Fisheries Research 186 (2017) 383–396

Contents lists available at ScienceDirect

Fisheries Research

journal homepage: www.elsevier.com/locate/fishres

Full length article

Threshold temperatures for performance and survival of American lobster larvae: A review of current knowledge and implications to modeling impacts of climate change

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ARTICLE INFO

Article history:
Received 12 January 2016
Received in revised form
20 September 2016
Accepted 21 September 2016
Handle by Chennai Guest Editor
Available online 5 October 2016

Keywords:
American lobster
Larvae
Temperature
Climate change
Thermal tolerance

ABSTRACT

Warming generally improves performance of life processes such as moulting and growth in ectotherms, but excessive warming can reduce performance and cause death, which in turn affects their demography. Previous studies of American lobster, *Homarus americanus*, have considered warming impacts on benthic adults, but little attention has been paid to performance of planktonic larvae at extremely high temperatures. Water column temperatures are expected to increase faster than bottom temperatures, so warming may compromise physiological performance of larvae sooner than that of adults. It is thus important to identify stressful and lethal temperatures for lobster larvae, and include these when estimating climate change impacts. Previous studies that observed survival, development, moulting, growth, and physiological performance of lobster larvae at extreme temperatures were reviewed. Mortality following short-term exposure to 28–36 °C from minutes to hours in duration has been reported, but more ecologically-relevant longer-term high-temperature exposures lasting days or weeks have rarely been tested for larvae of this species. Sub-lethal indicators of stress such as irregular heartbeat were reported in short- and long-term exposures between 20 and 26 °C, suggesting that perhaps extended exposure to these temperatures could be lethal. Over the next 10–50 years, larvae may experience temperatures up to 30 °C, which could negatively impact lobster populations if these temperatures are indeed stressful or lethal to them. Knowledge gaps identified highlight the need for further research into tolerance of lobster larvae to high temperatures.

1. Introduction

In ectotherms, performance and rates of chemical and enzymatic pathways mediating survival, heartbeat, activity level, growth, development, and moulting are all generally enhanced by warming (Bělehrádek, 1935; McGaw and Reiber, 2015; Webster, 2015). However, there are biological limits to the extent to which warming improves performance (Bělehrádek, 1935; Niehaus et al., 2012; Whiteley and Taylor, 2015). Life processes perform best at a particular optimum temperature, and then performance decreases at temperatures below and above this (Frederich and Pörtner, 2000; Jost et al., 2012; McGaw and Reiber, 2015; Pörtner et al., 2010; Fig. 1). Declines occur more rapidly as temperatures rise above the optimum (i.e., with warming) than when they sink to those below it (i.e., cooling) (Fig. 1). As environmental temperature moves away from the optimum, performance declines at a relatively slow and constant (linear) rate until a threshold stress temperature (*pejus* temperature; Frederich and Pörtner, 2000; Jost et al., 2012; Pörtner et al., 2010) is passed (Fig. 1). Beyond this threshold performance declines nonlinearly, worsening with each degree, but can recover if temperatures closer to the optimum are restored (Jost et al., 2012). Temperatures further still from the optimum pass another pair of thresholds, the "critical" or lethal temperatures, beyond which irreversible damage is inflicted on the organism and its life processes (Bělehrádek, 1935; Frederich and Pörtner, 2000; Jost et al., 2012; Pörtner et al., 2010; Fig. 1).

There is concern that ocean warming due to climate change will cause many marine organisms to be exposed to thermal conditions that are stressful or lethal to them (Byrne, 2011; Green et al., 2014; Niehaus et al., 2012; Walther et al., 2010). Developmental success of planktonic larvae in many marine invertebrates, including ascidians, cnidarians, crustaceans, echinoderms, molluscs, and others, was noted in a recent review by Byrne (2011) to be optimized at temperatures ranging from 5 to 32 °C but then impaired when temperatures were raised 1–6 °C above each species' opti-

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http://dx.doi.org/10.1016/j.fishres.2016.09.022
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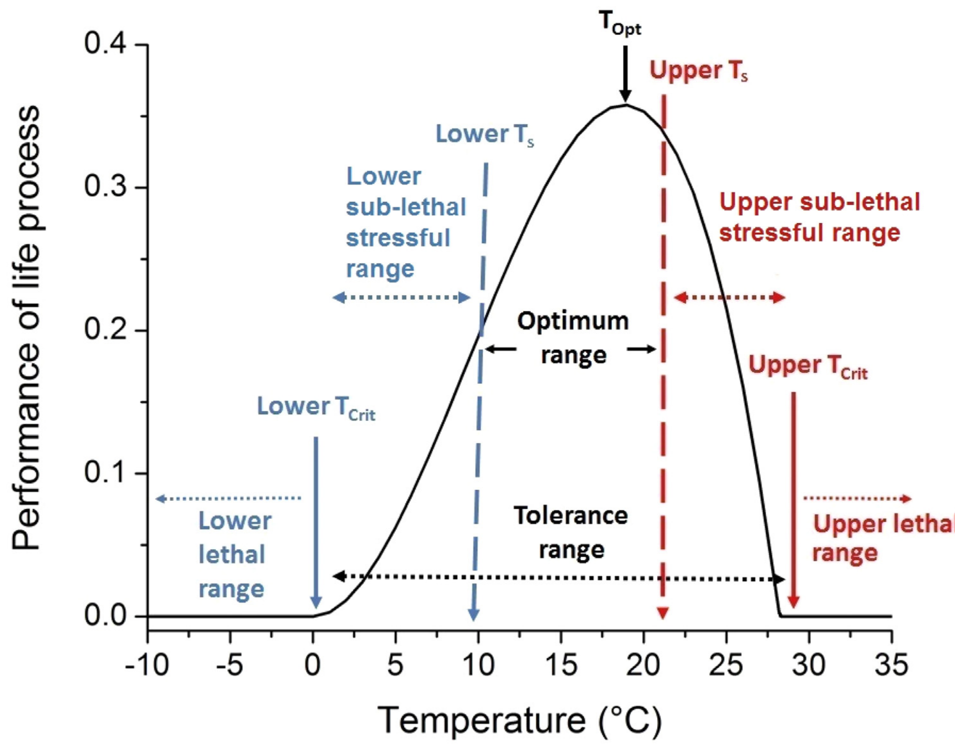

Fig. 1. Illustration of the relationship between environmental temperature and performance rate of a hypothetical life process (e.g., moulting rate or survival; performance units on y-axis and temperature values for illustration purposes only). Temperature ranges and thresholds are explained in detail in Section 1 and used throughout the present review. Abbreviations: T_{Opt} = optimum temperature (maximum performance); T_S = stress threshold; T_{Crit} = critical temperature, or lethal threshold temperature. Figure based on Jost et al. (2012), with modification. (For a colour version of this figure, the reader is referred to the web version of this article.)

mum. Tolerance to high temperatures is generally highest for embryos, lower in larvae, and progressively decreases over the course of development, especially in species with benthic adults (Byrne, 2011). Larvae usually inhabit more thermally-variable environments than embryos and adults and are thus perhaps the most likely to encounter limiting temperatures in nature (Byrne, 2011). Completion of all life history stages is required for persistence of populations and species (Byrne, 2011), so the larval phase may represent an important bottleneck to persistence of marine species in the face of future climate change (Walther et al., 2010). Studies on larvae of marine crustaceans, such as fiddler crabs (*Uca pugilator*: Vernberg et al., 1973) and spider crabs (*Hyas araneus*: Schiffer et al., 2014; Walther et al., 2010) have demonstrated stressful and lethal impacts of elevated temperatures on this life stage with implications to recruitment of adult stocks. Growth, development, and survival of larvae in many species of marine crustaceans (e.g., lobsters and crabs) that support major fisheries is generally enhanced by rising temperature until upper limits are reached, beyond which these processes are impaired (Green et al., 2014). Sustained high temperatures also compromise crustacean immune function (Le Moullac and Haffner, 2000), potentially leading to disease outbreaks and population declines in warm areas. As a result, climate warming is likely to initially lead to growth of populations supporting crustacean fisheries, but further warming may cause declines (Caputi et al., 2013; Green et al., 2014).

The American lobster, *Homarus americanus*, is a crustacean that supports major fisheries along the Atlantic coasts of Canada and the United States of America (Cobb and Castro, 2006; Wahle et al., 2013). Lobsters are found across a large latitudinal range, over which they historically experienced temperatures from −1 °C to 26 °C (Lawton and Lavalli, 1995; Quinn and Rochette 2015). Traditionally, survival and reproduction of lobsters have been thought to be limited by cold temperatures (e.g., Boudreau et al., 2015; Cobb and Catro, 2006), while studies of warming effects on lobsters have primarily viewed these as beneficial (e.g., MacKenzie, 1988; Waddy et al., 1995). For example, lobster fisheries landings have been increasing exponentially throughout most of the species' range since the 1980s, and one frequently suggested explanation for this trend has been that water temperatures have also been increasing throughout this period (Caputi et al., 2013). Warming is thought to have increased lobster abundances by enabling enhanced survival of lobsters and their larvae, faster growth to commercial size, expanded habitat area for juvenile lobsters, and decline of cold-adapted predators of lobsters (Boudreau et al., 2015; Caputi et al., 2013; Steneck and Wahle, 2013; Wahle et al., 2013). Recently, however, major collapses have occurred in lobster populations and fisheries in the southernmost and warmest portion of the species' range (e.g., Long Island Sound, southern New England) that have been tied to warming impacts on disease susceptibility and physiological stress (Caputi et al., 2013; Castro et al., 2006; Glenn and Pugh, 2006; Laufer et al., 2013; Pearce and Balcom, 2005; Shields, 2013). Work has since been initiated to investigate potential impacts of warming on lobster stocks (Caputi et al., 2013; Steneck and Wahle, 2013; Wahle et al., 2013).

There is potential for ocean warming to cause sudden and powerful impacts on lobsters. Importantly, most studies examining impacts of warming on lobsters thus far have focused on the benthic juvenile and adult stages of the lobster's life history (e.g., Castro et al., 2006; Glenn and Pugh, 2006; Laufer et al., 2013; Shields, 2013; Wahle et al., 2015). However, warming impacts on the important planktonic larval phase of the life cycle, on which recruitment of all later life phases to populations depends (Ennis, 1995), have thus far received very little attention. This is likely due partly to the fact that waters at and near the ocean surface and to which larvae are exposed are usually warmer than those at the bottom, where juveniles and adults live (Guo et al., 2013; Lawton and