Climate change effects on fishes and fisheries: towards a cause-and-effect understanding

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Ongoing climate change is predicted to affect individual organisms during all life stages, thereby affecting populations of a species, communities and the functioning of ecosystems. These effects of climate change can be direct, through changing water temperatures and associated phenologies, the lengths and frequency of hypoxia events, through ongoing ocean acidification trends or through shifts in hydrodynamics and in sea level. In some cases, climate interactions with a species will also, or mostly, be indirect and mediated through direct effects on key prey species which change the composition and dynamic coupling of food webs. Thus, the implications of climate change for marine fish populations can be seen to result from phenomena at four interlinked levels of biological organization: (1) organismal-level physiological changes will occur in response to changing environmental variables such as temperature, dissolved oxygen and ocean carbon dioxide levels. An integrated view of relevant effects, adaptation processes and tolerance limits is provided by the concept of oxygen and capacity-limited thermal tolerance (OCLT). (2) Individual-level behavioural changes may occur such as the avoidance of unfavourable conditions and, if possible, movement into suitable areas. (3) Population-level changes may be observed *via* changes in the balance between rates of mortality, growth and reproduction. This includes changes in the retention or dispersion of early life stages by ocean currents, which lead to the establishment of new populations in new areas or abandonment of traditional habitats. (4) Ecosystem-level changes in productivity and food web interactions will result from differing physiological responses by organisms at different levels of the food web. The shifts in biogeography and warming-induced biodiversity will affect species productivity and may, thus, explain changes in fisheries economies. This paper tries to establish links between various levels of biological organization by means of addressing the effective physiological principles at the cellular, tissue and whole organism levels.   © 2010 The Authors

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INTRODUCTION

Ocean warming is currently one of the main driving forces causing changes in species abundance and distribution and, thus, in species composition in marine ecosystems (Perry *et al.*, 2005). This appears as a consequence of the fact that temperature defines

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the large-scale geographical distribution of marine water-breathing animals, within conditions set by geomorphology, ocean currents, water depth and stratification or salinity. The fish fauna has been widely investigated in this context with long-term data series compiled due to fisheries interests. Such studies have focused on statistical analyses of how stock size or population structure, recruitment or spawning events are influenced by changes in climatic indices such as the North Atlantic Oscillation (NAO; Alheit *et al*., 2005). Shifts in geographical distribution occur in response to climate change and are generally most evident near the northern or southern boundaries of the geographic range of a species, where warming or cooling theoretically drives marine fishes to higher and lower latitudes, respectively. A number of studies have documented such changes within particularly well-studied ecosystems of the world's oceans including the North Sea and other parts of Europe (Beare *et al*., 2004; Perry *et al*., 2005; Rose, 2005). Furthermore, analyses have investigated whether there have been shifts in the seasonal timing (phenology) of crucial events such as spawning by fishes (Sims *et al*., 2005) and the spring blooms of phytoplankton and zooplankton (Wiltshire *et al*., 2008). Out-of-phase shifts between the former and latter can have large consequences for match and mismatch phenomena in, for example, food availability for larval and juvenile fishes (Beaugrand *et al*., 2002), possibly leading to regime shifts (Beaugrand, 2004).

It is important to recognize that the observed effects of global warming on fishes at the various levels of biological organization (organismal, population and community–ecosystem) result from physiological changes at molecular, cellular and whole organism levels and that the ultimate effects of global warming at the ecosystem level will build on species-specific responses (Pörtner, 2001, 2002). As a consequence, species interactions change with interactions at the community level (Pörtner & Farrell, 2008). Such a cause-and-effect understanding is needed to reliably project the effects of global warming on commercially important marine fish species and to disentangle these effects from the synergistic effect of fishing pressure on such populations. A fundamental concept which links the various levels of biological organization and also provides a matrix for integrating various environmental stressors is the concept of oxygen and capacity-limited thermal tolerance (OCLT).

Although purely statistical analyses of climate effects have provided evidence for climate-induced effects, only a few examples exist which demonstrate the relationship between climate sensitivity of particular species using physiological principles. In the following, appropriate examples are provided by discussing changes in specific populations of eelpout *Zoarces viviparus* (L.), Japanese anchovy *Engraulis japonicus* Temminck & Schlegel, Japanese sardine *Sardinops melanostictus* (Temminck & Schlegel) and Atlantic cod *Gadus morhua* L.

This review paper focuses attention on the need for a cause-and-effect understanding of climate interactions with marine fishes and the ecosystems in which they live. In the first section, a review is given of broad-scale patterns observed in (1) the effects of temperature on species and (2) climate-driven ecosystem-level changes. In the next section, coverage focuses on (3) an elaboration of the cellular and organismal-level physiological underpinning of species-specific responses to temperature and changes in other climate-driven factors (pH and hypoxia). Finally, in (4) a discussion is presented on current modelling methods that are based (at least in part) on physiological first principles and that are being utilized to understand historical and project future climate-driven changes in fish populations.

TEMPERATURE TOLERANCE AND OPTIMA AND CLIMATIC EFFECTS ON SPECIES

The literature is replete with studies that have measured lethal limits and, thus, tolerance to extreme temperatures by fish species (Appendix). Meta-analyses of the available data have demonstrated clear species-specific differences in both preferred and tolerable extreme temperatures (Jobling, 1981). These differences appear not only between species but also within species, for example related to differences in thermal windows due to acclimation or permanent population differences.

Measurements of the upper and lower lethal temperatures or critical thermal maxima or minima (Becker & Genoway, 1979) of fish species (T_{Cmax} and T_{Cmin} or T_{Lmax} and T_{Lmin}) can be used to illustrate the degree of specialization of species and populations on specific thermal environments. As a note of caution, these extreme limits may not be directly relevant in the ecosystem. They are, however, correlated with limits reached sooner and operative at ecosystem level. These limits, which are sublethal on shorter time scales, are not (yet) as widely available in the literature.

Extreme temperature limits and associated tolerance ranges within and among fish species change with latitude of the field population [Fig. 1(a)]. The range in tolerable temperatures is most narrow for fishes inhabiting high latitudes and relatively narrow for species at low latitude. In contrast, the tolerance range tends to be widest for fishes inhabiting mid-latitudes where seasonal differences in temperatures are, on average, largest. Figure 1 also depicts the preferred temperatures of such species. Naturally, these thermal endpoints are not static but depend to some degree on acclimation temperature. When a fish species can be acclimated to vastly different temperatures such as a range of 20° C, large differences in the upper and lower limits can be observed [Fig. 1(b)]. Compared to critical or lethal extremes, acclimation to different water temperatures has less effect on preferred temperatures. Within a species, preferred temperatures are often closely related to T_{Cmax} (Tsuchida, 1995) and often correspond to optimal growth temperatures (Jobling, 1981). Caution must be taken, however, not to oversimplify estimates of thermal limits and preferences (and their relation) since other environmental factors (*e.g.* prey availability and salinity) can modify each of these thermal values. Moreover, measurements of T_{Cmax} need to be interpreted with caution since experimental protocols may not have adequately accounted for the time dependence of such lethal thresholds. Nevertheless, overall, patterns of changes in tolerance may give a first approximation of the relative effects of increased temperatures due to global warming. The relationship also allows geographical distributions of species (Arctic, boreal, Lusitanian, tropical and Atlantic) to be used as a classification scheme to evaluate expected responses. In general, the analysis of physiological patterns on large scales, *e.g.* latitudinal clines as in macrophysiology (Gaston *et al.*, 2008), will help to unravel specialization on climate and associated limitations.

A second important feature of thermal physiology within fish species is ontogenetic change in the width of thermal tolerance windows. Two examples of this phenomenon are presented in Fig. 2, one based on a literature synthesis presented by Brewer (1976) for northern anchovy *Engraulis mordax* Girard inhabiting the California current, and the second from Rijnsdorp *et al.* (2009) based on a compilation of results for sole *Solea solea* (L.) in the North Sea. Patterns of thermal tolerance
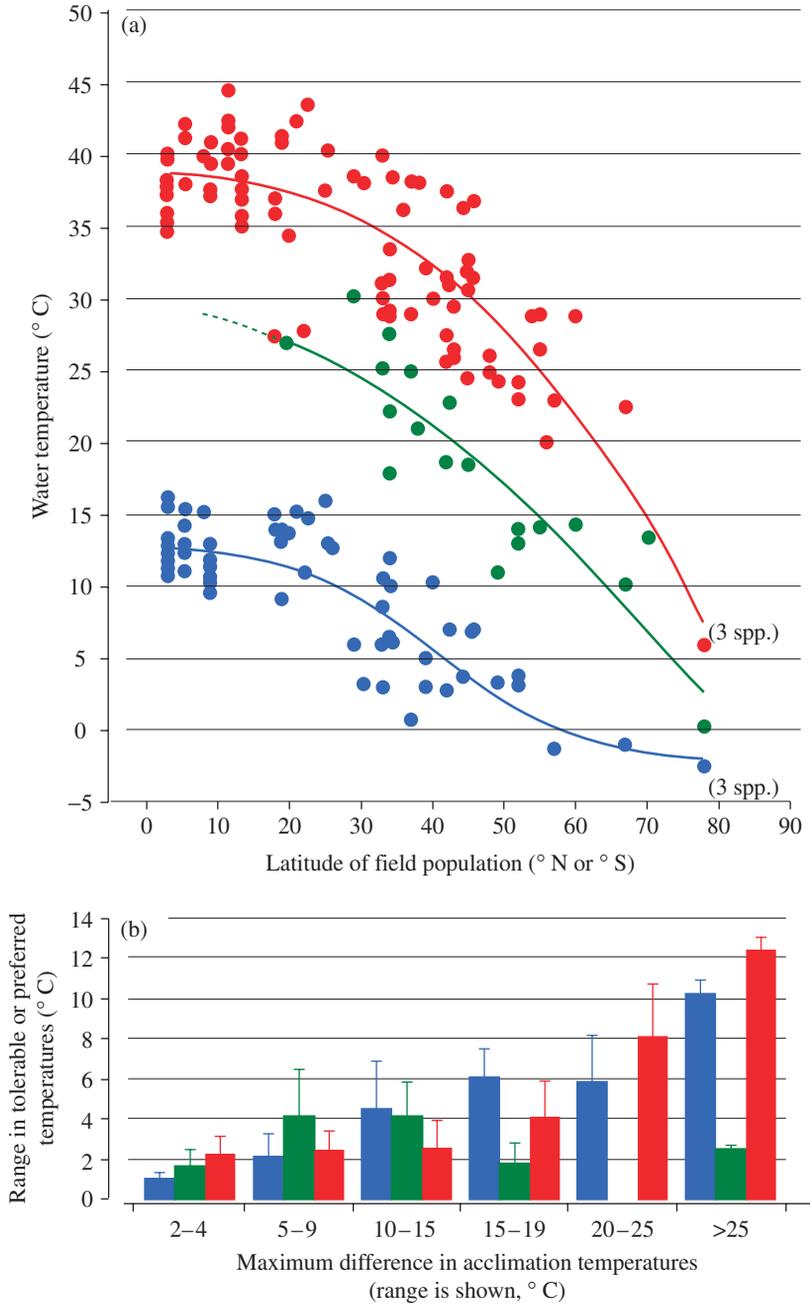
FIG. 1. (a) Thermal tolerance in marine fish species including upper (T_U, ●, 108 species), lower (T_L, ●, 61 species) and preferred (T_{PR}, ●, 21 species) temperatures and latitude of the fish population. Note that values of T_U or T_L are lethal or critical thermal maxima and minima (T_{Cmax} and T_{Cmin}). (b) Values of T_L, T_U or T_{PR} shift for fish acclimated to different water temperatures (grouped according to the magnitude of the difference between upper and lower acclimation temperatures). Note the increase (mean ± S.D.) in T_L (■) and T_U (■) ranges but not T_{PR} (■) for fishes studied over the broadest range of acclimation temperatures. Data were taken from published literature sources (see Appendix).
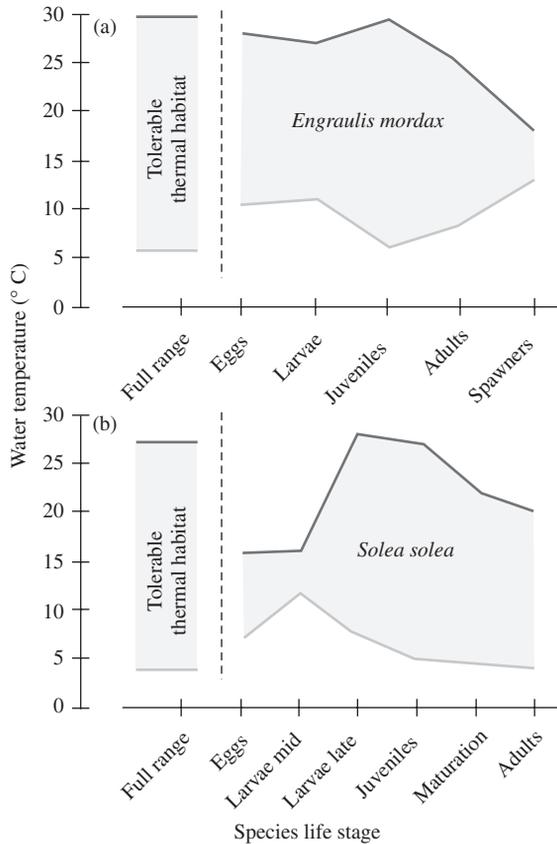
FIG. 2. Ontogenetic changes in thermal habitats or tolerance for *Engraulis mordax* in the California current (from Brewer, 1976) and *Solea solea* in the North Sea (from Rijnsdorp *et al*., 2009). In both cases, the earliest life stages were more sensitive (had a more narrow range in thermal tolerance) than later larvae and early juveniles that can exploit the largest range in thermal habitats compared to earlier or later (adult) life stages. In the *S. solea* example, maturation refers to the body size at which fish become sexually mature (first enter the adult stage) and does not refer to adult fish that are in spawning condition (displayed for *E. mordax* data).

by life stage in both these highly phylogenetically different species indicate thermal bottlenecks during the early life stages or in spawning stage. In the future and once available, such critical and lethal limits as depicted in Figs 1 and 2 will need to be replaced by more realistic limits (more narrow thermal ranges) beyond which ecological interaction sets in (Pörtner & Knust, 2007). Available knowledge of mechanistic principles already indicates that thermal windows are narrow in early life stages, due to developmental constraints and insufficient capacity of central organs in the larvae (Pörtner *et al*., 2006). Thermal windows widen in juveniles and young adults in line with rising performance capacity at small body size. Larger individuals then become more thermally sensitive, due to progressively falling oxygen supply capacity in relation to demand. Adult spawners need to provide oxygen to their large egg or sperm masses, at the expense of a narrowing of thermal tolerance windows and a lowering of tolerated extremes (Pörtner & Farrell, 2008).

Ecosystem effects are not only related to shifts in seasonal or annual mean temperatures. Currently, such shifts and their effects are prominent at high latitudes. Temperature maxima or minima, as opposed to mean temperatures, however, represent strong driving forces for ecosystem-level changes in population structure and in the community composition of marine areas. This is true on both the cold and the warm side of the temperature spectrum and, accordingly, on both sides of the thermal window of species. Here, ambient temperature exceeds the capacity of the individuals to acclimatize to lower or higher temperatures and, thereby, shift thermal limits. Long-term sustenance of species below their lower thermal limit is not possible. Among adult fishes, a prominent example is the sea bream *Sparus aurata* L. which cannot be cultured at $\leq 10^\circ$ C as it develops symptoms called 'winter syndrome' (Domenech *et al.*, 1997). This species cannot acclimate to those low temperatures and therefore suffers from fitness decrements and disease (Gallardo *et al.*, 2003; Ibarz *et al.*, 2010; Kyprianou *et al.*, 2010).

Sensitivity to cold appears as a very important characteristic in shaping community composition. Accordingly, winter exposure of fish larvae is seen as a key selective factor in setting the productivity of a species. The occasional occurrence of cold stress is probably effective in setting limits to the biogeography of cold-sensitive species. Low temperatures during winter may increase mortality, either because temperatures fall outside the thermal window or because energy reserves become limiting, especially in smaller individuals that have relatively fewer reserves compared to larger conspecifics (Post & Evans, 1989; Sogard, 1997). Extreme winter events cause reductions in species abundance and ecosystem changes, for example in the German Wadden Sea (Woodhead, 1964). The frequency of such events, however, has decreased during recent decades and the alleviation of winter cold has been paralleled by an increase in the frequency of warmer summers.

Conversely, cold-tolerant species will suffer from increasing exposure to summer heat. Observed shifts in geographical distribution of species such as *G. morhua*, snake blenny *Lumpenus lumpretaeformis* (Walbaum) and anglerfish *Lophius piscatorius* L. in the North Sea may involve the shifting frequencies of such weather conditions (Perry *et al.*, 2005). Specific life stages, however, may be especially sensitive during well-defined seasonal time windows as seen for *G. morhua* in the southern North Sea. Here, winter warming is closely correlated with the population shift (Perry *et al.*, 2005), indicating that adult spawners as well as eggs and larvae are the putative critical life stages sensitive to winter warming (Pörtner *et al.*, 2008; Pörtner & Farrell, 2008). As a result, recruitment of *G. morhua* in the North Sea falls during warming, but rises during cooling. In contrast, recruitment of the Barents Sea (north-east Arctic) *G. morhua* population decreases during cooling periods and increases upon warming. These trends emphasize that *G. morhua* in the southern North Sea live close to the upper and those in the Barents Sea to the lower thermal limits of the species, respectively. In line with these observations, correlations between climate-associated temperature change and *G. morhua* recruitment are stronger at the southern and northern borders of the geographical distribution area of the species in the north-east Atlantic Ocean. As a corollary, temperature defines the southern and northern distribution limits of the species.

A second example of the consequences of different thermal windows for growth and spawning productivity can be found in the oscillations between *E. japonicus* and *S. melanostictus* in the Pacific Ocean. In the Kuroshio–Oyashio current, alternating

periods of relatively cold and warm years are closely associated with alternating dominance of *S. melanostictus* and *E. japonicus*, respectively. These shifts are linked to the limited and different thermal windows of growth and of spawning productivity of the two species (Takasuka *et al.*, 2007, 2008). Performance capacity within a limited thermal window thus appears key to the successful survival and competition of a species.

Such climate-dependent functional specialization and differentiation even occurs between populations of the same species. *Gadus morhua* populations between the southern North Sea and the Arctic North Atlantic display different thermal windows of growth (Pörtner *et al.*, 2001, 2008). The key observation is that high latitude populations display an earlier reduction in growth during warming and are more cold tolerant. Their overall growth rates appear reduced, probably due to the metabolic cost associated with being cold tolerant and eurythermal at the same time. Such climate-driven functional differentiation may support the divergence of species from a common ancestor. For example, along the North American Atlantic coast between Nova Scotia, Canada, and Florida, U.S.A., the killifish *Fundulus heteroclitus* (L.) has split into two species with hybrids occurring in the middle of the range. To what extent adaptation to local or regional differences in climate has supported speciation is an active field of research (Fangue *et al.*, 2006). In this context, identifying physiological changes such as adaptations enhancing energy efficiency depending on local and regional variability in temperatures (Pörtner, 2006) will help clarify how metabolic adaptations are involved in specialization on the climate regime and may support speciation.

The success or fitness of a species is best measured in terms of its productivity in the field which, in terms of biomass, is determined by rates of growth and mortality and recruitment success. Most commercial fish species produce millions of eggs (Rothschild, 1986), and mortality rates of early life-history stages are very high and variable, generating large fluctuations in the survival of year classes destined to enter the adult population (Houde, 2008). Relatively small changes in rates of growth and mortality during the egg and larval phases can have a great influence on the recruitment success of populations. As early life-history stages are likely to be more sensitive to altered environmental conditions, climate change is expected to have a major effect on the distribution and abundance of fishes through its influence on recruitment. Apart from direct mortality of early life stages due to intolerable conditions, differences in rates of survival will be attributable to match–mismatch dynamics between the timing of reproduction relative to the production of larval food (*e.g. G. morhua*) and predators (Cushing, 1990; van der Veer *et al.*, 2000; Platt *et al.*, 2003; Temming *et al.*, 2007) or the connectivity (retention or transport) between spawning sites and required nursery areas of early life stages (Sinclair, 1988; Wilderbuer *et al.*, 2002).

Inter-stock comparisons often indicate dome-shaped relationships between recruitment strength and water temperature experienced during the spawning season, with maximum recruitment at an intermediate temperature in both demersal and pelagic fishes (Brander, 2000; MacKenzie & Köster, 2004). The effects of climate on recruitment, however, are not limited to processes acting during the egg and larval stages, but may extend to later (juvenile and adult) life stages and finally adult reproductive performance. For example, survival through the first, critical year of life in some species appears linked to feeding and temperature conditions experienced during the

postlarval or juvenile period (Baumann *et al*., 2007), particularly in fish species that feed exclusively on zooplankton and that can exert strong top-down control and exhaust that prey resource.

Productivity will also be influenced by the effect of temperature on growth rate (Brander, 1995; Teal *et al*., 2008). In a comparative study of 15 *G. morhua* stocks, seven-fold differences in the productivity among stocks corresponded to the differences in the temperature of the environment (Dutil & Brander, 2003). This effect adds to the finding of different performance rates (*e.g.* in growth) of *G. morhua* populations at the same temperature due to specialization on local or regional climate regimes. Fish species are generally plastic in the age and size at which they become sexually mature. An increase in juvenile growth as well as an increase in temperature may result in a decrease in the length and age at first maturation, affecting the growth of adults as surplus energy is channelled into reproduction at an earlier age and smaller size (Heino *et al*., 2002). The data available for *E. japonicus* and *S. melanostictus* in the Japan Sea indicate that recruitment processes and growth occur within the same species-specific range of temperatures (Takasuka *et al*., 2007, 2008).

As a consequence of thermal specialization, low productivity and high mortality will occur when temperature conditions reach extreme values. Further factors, however, interfere and interact with temperature. Mortality will be elicited or enhanced during hypoxic, or anoxic conditions, as has been reported for the Kattegat (Diaz, 2001). In some ecosystems, mass mortalities during summer have been reported in relation to harmful algal blooms (Yin *et al*., 1999; Heil *et al*., 2001). Climate change may have dramatic (negative) effects on the productivity of fish populations by increasing the frequency of these episodic extreme events that have acute, physiological consequences.

For some broadcast spawning fish species, there is evidence that the size of populations is determined by the size and availability of spawning and nursery habitats (Rijnsdorp *et al*., 1992; Gibson, 1994; Sparholt, 1996; MacKenzie *et al*., 2000). Limits on the availability of these habitats may act as a bottleneck for population size (and productivity). In these cases, the focus should be on the effect of climate change on the critical life-history stages. Whether this relationship is applicable will depend on the relative size of the habitat in relation to that of other life-history stages and is determined by the specific geographic setting. Finally, life cycle closure may be affected if climate change influences the connectivity between the habitats of successive life-history stages (Sinclair, 1988; Rijnsdorp *et al*., 2009). For instance, changes in ocean climate may affect the transport of eggs and larvae between spawning grounds and nursery areas (Corten, 1986; van der Veer *et al*., 2000; Wilderbuer *et al*., 2002) or may change the timing of spawning migrations and arrival of adults at the spawning grounds (Sims *et al*., 2005).

EXTENDING BEYOND SPECIES: COMMUNITY AND ECOSYSTEM EFFECTS

The principles behind species specialization and sensitivity also extend to the community level and ecosystem functioning. Different thermal windows of species probably influence the quality and intensity as well as the seasonal timing of their

interactions in an ecosystem (Pörtner & Farrell, 2008). In general, species coexist where their thermal windows overlap and their thermal windows are not necessarily identical. This physiological feature explains why climate sensitivity differs among species and may be one principal reason for climate-induced changes in community composition and food-web interactions. The limited window of whole organism performance capacity will then directly affect the productivity of a species in an ecosystem, as well as indirectly by influencing its interactions with other species (in predator–prey and competitive interactions) in that ecosystem. Alterations in community composition may result as direct effects of temperature on individual species and lead to higher level effects in the ecosystem. For example, a regime shift among copepods in the *Calanus* genus, from colder water *Calanus finmarchicus* to warmer water *Calanus helgolandicus* was correlated with the timing of the decrease in North Sea *G. morhua* stocks due to reduced food availability for juvenile *G. morhua* (Beaugrand *et al*., 2002). In the adjacent Baltic Sea, a similar regime shift occurred among copepods with a reduction in *Pseudocalanus acuspus* and the increase in smaller, warmer water *Acartia* and *Temora* spp. The resulting alteration in predator–prey relationships favours the early (larval) survival of sprat *Sprattus sprattus* (L.), one of the two dominant clupeid species in the Baltic, over that of larval cod. Adult *G. morhua* are the major predator of Baltic *S. sprattus* (Möllmann *et al*., 2009).

These regime shifts occurring in copepods represent a similar phenomenon as the one described for the regime shift between *S. melanostictus* and *E. japonicus*. These examples emphasize that the differential physiological effects of temperature on individual species in relation to their limited window of whole organism performance capacity are key to understanding and projecting climate-induced changes in species interactions and, furthermore, in community composition (Pörtner & Farrell, 2008). The fundamental insight here is that higher level processes (at population, community or ecosystem levels) are driven by the similarities, differences and relationships between niches of the various species that make up a community.

Finally and as exemplified above, climate change is expected to affect a number of different attributes of ecosystems including the dynamics of marine fish prey resources. When the mismatch between predators and prey is not so severe, food-limited (lower) growth rates may be observed which may shift thermal sensitivity or make mortality due to predation more likely. The processes are indeed complex and highly interactive. As a first step, the effects of global warming on marine fish species can be inferred from empirical comparisons made among populations inhabiting environments with different mean characteristics. This would then be the basis for elaborating the contributing mechanisms to patterns observed among populations of a species (Brander, 1995; Drinkwater, 2005).

As a corollary, an overarching pattern in this complexity is the specialization of marine fauna on climate-related temperature windows. This causes sensitivity to temperature extremes, due to decrements in performance (*i.e.* the capacities to forage, migrate, grow or reproduce). Temperature change is currently the main driving force causing shifts in the geographical distribution of species and in the species composition of marine ecosystems. Increasingly, temperature interacts with other stressors operating at large scales such as carbon dioxide induced ocean acidification and hypoxia in warming, more stratified oceans. As outlined below and elsewhere (Pörtner, 2010), the thermal window comprising temperature-dependent

performance and passive resistance may act as a suitable matrix to address such relationships and then build a foundation on which ecosystem-level complexities can be addressed.

PHYSIOLOGICAL EFFECTS OF CLIMATE CHANGE ON ECOSYSTEMS

OXYGEN AND CAPACITY-LIMITED THERMAL TOLERANCE

Specialization of marine fauna and their life stages on climate-related thermal windows emerges as one overarching reason for the sensitivity of marine fauna to temperature extremes. As previously discussed, thermal windows differ between life stages of one species as well as between species and thereby co-define changes in higher level processes at ecosystem level in response to climate change (Pörtner & Farrell, 2008). For animals, the concept of oxygen and capacity-limited thermal tolerance (OCLT; Fig. 3) provides a mechanistic explanation of why and how thermal limitation occurs. It also provides access to the differentiation between the thermal range of permanent, active survival through temperature-dependent performance and the range of time-limited passive tolerance to temperature extremes. This concept also explains the transition between those ranges. It is a suitable candidate to define the borders of the niche of functional capacity of a species with respect to temperature and to species interactions (Pörtner *et al*., 2010).

The concept implies that oxygen supply to tissues is optimal between limits called lower and upper pejus temperatures (pejus means getting worse). Between pejus limits, oxygen supply can also be increased to levels above maintenance demand at which point aerobic metabolism can sustain performances such as growth, foraging, migration and reproduction that support the fitness of species. The excess in oxygen availability supporting such performances is reflected in an animal's aerobic scope (the difference between the lowest and highest rates of aerobic respiration) with an optimum close to the upper pejus temperature. These considerations match earlier definitions by Fry (1971) who classified environmental factors based upon their influence on aerobic metabolism and aerobic scope. The latter represents the energy available for all life processes and is, more precisely, the difference between standard levels (or costs) and the rate caused by environmental stimuli or activity increments. According to Fig. 3, temperature co-defines the scope, due to limitations on capacity, and other factors also act to increase or decrease (limit) the aerobic scope.

The kinetic stimulation of performance by warming causes the curve of the relationship to be tilted to the right. The kinetic slowing of performance by cooling below the optimum leads to a lower pejus limit, which is characterized by performance significantly below optimum levels. Some polar fishes live permanently below their acclimated optimum (Lannig *et al*., 2005; Brodte *et al*., 2006), indicating that the temperature range below the optimum but above lower pejus temperature is still ecologically viable. Beyond upper pejus limits, oxygen supply capacity becomes limiting, maintenance demand rises and aerobic scope starts to decrease in due course. Hypoxaemia develops and whole organism functional capacity (*e.g.* exercise or growth performance) declines. Once critical temperatures are reached, extreme hypoxaemia causes a transition to anaerobic metabolism. Finally, thermal damage to the integrity of molecular structures (denaturation) may occur.

Figure 3 distinguishes between the temperature range associated with long-term survival, growth and reproduction due to maintained performance (the active range) and the subsequent time-limited endurance of temperature extremes (passive range). The transition between the two and the loss in performance is progressive, leading to a progressively severe time limitation of thermal tolerance. The point where this transition starts is defined as the pejus temperature (T_p, the temperature at which aerobic scope begins to decline). Organisms would not survive long term at temperatures higher than the upper T_p or below the lower T_p; time constraints become more and more severe as temperatures approach and reach beyond T_C where aerobic scope approaches zero. The combination (product) of time and heat load beyond T_p (Fig. 4) would then set the lethal temperature, which indicates the ultimate limits of passive tolerance (Pörtner, 2010). The lethal temperature is thus time dependent, such that short-term heating protocols will lead to higher lethal temperatures than long-term heating protocols. In laboratory studies, lethal tolerance limits of fishes have traditionally been determined as the onset of spasms
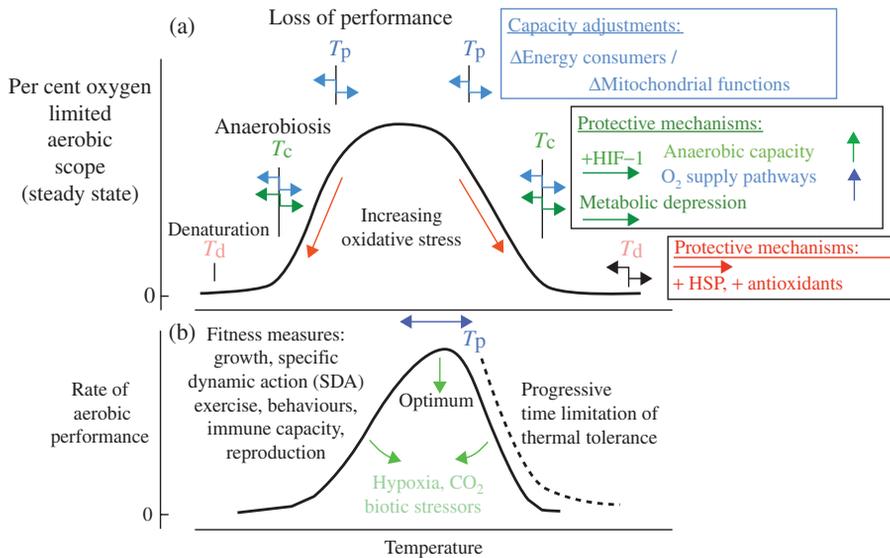

Fig. 3. Conceptual model of how ocean warming, hypoxia and acidification, as interacting stressors, shape the thermal window of performance of a species at a specific life stage, based on the concept of oxygen and capacity-limited thermal tolerance (OCLT). Oxygen supply to tissues is (a) optimal between low and high pejus temperatures and (b) supports temperature-dependent performance capacity. Critical temperatures (T_C) characterize the onset of anaerobic metabolism and denaturation temperatures (T_d) the loss in integrity of molecular structures. Critical thermal maxima and minima (T_{Cmax} and T_{Cmin}) delineate the outermost limits where whole organism function ceases. The kinetic stimulation of performance by warming leads to a tilted curve with a functional optimum close to the upper pejus temperature. This performance curve reflects the role or functional capacity and associated aerobic scope in ecosystem-level processes such as competition, foraging, immune response, growth and behaviours. Ambient hypoxia and elevated carbon dioxide levels both cause a narrowing of thermal windows and possibly, lower performance optima through lower functional capacities and reduced systemic oxygen tensions (→). The graph depicts acute performance levels and limitations in response to short-term temperature fluctuations. Seasonal acclimatization causes a shift and changing widths of acute performance windows within the limits of the thermal niche of a species (←→) (after Pörtner, 2010).
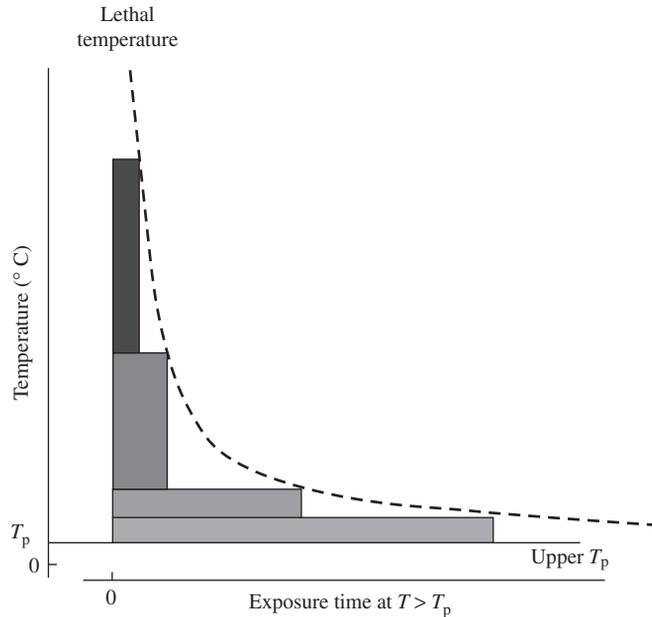
FIG. 4. Projection of how lethal tolerance limits depend on the time duration of heat exposure building on
    the oxygen and capacity-limited thermal tolerance (OCLT concept) (see Fig. 3). The upper pejus limit
    delineates the onset of time limitation in thermal tolerance. The tolerable heat budget is shaped by the
    capacity of protective mechanisms and equals the integral of excess temperature or heat experienced
    above T_p over time $[(T - T_p) \times$ time (h, days or weeks)]. This integral is assumed to remain constant
    between short-term exposures to high temperatures and long-term exposures to mild temperature changes.
    The integral may change with acclimation in protective capacity (after Pörtner, 2010). ...., heat excess
    tolerated over time $[(T - T_p)$ h].

at critical thermal maxima or minima (T_{Cmax} and T_{Cmin}). These limits have been
found beyond T_C values as defined by the OCLT concept, but again, are strongly
influenced by the rate of temperature change to which the organism is exposed
(Fig. 4). T_{Cmax} and T_{Cmin} are the temperatures at which fish are definitely unable
to escape conditions that will ultimately lead to thermal death. This view already
emphasizes the time component, which needs to be systematically considered dur-
ing evaluation of such limits. During exposures to extreme temperatures beyond
T_p, animals will progressively enhance their exploitation of protective mechanisms
such as the capacity of anaerobic metabolism (beyond T_C), of antioxidative defence
and of the heat-shock response. All these contribute to extend the period of pas-
sive tolerance. The relevance of these processes varies between species and would
be under strong selection in some environments where organisms are regularly
exposed to thermal extremes. For example, such passive extension of the range
of tolerance appears crucial in thermally variable environments such as the intertidal
zone.

   Pejus limits reached acutely on short time scales may shift over time when the
organism has the capacity to acclimate to temperature change (Lucassen *et al.*, 2006).
Acclimation capacity is limited, however, such that during exposure to tempera-
ture on long time scales (as in growth studies), performance decrements occur at

the limits of thermal acclimation capacity. Beyond these long-term thermal limits, the loss in fitness remains uncompensated and leads to various phenomena at the ecosystem level, *i.e.* a loss of growth performance and reduced population abundance. Such effects were observed in *Z. viviparus* in the German Wadden Sea (Pörtner & Knust, 2007), where abundance decreases upon exposure to extreme summer temperatures, in the same range of temperatures where growth performance decreases and the capacity of the circulatory system to supply oxygen becomes limiting. Large individuals are lost first from the population since they are affected most by the heat stress, in line with the exacerbation of oxygen limitation at larger body sizes. The combination of physiological studies in the laboratory with results from field surveys indicates that heat exposure in these fish leads to decreased abundance due to reductions in performance. It remains to be explored whether the largest individuals exposed to temperature extremes exploit their capacity of passive resistance.

While these phenomena identify the physiological processes limiting thermal tolerance at ecosystem levels, these observations clearly indicate the importance for an understanding of why animals specialize on limited thermal environments. Such specialization on a climate regime seems to involve savings of metabolic energy. The benefits of such specialization are so large that temperate zone species shift their thermal windows between winter, spring and summer or between life stages according to their season of existence. Permanent differences between thermal windows have even been detected between adults from various populations of the same species (fishes including *G. morhua* and marine invertebrates) in a latitudinal cline along the east Atlantic coast between the North Sea and the Arctic. The complexity increases further when considering that thermal specialization differs among life stages and influences the key processes shaping population size and structure, fecundity, growth and mortality.

Available data suggest that aerobic scope, which is limited to the window of tolerance, sets the environmental niche either acutely, *e.g.* as the niche of the respective life stage, or as a longer-term average of the species. A minimum level of aerobic performance characterizes the limits of this niche and supports minimum functional rates and competitiveness within an ecosystem. The concept of aerobic scope has a long-standing history in comparative physiology and has only recently been demonstrated to underpin climate-induced ecological shifts observed in the field. The concept of OCLT provides explanations of thermally limited aerobic scope. It relates the level of aerobic scope to climate and lifestyle; it explains the width and the tilted shape of the temperature-dependent aerobic performance curve (Fig. 5). Such mechanistic knowledge specifies the more empirical descriptions of thermally limited performance in evolutionary thermal biology (Angiletta, 2009).

PERFORMANCE PATTERNS AND ENERGY BUDGET

Thermal specialization attempting to match the local climate conditions occurs at molecular, cellular and whole organism levels. This has performance implications (*e.g.* due to changes in metabolic rates and capacity for acid–base regulation) at the level of the whole organism. Species-specific rates of body growth, feeding and special features of behaviour and activity can be expected as overarching consequences
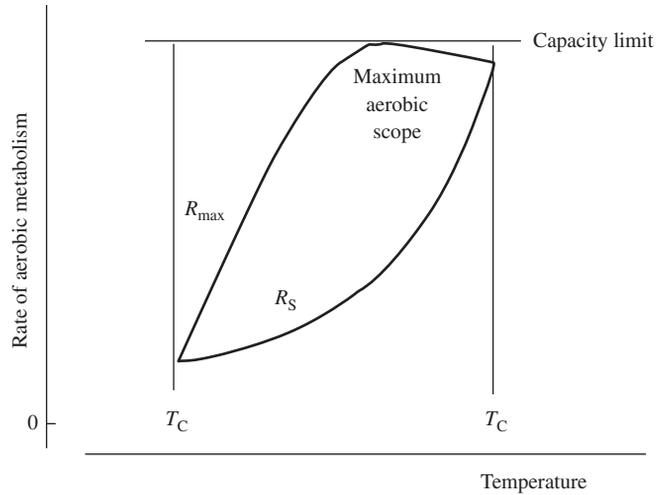
FIG. 5. Conceptual model of how standard and maximal metabolic rates fit the thermal window of oxygen and capacity-limited thermal tolerance (projected from mechanistic knowledge as in Fig. 2). The exponential phase of standard metabolism R_S is bordered by critical temperatures (T_C). The performance curve as in Fig. 3 results from the difference between maximum (R_{max}) and R_S rates.

of specialization according to climate, leading to species-specific responses to environmental changes associated with climate change. The answers relate to how the available excess in aerobic energy is allocated to specific functions and processes at the whole organism level. Following the second law of thermodynamics, these physiological effects at the organismal level have been addressed using balanced bioenergetics budgets that include specific pathways for energy gain and loss:

$$C = G + R + E + F \tag{1}$$

where C = energy gained from food consumption, G = the energy gained in growth, R = energy lost *via* respiration, E = energy lost *via* nitrogenous excretion and F = the energy lost in egested faecal material (Brett & Groves, 1979). All variables have common energetic units (*e.g.* joules day^{-1}). Rates of R (and E) can be subdivided to include different levels of energy loss due to basal (standard R_S), feeding (specific dynamic action, R_{SDA}), sometimes referred to as apparent heat increment (Blaikie & Kerr, 1996), and active (R_A) metabolism. The scope (maximum−minimum) of these rates thus follows the temperature-dependent window of aerobic scope, but the relative magnitude of these rates may change over time (Fig. 6). Growth can also be subdivided to partition between gonadal (G_G) and somatic (G_S) growth. This balanced equation is most commonly used to estimate either growth or food consumption after the other variables are determined (Hanson *et al.*, 1997). Rates of these various variables are affected by a number of factors including water temperature, fish body size and feeding level (Brett & Groves, 1979). Thus, balanced budgets provide a route for exploring possible effects of environmental changes at the level of the individual. For a true cause-and-effect understanding, however, the question requires
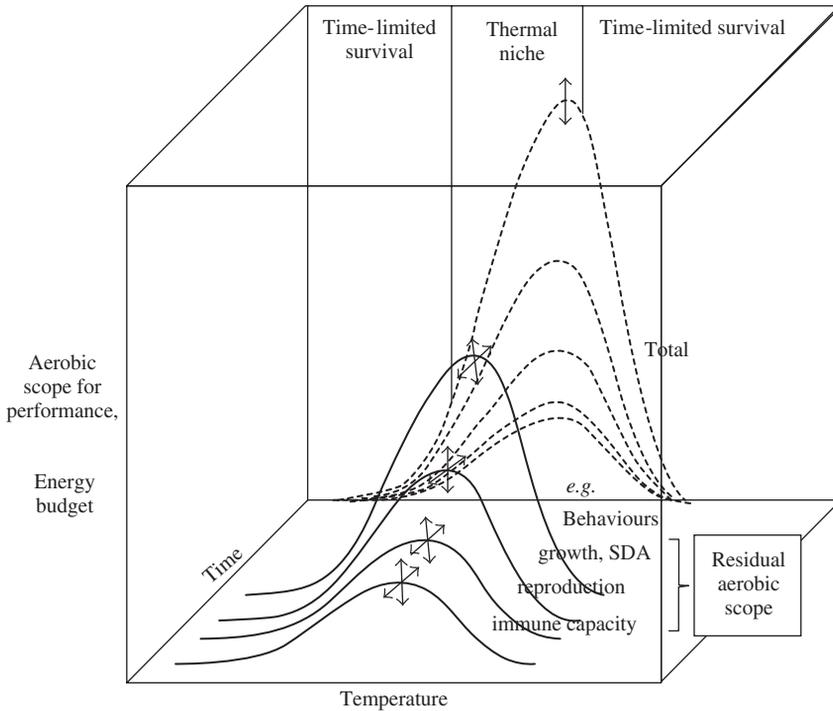
FIG. 6. Energy budget for processes beyond maintenance comprising fractions of overall performance fuelled by the temperature-dependent window of aerobic scope (Fig. 3). ←→, shifting fractions of various processes in the energy budget over time (SDA, specific dynamic action) (order and timing arbitrary) (after Pörtner *et al.*, 2010).

the consideration of which variables are dependent variables and, thus, follow from the relationships between climate specialization and climate sensitivity.

The effect of temperature on growth rate (*G*) follows the aerobic performance curve with net growth performance only possible above and below critical thresholds (Fig. 3). Sensitivity to temperature extremes rises when energy gained from *C* is much less than that lost *via R*, *E* and *F* (metabolic costs cannot be met by feeding). Above the lower threshold, when *C* is maximal (well-fed fishes), growth rates increase with increasing temperature until an optimal temperature is reached. With further increases in temperature, *G* often rapidly declines until mortality occurs. At sub-optimal high temperatures, fishes cannot consume enough food to meet increasing metabolic costs; available evidence suggests that there is not enough aerobic scope available to cover the postprandial increase in oxygen demand (Fig. 3). Losses in appetite occur at the highest temperatures, rapidly leading to mortality. Existing evidence suggests that the availability of aerobic power and its budgeting are crucial for the fitness of a species at the ecosystem level and for co-defining the niche of a species (Pörtner *et al.*, 2010; Guderley & Pörtner, 2010).

For some marine fishes, particularly traditional aquaculture species, relationships between growth rate and temperature have been determined at optimal (*ad libitum*) food supply (*e.g.* temperature-growth curves; Fonds *et al.*, 1992; Peck *et al.*, 2003). In

the wild, however, some fishes may not always experience unlimited prey resources, food supply may even become limiting to growth, particularly in young larvae (Buckley & Durbin, 2006) that have relatively poor foraging ability or in young juveniles that have high foraging ability and may occur at high enough abundances to exert top-down control of their prey, leading to reduced rates of growth and starvation (Baumann *et al.*, 2007). Food-limited growth, however, may be difficult to detect since these slower growing individuals of early life stages have an increased risk of predation mortality and tend to be removed from fish populations. Furthermore, some fishes may not live at their optimum temperature for the whole year or not even for their whole life as indicated by maximum growth at higher than ambient temperature in an Antarctic fish *Pachycara brachycephalum* (Pappenheim) (Brodte *et al.*, 2006). Therefore, observed growth rates in the field are quite dynamic both spatially and temporally (particularly in temperate environments), for reasons associated with temperature-dependent kinetic rate limitations or since other energy budget components take precedence and restrict energy allocation to growth. In the case of adult *G. morhua*, however, food limitations did not become visible in field samples collected in a latitudinal cline of the eastern North Atlantic Ocean. A reduced growth capacity in sub-Arctic compared to southerly populations was rather related to the metabolic costs associated with eurythermal cold adaptation (Pörtner *et al.*, 2001).

Insight from Fig. 3 suggests that growth rate depends on the availability of aerobic scope. Using the terminology of the energy budget (equation 1), a key process related to differences in environmental (*e.g.* thermal) tolerance is the rate of energy loss due to metabolism (R). The rate of metabolic loss tends to increase exponentially with increasing temperature, between limits set by critical temperatures of the OCLT window (Figs 3 and 5). Climate specialization and the width of thermal window cause R to vary if compared at specific temperatures. Specifically, if standard metabolic rate changes in response to thermal acclimatization or adaptation, then maximum metabolic rate and thus aerobic scope and in consequence R also vary accordingly. This might cause growth rate to vary depending on climate as described above for *G. morhua*. For a deeper understanding, the mechanistic background of such relationships requires consideration such as that indicated in Fig. 3.

Fry (1971) classified environmental factors based upon their influence on aerobic metabolism and aerobic scope. Thermal or other stimuli either act to increase (unload or release) or decrease (*e.g.* limit) the aerobic scope. The reasons for these changes can be linked to patterns and processes mentioned in Fig. 3 as well as to the role of temperature in reaction kinetics. At the most basic level, suitable environments are those where an organism's metabolic scope is positive and various controlling factors (*e.g.* temperature, pressure or water pH and carbon dioxide levels) determine the range of metabolic scope and hence reflect the active tolerance range (Figs 3 and 6). Thus, other factors interact with the controlling effect of temperature and either increase or decrease the metabolic rate and metabolic scope of an organism. Factors like carbon dioxide (ocean acidification) or hypoxia interact with the thermal window of OCLT (Pörtner, 2010). Existing knowledge suggests that these factors elicit metabolic depression that would support passive tolerance to thermal extremes but, at the same time, cause a reduction in aerobic scope. These mechanisms thereby cause a narrowing of thermal performance windows as in Fig. 3 and lead the organism earlier to the limits of its thermal acclimation capacity. In this context, several

authors have stated that marine fishes are likely to be less affected by an increase in oceanic carbon dioxide and a corresponding decrease in pH than invertebrate groups such as molluscs and corals (Pörtner, 2008). Synergistic effects of temperature extremes and carbon dioxide, however, have rarely been studied and require consideration when assessing climate sensitivity. Studies in coral reef fishes have confirmed the hypothesis that carbon dioxide levels as expected from anthropogenic emissions would exacerbate the effects of temperature extremes and cause further reductions in aerobic scope (Munday *et al.*, 2009*a*).

As a corollary, the relationships between the levels of energy turnover, the capacities of activity and other functions and the widths of thermal windows support an integrative understanding of specialization on climate and of sensitivity to climate change. The balance between oxygen demand for maintenance and the level of aerobic scope available to crucial performances between critical temperatures therefore appears essential for defining sensitivity and responses to abiotic and biotic environmental factors (Fig. 6). Pejus limits encompass the optimal range in temperatures (*i.e.* the temperatures where metabolic scope and thus performance is highest) and therefore delineate the window of highest competitiveness. In line with the predictions resulting from Fig. 3, aerobic scope closely describes the range of performance sensitivity to environmental changes.

As outlined above, the range of tolerable temperatures is both species and often life-stage specific and is a key attribute defining the observed distribution (niches and habitats utilized) by marine fish species. Global warming is not expected to affect all life stages of marine fishes in the same manner. For example, evidence for *S. solea* and *G. morhua* suggests that the optimum temperatures for growth decrease with increasing body size of juveniles and adults (Pörtner *et al.*, 2008). Decreases in oxygen-limited tolerance to warm temperatures with increasing body size can be used to explain the ontogenetic shift in habitats observed in several fish species where young stages occur in shallower (warmer) waters than larger stages. In some species, egg and larval stages have a narrower range in tolerable temperatures than other life-history stages (particularly juveniles), making these early life stages more vulnerable to the effects of global warming (Figs 2 and 7). As outlined above, the sensitivity of larval stages to global warming probably relates to the ontogenetic development of convective oxygen transport during a period of when diffusive oxygen supply becomes limiting (Pörtner *et al.*, 2006). In larvae, behavioural compensation is constrained by limited swimming abilities (particularly in temperate and polar species), making individuals less capable of selecting and migrating towards more suitable habitats. Furthermore, their relatively high (mass-specific) metabolic rates and lower energy reserves make these young life stages more vulnerable to mortality due to starvation during periods of adverse environmental condition (*i.e.* periods of food shortage). Another sensitive life stage is the mature spawner, where the egg mass is the largest tissue to be supplied with oxygen, which will narrow its tolerance range to temperature fluctuations due to the allometry of oxygen limitation. This may contribute to setting relatively low temperature limits to *G. morhua* during their winter and spring spawning (Pörtner *et al.*, 2008) and also contribute to limiting the heat tolerance of Pacific salmon *Oncorhynchus* spp. during their spawning migrations (Farrell *et al.*, 2008). In line with Fig. 2, Fig. 7 outlines these patterns expected from the principles of the OCLT concept.
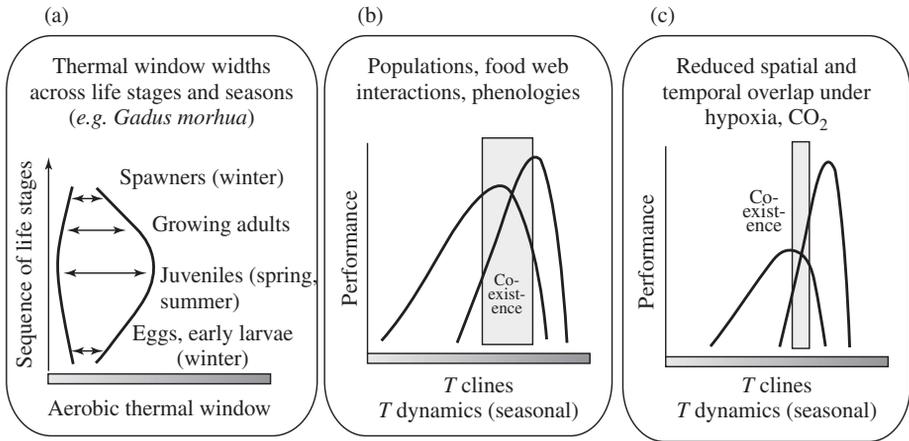
FIG. 7. Ecosystem-level perspective of how (a) thermal windows develop during ontogeny in relation to sea-sonal temperature dynamics (as in *Gadus morhua*, for further examples see Fig. 3). Furthermore, the synergistic effects of shifting temperatures, carbon dioxide and hypoxia levels affect species interactions, starting from (b) undisturbed conditions through (c) changes in temporal and thermal overlap as well as in relative performance (after Pörtner & Farrell, 2008).

In juvenile and (young) adult life stages, individual fishes can clearly respond to a change in temperature and in many cases exhibit active temperature preference. Some elasmobranchs respond to quite subtle changes in temperature (*i.e.* to changes of $<0.001°$ C; Brown, 2003). Naturally, even for individuals in these later life stages that have strong swimming capacity, information concerning the location of optimal habitats will not be perfect. Moreover, behavioural changes may have unexpected consequences. For example, as a result of an increase in temperature, the swimming speed of *G. morhua* and other species increases (Peck *et al.*, 2006) and animals may behave differently in response to oncoming fishing gear making them more (or less) vulnerable to capture. Finally, over longer time periods, climate-driven changes in temperature can modify the phenology of annual migrations to feeding and spawning grounds as observed and predicted for temperate marine species. It can be inferred that the behavioural response to changes in environmental conditions brought on by global warming or ocean acidification (Munday *et al.*, 2009*b*) will depend on the rate of change and the spatial scale over which conditions change relative to fish body size or developmental stage since the capacity for avoidance responses will increase with increasing body size.

Changes in species interactions and competitiveness at the ecosystem level may also reflect these principles and may result from relative changes in performance due to different thermal sensitivities (Fig. 7; Pörtner & Farrell, 2008). The regime shifts described then not only relate to the principle effects of temperature according to thermal windows. Shifts may be accelerated by the relative changes in performance and the associated shift in competitiveness once species compete for the same resource or ecological niche.

PHYSIOLOGY-BASED PROJECTIONS OF EFFECTS

Projections have been made of the effects of global warming on marine fishes using a variety of methods that range from simple to complex, each of which has its own caveats and only some of which incorporate physiological mechanisms. Most projections of the effects of global warming on fish populations, aside from simple what if hypothesis testing, rely on the outputs of global climate models (GCM).

In the most simple example, outputs from GCMs are used to adjust environmentally sensitive stock–recruitment relationships which are essentially functions estimating year class survival (recruitment) from key population and environmental factors (*e.g.* spawning stock biomass and temperature), as in the dome-shaped relationships described above. Such predictions do not reveal mechanisms but, nonetheless, provide short-term estimates of population strength in the face of climate effects, all other elements of the ecosystem being equal.

'Bioclimatic envelope modelling' represents a second approach which is more physiology-based, in that it makes projections based upon changes in environmental conditions correlated with the survival (or current distribution) and productivity of individual species (Beaumont *et al.*, 2005). Projected global or regional changes in key physical features of marine habitats (water temperature and circulation patterns) in various ecosystems have thus been translated into broad-brush projections of changes in distribution (and productivity) based upon a species' bioclimate envelope. Recent modelling results for >800 commercially important marine fish species (Cheung *et al.*, 2009) suggested that climate change could lead to numerous local extinction events by the year 2050, particularly in subpolar regions, the tropics and semi-enclosed seas (*e.g.* the Mediterranean Sea), with the distribution of pelagic fish species (Clupeiformes) and demersal species [such as *G. morhua*, haddock *Melanogrammus aeglefinus* (L.) and flatfishes] moving pole-wards by an average of 600 and 223 km, respectively. Similar to the simple stock–recruitment relationships described above, however, such predictions do not take into account other changes that may occur in marine habitats that place constraints on the survival and persistence of populations of marine fishes.

Biophysical individual-based models (IBM) represent a third example of methods available for climate model-based projections. To date, most IBMs constructed for marine fishes have been used to help understand the processes affecting the survival and growth of early life stages and recruitment success (Miller, 2007). Many IBMs are physiology-related and estimate growth and survival using balanced bioenergetics and foraging potential (Peck & Daewel, 2007; Hinrichsen *et al.*, 2010). Recently coupled ecosystem-larval fish IBMs have been developed that allow climate-driven changes in factors that may directly (water currents and temperatures) and indirectly (prey productivity) affect fish survival and growth to be included (Daewel *et al.*, 2008, in press). Finally, end-to-end biophysical models are now being applied that include juvenile and adult behaviour and growth bioenergetics to assess climate-driven effects in zooplanktivorous species such as Pacific herring *Clupea pallasii* Valenciennes (Kishi *et al.*, 2007). The reliability of this modelling approach to project future results, however, depends upon obtaining robust estimates of hydrographic changes resulting from global warming. The latter is a rapidly advancing field of climate research. Furthermore, such modelling efforts would benefit from a robust

understanding of the mechanisms shaping climate-dependent evolution, specialization on climate and the associated trade-offs and constraints in adaptation.

As a corollary, future studies need to move beyond correlative approaches and should attempt to reveal a cause-and-effect understanding of the underlying mechanisms; otherwise, consensus on the ecological implications of climate change will remain elusive. Such a cause-and-effect understanding needs to be improved. Ideally, investigations need to be integrative and address how mechanisms interact across various levels of biological organization, from genome to molecule, cell, tissue, organism and ecosystem. For an assessment of fitness in the natural habitat, these approaches should include an assessment not only of performance (and performance variability) in individual species but also of relative changes in performance of interacting species and of the respective consequences at ecosystem levels (Pörtner & Farrell, 2008). This will advance a mechanism-based understanding of the constraints and trade-offs in adaptation as well as of the limits in acclimatization and adaptation processes, which are closely linked to ecosystem-level phenomena and responses to climate change (Pörtner & Knust, 2007; Farrell *et al.*, 2008). Such knowledge would need to be extended and applied to many more examples than are currently available. This conceptual framework also needs to be considered and, when possible, integrated within modelled projections, both for improved reliability of those projections and for developing further hypotheses for a deepening of the integrative understanding.

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APPENDIX. Table summarizing the critical or lethal thermal maxima and minima for various species of teleosts, together with other relevant information including acclimation temperature (acclim.). Life stages include larvae (L), juvenile (J) and adult (A). Fish types include freshwater (F), marine (M), estuarine (E) and anadromous (A)

| Teleost | | Life stage (L, J, A) | Type | Latitude of field collection (° N or ° S) | Acclim. | Temperature (° C) | | | | | | Preferred mean | Reference |
| Species | Common name | | | | | Critical | | Lethal | | | | | |
						Mini-mum	Maxi-mum	Mini-mum	Maxi-mum	Mini-mum	Maxi-mum		
Apogon pacifici	Cardinalfish	A	M	3·0	26·5	10·8	35·2						Graham (1971), Mora & Ospina (2001, 2002)
Plagiotremus azaleus	Sabertooth blenny	A	M	3·0	26·5	13·4	38·2						Mora & Ospina (2001, 2002)
Cirrhiitichthys oxycephalus	Pixy hawkfish	A	M	3·0	26·5	11·4	35·4						Mora & Ospina (2001, 2002)
Bathygobious ramosus	Goby sp.	A	E	3·0	26·5	12·0	35·8						Mora & Ospina (2001, 2002)
Coryphopterus urospilus	Redlight goby	A	E	3·0	26·5	12·3	36·0						Mora & Ospina (2001, 2002)
Haemulon steindachneri	Chere-chere grunt	A	M	3·0	26·5	13·2	38·1						Mora & Ospina (2001, 2002)
Halichoeres dispilus	Chameleon wrasse	A	M	3·0	26·5	15·6	39·7						Mora & Ospina (2001, 2002)
Thalassoma lucasanum	Cortez Rainbow Wrasse	A	M	3·0	26·5	16·2	40·1						Mora & Ospina (2001, 2002)
Malacoctenus zonifer	Glossy blenny	A	M	3·0	26·5	12·5	37·3						Mora & Ospina (2001, 2002)
Lutjanus guttatus	Spotted rose snapper	A	M	3·0	26·5	12·0	35·9						Mora & Ospina (2001, 2002)
Eucinostomus gracilis	Mojarra	A	M	3·0	26·5	12·5	36·0						Mora & Ospina (2001, 2002)
Mugil curema	White mullet	A	M	3·0	26·5	10·7	34·7						Mora & Ospina (2001, 2002)
Chromis atrilobata	Scissortail damselfish	A	M	3·0	26·5	11·2	35·3						Mora & Ospina (2001, 2002)

APPENDIX. Continued

Species	Common name	Life stage (L, J, A)	Type	Latitude of field collection (° N or ° S)	Acclim.	Critical Minimum	Critical Maximum	Lethal Minimum	Lethal Maximum	Preferred mean	Reference
Stegastes acapulcoensis	Acapulco damselfish	A	M	3·0	26·5	12·6	37·5				Mora & Ospina (2001, 2002)
Apogon dovii	Tailspot cardinalfish	A	M	3·0 and 9·0	26·5	13·1	37·8				Mora & Ospina (2001, 2002)
Apogon novenfasciatus	Nine-banded cardinalfish	np	M	5·5	17–32	15·4	38·0				Eme & Bennett (2009)
Bathygobius fuscus	Duskyfrill goby	np	E	5·5	20–35	11·1	41·2				Eme & Bennett (2009)
Bathygobius sp.	Sandflat goby	np	E	5·5	17–34	12·4	41·4				Eme & Bennett (2009)
Liza vaigiensis	Squaretail mullet	np	M	5·5	20–35	13·0	42·2				Eme & Bennett (2009)
Dascyllus aruanus	White-tailed humbug	np	M	5·5	17–31	14·3	38·0				Eme & Bennett (2009)
Horabagrus brachysoma	Yellow catfish	np	F	8·0	15–36	15·2	40·0				Dalvi *et al.* (2009)
Apogon maculatus	Spotted cardinalfish	A	M	9·0	26–28	13·0	37·7				Graham (1971)
Bathygobius ramosus	Panamic frillfin	A	E	9·0	17–28	9·5	39·5				Graham (1971)
Bathygobius soporator	Frillfin goby	A	E	9·0	26–28	10·1	40·9				Graham (1971)
Abudefduf saxatillis	Sergeant major	A	M	9·0	26–28	11·6	39·3				Graham (1971)
Abudefduf troschelii	Pan. sergeant major	A	M	9·0	26·5–29	11·9	39·4				Graham (1972)
Ambasis commersoni	Glass fish	A	E	11·5	28		40·5				Rajaguru & Ramachandran (2001)
Lates calcarifer	Barramundi	A	E	11·5	28		44·5				Rajaguru & Ramachandran (2001)

APPENDIX. Continued

| Teleost | | Life stage (L, J, A) | Type | Latitude of field collection (° N or ° S) | Acclim. | Temperature (° C) | | | | | Reference |
| Species | Common name | | | | | Critical | | Lethal | | Preferred mean | |
						Mini-mum	Maxi-mum	Mini-mum	Maxi-mum		
Liza dussumeri	Mullet sp.	A	M	11·5	28		44·5				Rajaguru & Ramachandran (2001)
Etroplus suratensis	Pearlspot	A	M	11·5	20–35		42·3				Rajaguru & Ramachandran (2001)
Scatophagus argus	Spotted scat	A	M	11·5	28		42·5				Rajaguru & Ramachandran (2001)
Siganus javus	Streaked spinefoot	A	E	11·5	28		39·5				Rajaguru & Ramachandran (2001)
Therapon jarbua	Three-striped tigerfish	A	M	11·5	20–35		42·0				Rajaguru & Ramachandran (2001)
Ambassis kopsii	Freckled hawkfish	np	M	13·3	22·8 and 26·0			38·6	38·6		Menasveta (1981)
Apogon aureus	Ring-tailed cardinal fish	np	M	13·3	23·0–27·3				38·4		Menasveta (1981)
Chaetodon rostratus	Butterfly fish	np	M	13·3	23 and 29			37·8	37·8		Menasveta (1981)
Lutianus melabaricus	Snapper	np	M	13·3	23–28			37·0	37·0		Menasveta (1981)
Lutianus vitta	Black-striped snapper	np	M	13·3	23–28			37·0	37·0		Menasveta (1981)
Monocanthus chinensis	File fish	np	M	13·3	22·5–28·0			35·2	35·2		Menasveta (1981)
Mugil dussumerii	Mullet	np	M	13·3	22·5–29·5			38·4	40·2		Menasveta (1981)
Plotosus anguillaris	Sea catfish	np	M	13·3	25 and 28			38·2	38·2		Menasveta (1981)
Halichoeres nigreceus	Parrot fish	np	M	13·3	22·7–28·0			37·6	35·0		Menasveta (1981)
Epinephelus tauvina	Greasy grouper	np	M	13·3	22·7–28			37·6	37·6		Menasveta (1981)

APPENDIX. Continued

| Teleost | | | | | | Temperature (° C) | | | | | |
Species	Common name	Life stage (L, J, A)	Type	Latitude of field collection (° N or ° S)	Acclim.	Critical Minimum	Critical Maximum	Lethal Minimum	Lethal Maximum	Preferred mean	Reference
Siganus oramin	Spinefoot	np	M	13.3	22.7–25.0			35.9	35.9		Menasveta (1981)
Sillago sihama	Silver sillago	np	M	13.3	22.8 and 29.5			37.8	37.8		Menasveta (1981)
Therapon theraps	Largescaled terapon	np	M	13.3	22.7				41.2		Menasveta (1981)
Cyprinodon dearborni	Ocellated killifish	J and A	E	18.0				14.0	37.0		Brett (1970)
Ocyurus chrysurus	Yellowtail snapper	J	M	18.0	20–32				32.8	27.4	Wallace (1977)
Poecilia sphenops	Molly	J and A	F	18.0				15.0	37.0		Brett (1970)
Rivulus marmoratus	Mangrove rivulus	J and A	E	18.0				14.0	37.0		Brett (1970)
Haemulon flavolineatum	French grunt	np	M	18.0	27				36.0		Sylvester (1973)
Labeo rohita	Roho	J	F	18.9	25–35	14.0	41.3				Chatterjee *et al.* (2004)
Cyprinus carpio	Common carp	J	F	18.9	25–35	9.1	41.0				Chatterjee *et al.* (2004)
Anabas testudineus	Climbing perch	np	F	18.9	25–35	13.1	41.1				Sarma *et al.* (2010)
Canthigaster jactator	Whitespotted toby	J/A	M	19.4	np					27	Casterlin & Reynolds (1980)
Kuhlia sandvicensis	Hawaiian flagtail	J and A	M	20.0	23			13.8	34.4		Brett (1970)
Catla catla	Catla	J	F	21.0	30–38	15.2	42.4				Das *et al.* (2004)
Pagrus major	Red seabream	np	M	22.0	9–28			11.0	27.8		Woo & Fung (1980)
Pangasius pangasius	Yellowtail catfish	J	F	22.6	30–38	14.7	43.5				Debnath *et al.* (2006)
Tilapia mossambica	Mozambique tilapia	np	F	25.0	22–36			16.0	37.6		Allanson & Noble (1964)
Xiphophorus maculatus	Platyfish	J and A	F	25.4	15–30	12.9	40.4				Prodocimo & Freire (2001)
Centropomus undecimalis	Snook	J and A	F	26.0	15–25	12.7		10.1			Shafland & Foote (1983), Howells *et al.* (1990)

APPENDIX. Continued

| | | | | | | Temperature (°C) | | | | | |
| | | | | | | Critical | | Lethal | | Preferred | |
Species	Common name	Life stage (L, J, A)	Type	Latitude of field collection (° N or ° S)	Acclim.	Mini-mum	Maxi-mum	Mini-mum	Maxi-mum	mean	Reference
Sardinops sagax	Pacific sardine	J	M	28·0 and 34·0	15·5 and 20·5	6·3	31·3			17·9	Martínez-Porchas *et al.* (2009)
Heteropneustes fossilis	Indian stinging catfish	A	F	29·0	16 and 29			6·0	38·6	30·2	Vasal & Sundararaj (1978)
Fundulus heteroclitus heteroclitus	Common mummichog	A	E	30·5	2–34	3·2	38·2				Fangue *et al.* (2006)
Atherinops affinis	Topsmelt silverside	L, J and A	E	33·0	14·5–25·5			10·6	31·1	25·2	Doudoroff (1945), Ehrlich *et al.* (1979)
Clinocottus analis	Woolly sculpin	np	M	33·0	11–23		31·3	4·0	27·5	18	Graham (1970)
Fundulus parvipinnis	California killifish	J	E	33·0	20			3·0			Doudoroff (1945)
Girella nigricans	Opaleye	np	M	33·0	12–28			8·6	30·1		Doudoroff (1942)
Scomber japonicus	Chub mackerel	J and A	M	33·0	16·5			6·0	29·0		Schaefer (1986)
Sebastes dalli	Calico rockfish	np	M	33·0	13 and 16		25·9			13	Shrode *et al.* (1982)
Rypticus nigripinnis	Blackfin soapfish	A	E	33·0	17–28	8·6	40·0				Graham (1971, 1972)
Hypsoblennius gilberti	Rockpool blenny	L	M	34·0	11–23			6·5	28·8	22·2	Graham (1970)
Engraulis mordax	Northern anchovy	L	M	34·0	12–24			10·0	29·2		Brewer (1976)
Engraulis mordax	Northern anchovy	J and A	M	34·0	8–24			12·0	33·5		Brewer (1976)
Citharichthys stigmaeus	Speckled sanddab	J and A	M	34·0	10–19					11·1	Ehrlich *et al.* (1979)
Cheilotrema saturnum	Black croaker	J and A	M	34·0	17					27·6	Ehrlich *et al.* (1979)
Ictalurus punctatus	Channel catfish	J	F	34·5	20–30	6·3	38·5				Currie *et al.* (1998)

APPENDIX. Continued

Species	Common name	Life stage (L, J, A)	Type	Latitude of field collection (° N or ° S)	Acclim.	Temperature (° C)				Preferred mean	Reference
						Critical		Lethal			
						Mini-mum	Maxi-mum	Mini-mum	Maxi-mum		
Micropterus salmoides	Largemouth bass	J	F	34·5 and 45·8	8–32	7·1	36·9				Currie *et al.* (1998), Fields *et al.* (1987)
Fundulus heteroclitus	Common mummichog	J and A	E	37·0	5–36		38·2		32·3	25	Bulger & Tremaine (1985), Garside & Chin-Yuen-Kee (1972), Garside & Morrison (1977)
Oncorhynchus mykiss	Rainbow trout	J	A	37·0	10–20	0·7	29·0				Currie *et al.* (1998)
Gillichthys mirabilis	Longjaw mudsucker	J and A	E	38·0	13 or 27		38·2	3·8		21	de Vlaming (1971)
Brevoortia tyrannus	Atlantic menhaden	L	M	38·0	7–15			5·1			Lewis (1965)
Menidia menidia	Atlantic silverside	A	E	39·0	7–28		32·2		27·3		Hall *et al.* (1982), Brett (1970)
Micropogonias undulatus	Atlantic croaker	L and J	E	39·0	8			3·0			Lankford & Targett (2001)
Sphoeroides maculatus	Northern puffer	np	M	40·0	10–28			10·3	30		Brett (1970)
Lucania parva	Rainwater killifish	np	F	42·0	35				37·5		Brett (1970)
Apeltes quadracus	Fourspine stickleback	np	E	42·0	25–30				31·5		Brett (1970)
Gobiesox strumosus	Skilletfish	np	M	42·0	20				31·5		Brett (1970)
Tautogolabrus adspersus	Cunner	np	E	42·0	1–22			2·8	27·5		Brett (1970)
Oncorhynchus tshawytscha	Chinook salmon	J	A	42·0	20 and 24		25·1			13	Brett (1970)
Pseudopleuronectes americanus	Winter flounder	np	M	42·0	7–28			2·7	25·6	18·7	Brett (1970)

APPENDIX. Continued

Species	Common name	Life stage (L, J, A)	Type	Latitude of field collection (° N or ° S)	Acclim.	Critical Minimum	Critical Maximum	Lethal Minimum	Lethal Maximum	Preferred mean	Reference
Alosa pseudoharengus	Alewife	J	E	42.4	5–25		31.0	7.0		22.8	Otto et al. (1976)
Clinocottus globiceps	Mosshead sculpin	np	M	43.0	21–37				26.0		Brett (1970)
Leptocottus armatus	Pacific staghorn sculpin	np	M	43.0	21–37				29.5		Brett (1970)
Oligocottus maculosus	Tidepool sculpin	np	M	43.0	21–37				26.5		Brett (1970)
Fundulus heteroclitus macrolepidotus	Common mummichog	A	E	44.3	2–34	3.8	36.4				Fangue et al. (2006)
Coregonis clupeaformis	Lake whitefish	J	F	44.9	5–22.5				24.5		Edsall & Rottiers (1976)
Anguilla rostrata	American eel	J and A	A	45.0	5–20					18.5	Haro (1991)
Gobius paganellus	Rock goby	np	E	45.0	22–25				31.8		Brett (1970)
Crenilabrus ocellatus	No common name	np	E	45.0	22–25				32.8		Brett (1970)
Mullus barbatus	Red mullet	np	M	45.0	22–25				32.0		Brett (1970)
Mullus surmuletus	Striped red mullet	np	M	45.0	22–25				30.7		Brett (1970)
Scorpaena porcus	Black scorpionfish	np	M	45.0	22–25				32.5		Brett (1970)
Box salpa	Salema	np	M	45.0	22–25				32.5		Brett (1970)
Sargus vulgaris	Two-banded seabream	np	M	45.0	22–25				32.8		Brett (1970)
Morone saxatilis	Striped bass	J	E	45.5	5–30			6.9	31.6	24.5–36.1° N	Cook et al. (2006), Coultant et al. (1984)
Gadus morhua	Atlantic cod	J and A	M	47.2						5.5	Despatie et al. (2001)

APPENDIX. Continued

| Teleost | | Life stage (L, J, A) | Type | Latitude of field collection (° N or ° S) | Acclim. | Critical | | Lethal | | Preferred mean | Reference |
Species	Common name					Minimum	Maximum	Minimum	Maximum		
Lepidopsetta bilineata	Rock sole	J and A	M	48·0	6·9–13				24·9		Ames *et al.* (1978)
Parophrys vetulus	English sole	J and A	M	48·0	6·9–13				26·1		Ames *et al.* (1978)
Oncorhynchus kisutch	Coho salmon	J	A	49·2	5–23	3·3	24·2			11	Brett (1952), Konecki *et al.* (1995)
Oncorhynchus keta	Chum salmon	J	A	52·0	5–23	3·8	23·0			14	Brett (1952)
Oncorhynchus nerka	Sockeye salmon	J	A	52·0	5–23	3·1	24·2			13	Brett (1952)
Zoarces viviparus	Common eelpout	np	M	54·0	12		28·8				Zakhartsev *et al.* (2003)
Pleuronectes flesus	European flounder	np	M	55·0	12–14				29·0		Brett (1970)
Pleuronectes platessa	European plaice	np	M	55·0	12–14				26·5	14·2	Jobling (1981)
Clupea harengus	Atlantic herring	L and A	M	56·0	7·5–15			−1·25	20·1		Blaxter (1960), Brawn (1960)
Pomatoschistus minutus	Sand goby	A	E	60·0	5–17		28·8			14·3	Hesthagen (1979)
Salvelinus alpinus	Arctic charr	np	A	63·5–70·0	0·5–20		22·5	−1·0		11·4 and 10·2	Baroudy & Elliott (1994), Larsson (2005), Mortensen *et al.* (2007)
Pagothenia borchgrevinki	Bald nototHen	np	M	78·0	−1·9		<−2·5		6·0		Somero & DeVries (1967)
Trematomus bernacchii	Emerald rockcod	np	M	78·0	−1·9			−2·5	6·0		Somero & DeVries (1967)
Trematomus hansoni	Striped rockcod	np	M	78·0	−1·9		<−2·5		6·0		Somero & DeVries (1967)

np, not provided.