

temperatures can even denature proteins and shut down cellular function. One might expect that physiological stress from temperature would increase toward lower latitudes, but this expectation might be strongly modulated by the timing of the tides. On the west coast of North America, the latitudinal thermal gradient of water temperature is not strong, and waters of southern California are just a few degrees warmer than those of Oregon and Washington. However, Helmuth et al. (2002) found that

more northerly intertidal sites such as Friday Harbor, Washington, had low tide in midday in some years, when high temperature stress was likely, but in the same years, southerly locales such as Monterey, California, had more low tides at night, which reduced total temperature stress. These differences can change from year to year, so the location of maximum temperature stress is variable. In some years, therefore, global warming could exert maximum stress and cause mass mortality in different latitudes.

HOT TOPICS IN MARINE BIOLOGY 4.1



Global Climate Change: How Can We Tell If We Are at the Edge?

As we showed in Chapter 2, there is very strong evidence that many parts of the ocean have been warming over the past few decades. It is, of course, important to know why, but the trend is of sufficient concern to take a close look at how it might be imposing temperature stress on marine species. We should focus on cases where species might be at the edge of their tolerance or geographic distribution: (a) Temperature could be beyond the tolerance limits of individuals; and (b) temperature change might strongly affect the geographic range of a species.

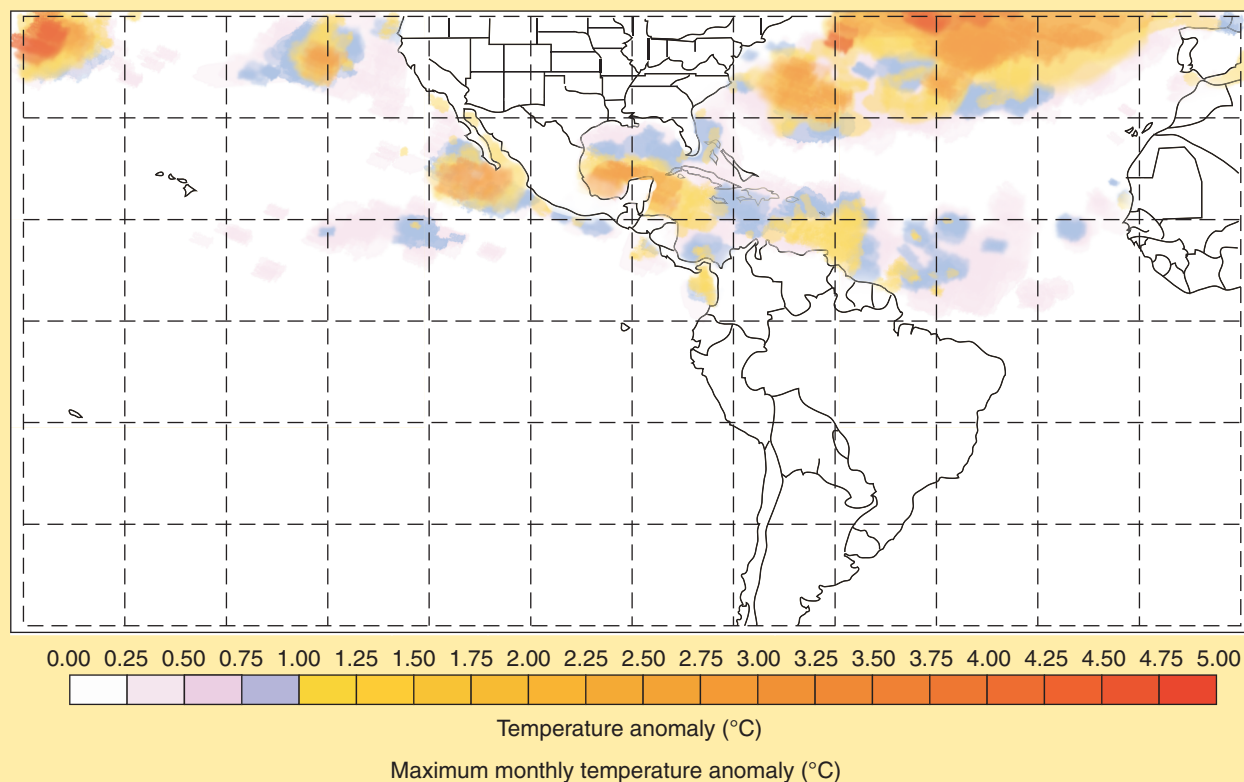
Will ocean warming take any locations past the point that species can survive? To answer this question, we need to admit our ignorance of the mechanisms of upper limits. We mentioned in the text a number of ways that temperature stress can be investigated—concentration of heat-shock proteins and membrane order, for example—but in truth, we do not know exactly when these measures indicate that a species is on the edge of doom.

A great surprise has been the effect of warming of sea-surface temperatures on corals and coral reefs throughout the world. This first became apparent after the pioneering studies of Peter Glynn on the effect of the very strong El Niño of 1982–1983 on the Pacific coral reefs of Panama. This was a particularly strong event lasting about 1.5 years, and sea-surface temperatures in Panama rose to as much as 9°C over average. Coral reefs on the Pacific coast of Panama live in fairly cool waters, but El Niño clearly put the corals in great stress. A phenomenon known as coral bleaching immediately spread throughout Panamanian coral reefs. We discuss bleaching in more detail in Chapter 15, but it involves the loss of symbiotic algae known as zooxanthellae, which normally are crucial for coral growth. Corals in Costa Rica, Panama, and Colombia experienced 50–80 percent mortality. In 2007, the World Conservation Union (IUCN) listed three coral species from the Galapagos Islands as endangered, and this probably stems from a series of reductions due to recent ENSO (El Niño–Southern Oscillation) events. Why is this related to global warming? Some models predict that global warming is increasing the frequency and intensity of ENSO events. The climate of the North Pacific is complex, so it is difficult to give an easy answer to the question of temporal trends (Trenberth, 1990). On the other hand, one thing is clear: Since the 1970s, ENSO events have been more prolonged and have often occurred in series with no intervening cooling event, known as La Niña (Trenberth and Hoar, 1996). It was also clear from Glynn's work that warming was potentially damaging.

What we have seen since then is a general trend toward sea-surface warming throughout the world, and this warming correlates with bleaching observed in coral reefs. The widespread whiteness that has been observed on coral reefs may be a harbinger of massive coral reef extinction. What needs to be better understood is the specifics of physiological stress that affect the coral–zooxanthellae symbiosis. Lacking this, we nevertheless have some data showing a strong correlation of temperature increase with bleaching. First, we need temperature records. These have become available fairly continuously since the 1970s because of satellite data. We can plot the data in terms of **anomalies**, or deviations from the mean temperature, at a given date and place over the years for which records are available. Alternatively, some have used the degree heating week (DHW): One DHW is equivalent to 1 week of sea-surface temperatures 1°C greater than the expected summertime maximum. Box Figure 4.1 shows a map of coral reef bleaching hot spots in 1998. Current data suggest that coral bleaching ranges from being present to severe for DHW values of 4–8. Donner and colleagues used a theoretical model of ocean circulation combined with known temporal trends of ocean-surface temperature to evaluate the extent of future coral bleaching and concluded that worldwide threats of bleaching would occur annually in the next 30–50 years unless the corals evolved greater thermal tolerance (Donner et al., 2007). It is important to realize that dominant corals will grow vigorously only in well-lit shallow water, so there is no deep-water refuge where they can hide; they will simply die.

Apart from geographic distributions, we need to know what specific physiological and biochemical processes might be threatened by global warming. This is likely to be a difficult undertaking because temperature affects so many biological functions differently. An insight into this difficulty comes from an important breakthrough in understanding the relationship of high temperature to oxygen delivery from the environment to cells by fishes. Beyond a critical upper and lower threshold, an animal cannot deliver enough oxygen by means of its cardiovascular system to satisfy demand. Past the upper threshold, for example, the animal may need to rely on anaerobic sources of metabolism, which in the long run are insufficient long-term for functions such as swimming, growth, and reproduction by fishes. As we discussed in the temperature section, many animals living in seasonal environments can acclimate successfully

HOT TOPICS IN MARINE BIOLOGY 4.1 CONT



BOX FIG. 4.1 A map of locations where coral bleaching is predicted to be likely based on a map of temperature anomalies from satellite detectors. Hot spots are determined on the basis of localities where the temperature is greater than 1°C over that expected for the average. Coral reefs live in only a fraction of areas where such anomalies exist. (From NOAA coral bleaching analysis, <http://www.osdpd.noaa.gov/>)

between winter and summer conditions. But what happens if the summer waters become too hot? The interesting prediction is that limits to growth and survival will be reached at temperatures below an immediate acute lethal limit that would normally be measured by placing the fish in increasingly warm water. This latter threshold could be far lower than the lethal limit, so we need a new perspective on how warming will affect marine animal species.

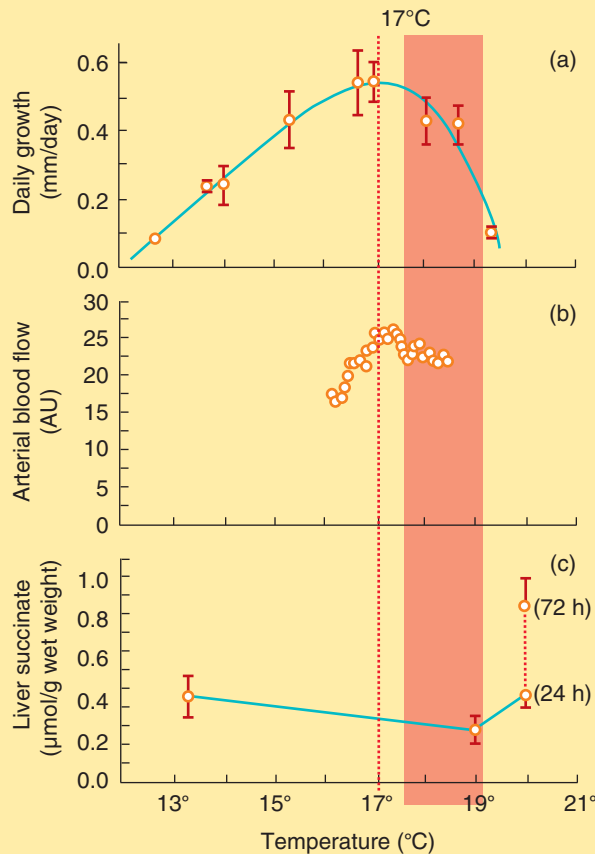
Hans Pörtner and Rainer Knuth investigated this problem in the southern North Sea, where sea-surface temperature has been increasing in the past century (Pörtner and Knuth, 2007). On average, water temperature has increased 1°C in the past 40 years, and extreme winter low temperatures have become less common over this period. A common fish, the eelpout *Zoarces viviparus* (Box Figure 4.2), had nonmigratory populations that declined in times when summer water temperatures were higher than average. Body growth increased with increasing temperature (Box Figure 4.3), but growth declined above about 17°C, which was far below the acute lethal upper temperature limit. Using



BOX FIG. 4.2 The eelpout *Zoarces viviparus* is found living on the bottom of shallow soft-sediment coastal waters and estuaries. (Photograph used with permission, Alfred Wegener Institut, Germany)

a noninvasive nuclear magnetic resonance technique (Pörtner et al. 2004), they showed that blood flow also peaked at about the same temperature as that of maximum growth. Calculations demonstrated oxygen stress above this temperature, and direct measurements showed that the fish was switching to anaerobic metabolism just at the maximum temperature when growth stopped completely.

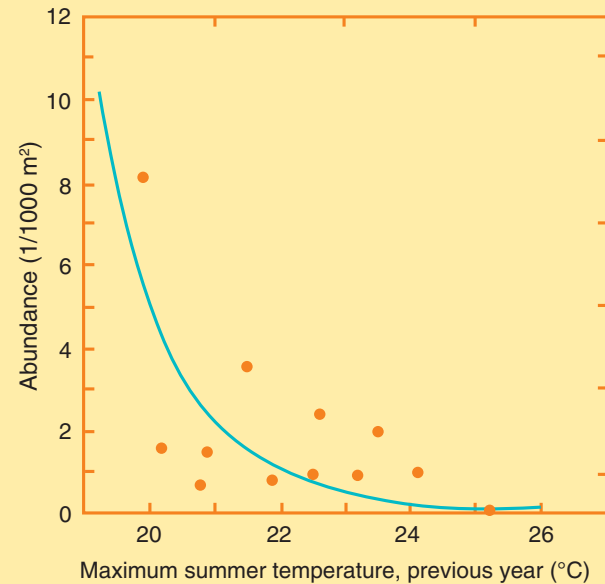
HOT TOPICS IN MARINE BIOLOGY 4.1 CONT



BOX FIG. 4.3 How the eelpout *Zoarces viviparus* is affected by temperature. (a) Growth increases with increasing temperature but drops dramatically between 17° and 21°C. (b) Blood flow also drops dramatically above about 16°C. (c) Succinate, which is an indicator of cellular oxygen limitation and anaerobic metabolism, starts to increase greatly between 20° and 24°C, which is where growth effectively stops. (After Pörtner and Knust, 2007)

This demonstrates that the upper limit for growth represents a loss of scope for aerobic activity, meaning the fish can no longer actively move around to feed. The most compelling result is their discovery that fish population size seems to respond directly to temperature: Abundance of eelpouts was negatively correlated with the temperature of the previous summer (Box Figure 4.4). Regional predictions in the next decades in this area are for an increase of as much as 3–4°C, which suggests that regional warming will have strongly negative effects on eelpout populations. Migratory species that are affected in the same way at least have the possibility of escaping to the north, but we can expect from regional warming a loss of less mobile species and a strong reorganization of communities.

Some species, especially those near the poles, will be trapped and are likely to decline because of physiological stress. But many other species, such as those in the temperate zone, are likely to extend their northerly ranges into higher latitudes. Such range



BOX FIG. 4.4 The temperature effect results in a negative correlation between eelpout abundance and summer temperature of the previous year. (After Pörtner and Knust, 2007)

extensions are happening on a massive scale in many marine and terrestrial organismal groups, and the response in many cases can be clearly related to temperature increases in recent decades (Parmesan and Yohe, 2003). In one case, a marine copepod has extended its range northward over 1,000 km. The readjustments of ranges will cause a reshuffling of the deck when it comes to interspecific interactions. At any one site, species will be lost and gained because of their individual temperature preferences and tolerances, which will bring new competitors into contact and new predators and prey to combine into new food chains. Sagarin and colleagues (Sagarin et al., 1999) were able to compare species on rocky shores of Monterey, California, living in the late 1990s with those surveyed previously in the 1930s. The differences were striking. Overall, higher latitude species (5 of 7) became less abundant while species generally living south of Monterey (10 of 11) had increased in relative abundance. Summer temperatures had increased nearly 2°C over this period.

The trend of sea-surface temperature change is worldwide in the coastal ocean. One of the fastest increasing areas in the Southern Hemisphere is the Tasman Sea, a broad area between New Zealand and southeast Australia. Neuheimer and colleagues investigated growth of the common temperate reef fish *Cheilodactylus spectabilis* by looking at a historical collection of otoliths over 90 years (Neuheimer et al., 2011). Otolith size correlates closely with overall size. Temperature increased steadily in the Tasman Sea, and fish growth actually increased in the middle of the geographic range. But at the northern and hottest end of the range, otolith size declined in collections closer to the present day, showing that stress was already increasing and likely to truncate the range eventually. What once was a normal area is now a thermally stressful zone. ■