during the early life history of fishes. ↑ = increasing rate, ↓ = decreasing rate, ↕ = rate may increase or decrease depending on other environmental parameters.

current-day CO_2 controls, did not suffer higher mortality, and exhibited no differences in skeletal or otolith development compared with controls (Munday *et al*. 2011). Although more studies are required, the limited evidence available to date suggests that pCO_2 levels predicted to occur in the ocean during the next 50–100 years might not have a serious effect on the growth and development of larval fishes.

A potentially serious consequence of rising pCO_2 is that it can affect the olfactory system of some marine fishes, rendering them unable to distinguish between ecologically important chemical cues (Munday *et al*. 2009*d*). Clownfish larvae reared at 1000 ppm CO_2 exhibited a broad attraction to any chemical cue presented in binary-choice flume trials and became attracted to chemical cues that they avoided when reared in control seawater. At 1000 ppm CO_2, they became attracted to the smell of inappropriate habitats (Munday *et al*. 2009*d*), could no longer discriminate the smell of kin versus non-kin (Munday *et al*. 2009*d*), and became attracted to the smell of predators (Dixson *et al*. 2010). At even higher pCO_2 (~1700 ppm), they failed to respond to any chemical cues, indicating complete impairment of the olfactory system. In subsequent experiments, Munday *et al*. (2010) showed that: (1) olfactory impairment of larval clownfishes and damselfishes (*Pomacentrus wardi*) occurred at 700–850 ppm CO_2, (2) behaviour of larval damselfish was altered in their natural coral reef habitat, and (3) that this caused a 5- to 9-fold increase in mortality from predation compared with controls. These results suggest that increased pCO_2 in the ocean could have a significant effect on the successful replenishment of reef fish populations, although the effects on predators and the outcome of predator–prey interactions when both partners have been exposed to elevated CO_2 have not yet been tested. Ecological connectivity between fish populations could also be significantly affected if exposure to elevated CO_2 impairs navigation and homing abilities of larval fishes, as suggested by the original studies (Munday *et al*. 2009*c*).

The physiological mechanisms responsible for impairment of olfactory sensitivity and changes in behaviour of larval fish exposed to elevated CO_2 are currently unknown, but do not appear to be related to changes in the chemical stimuli or abnormal developmental of the sensory system. Neither control nor CO_2-treated fish altered their responses to chemical cues when presented in CO_2-acidified versus control water (Munday *et al*. 2010; Dixson *et al*. 2010), indicating that elevated CO_2 affects the fish, not the chemical cue itself. No modification of the sensory epithelium was apparent in CO_2-treated fish (Munday *et al*. 2009*d*) and these fish regained their normal sensory ability after two days in control water (Munday *et al*. 2010). It is possibly that the effects on behaviour and olfactory ability be related to incomplete acid–base compensation or some other effect of elevated CO_2 on the nervous system, but this has yet to be examined.

Acclimation and adaptation

Many fish species have geographic ranges spanning a considerable gradient in average, maximum and minimum temperature, suggesting some capacity for acclimation or adaptation to temperature change (Munday *et al*. 2008*a*). There is evidence that thermal exposure history can moderate subsequent responses to increasing temperature. Populations of bullhead, *Cottus gobio*, harvested from a stream system which had a less variable annual thermal range (4.5–11.5°C) than another (0.5–19.2°C) were found to be less robust in resisting the inhibitory effects of high temperature (Reyjol *et al*. 2009). Similarly, populations of four species of reef fish from two families (Apogonidae and Pomacentridae) on the northern Great Barrier Reef (GBR) exhibited poorer performance at high temperatures compared with fish from the southern GBR, which experience a more variable thermal range (Gardiner *et al*. 2010). This indicates that local populations of these species are either acclimated or adapted to the local thermal environment, and that populations from more variable environments might have enhanced capacity to cope with future thermal stress.

Although acute thermal stress often depresses reproduction, long-term exposure to higher temperatures can confer some improvement through acclimatory processes. For example, laboratory experiments on spiny damselfish show that fish reared at higher temperature since birth have a greater capacity to maintain reproduction at temperatures over 30°C compared with individuals that have only a few weeks thermal acclimation (J. Donelson *et al*. 2011). Furthermore, the thermal

history of the parents is important, with embryos and larvae from parents reared at high temperatures exhibiting greater thermal tolerance or improved performance at high temperatures in several species (Rombough 1997).

In addition to acclimatory responses owing to thermal exposure history, individuals within a population can exhibit different thermal preferences (i.e. individual genetic variability), and different populations can be locally adapted to different thermal regimes (Crawshaw and O'Connor 1997; Farrell *et al*. 2008; Munday *et al*. 2008*a*). This variation provides the raw material for selection of genotypes that are more tolerant. The potential for genetic adaptation to rapid climate change depends on a range of factors, including the amount of adaptive genetic variation present, effective population sizes, generation time, and connectivity between populations that can aid in the spread of tolerant genotypes (Skelly *et al*. 2007; Munday *et al*. 2008*a*, 2009*c*). Unfortunately, much of this information is unknown for both marine and freshwater fishes and should be a priority area for future research.

Conclusion

Climate change will, or is already, affecting reproductive and early life history events of most fishes. This is occurring at a variety of levels and through a range of mechanisms which as our understanding develops are emerging as increasingly complex. These include the interplay of changes in physical variables with habitat, when in the reproductive cycle the thermal challenge occurs, the timing of spawning, whether events are extreme enough to initiate a physiological stress response, the energy status and reproductive age of the fish, and the thermal exposure history and adaptive capacity of the individual or the population. There is also the very strong suspicion that we are substantially under-informed to make useful predictions about likely effects beyond general assumptions, except for the relatively few species that have received the bulk of research attention. This in turn limits our capacity to develop specific options as management strategies. Temperature is one of the most fundamental variables affecting the lives of fishes but we still know discouragingly little about its effects.

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