

Review of existing literature on temperature sensitivity in the Baltic trollin, *Macoma balthica*

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Stefan Bolam and Julie Bremner

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tidal heights and sediment types) was conducted every year from 1969 to 2007 and *Macoma* numbers, weights and lengths determined. Various studies have been conducted using this dataset (e.g., Honkoop et al., 1998; Philippart et al., 2003; Beukema et al., 2009). These have highlighted short-term changes in *Macoma* population dynamics in response to warmer than average seasons occurring in recent years. These studies indicate that *Macoma* exhibits:

- A reduction of reproductive output and recruitment in years starting with mild winter-spring periods
- A reduction of adult survival in years with warmer summers
- A reduction of annual migration of approximately 8 month olds to more favourable areas during mild winters
- A reduction in growth rates in warmer than average growing seasons
- An enhancement of seasonal weight loss in milder than average winters.

These findings illustrate that there are a number of mechanisms underlying thermal effects on *Macoma*. That the Wadden Sea populations are situated relatively far north of the species' current southern distribution limit is particularly striking. This suggests that thermal stress can be manifest well within the species geographical range. The variety of responses seen in the Wadden Sea populations also signifies that temperature stress has complex effects on *Macoma*. Understanding the mechanisms underlying species' responses in such situations is challenging (Helmuth et al. 2006) and requires detailed analysis, but some individual factors can be identified.

4 Mechanisms underlying temperature effects

4.1 Mortality

- High temperature can induce mortality in *Macoma*, though this is most likely due to a combination of sub-lethal effects.

The most extreme temperature response provoked in individuals is death. Studying *Macoma* populations from Canada, Henderson (1929) recorded a lethal temperature for *Macoma* of 42.3°C, while Kennedy and Mihursky (1971), using 24-hour exposure experiments on *Macoma* individuals from Chesapeake Bay, found LC50 temperatures of between 30°C and 34°C, depending upon acclimation temperature. However, the species' thermal history (season, geographic distribution, shore height) is important in modifying its temperature limit. For example, Wilson (1981) indicated that the lethal water temperatures for *Macoma* from Dublin Bay varied between 27.5°C and 37.5°C for winter and summer populations, respectively. Lethal temperatures for longer periods appear to be somewhat lower, however. De Wilde (1975), for example, stated that individuals from the Wadden Sea suffered 70-100% mortality at 25°C.

Biological factors such as condition and, more importantly, developmental stage, also have important effects on *Macoma* mortality rate at different water temperatures. In the larval stages, survival is negatively related to increased temperature. For example, Drent (2002) found that the instantaneous survival rate of *Macoma* larvae from two populations with different natural temperature regimes (i.e., Balsfjord, Norway and the Gironde Estuary, France) declined with increasing temperature (above 10°C). Although growth rates of *Macoma* larvae increase with increasing temperature, mortality rates increase faster; the resulting mortality between egg and metamorphosis increases with temperature (Drent, 2002).

Mortality can result from the direct effects of acute exposure to temperatures beyond a species' thermal limits. However, it may also be caused by the multiplicative effect of a number of sub-lethal factors acting in concert. For example, increased *Macoma* mortality on the Wadden Sea tidal flats was observed in years with warmer summers (Beukema et al., 2009). Although the exact mechanism is unclear, it appears that it may have been associated with the reduced growth rates observed in years with elevated spring temperatures and greater weight loss in mild winters (when metabolic activity is raised (Beukema et al., 2009).

These mortality studies show the animals are capable of resisting (for short periods at least) temperatures well above those they may be exposed to in nature; while sediment surface temperatures on intertidal flats (particularly at high shore levels) during summer days may reach mortality-inducing levels, seawater and deeper sediment temperatures are unlikely to do so. Given the temperature-range differential between the intertidal and subtidal, different mechanisms may operate on subtidal and intertidal populations. In subtidal populations, the mechanisms underlying temperature sensitivity in *Macoma* are likely to be related to sub-lethal biological population processes, rather than acute death of individuals.

4.2 Recruitment

- *Macoma* recruitment varies in response to increasing temperature, though it is likely to be caused by a combination of intra- and inter-specific factors

The reduced annual recruitment after warmer than average winter-spring seasons observed in the intertidal flats of the western Wadden Sea may have multiple causes acting at different developmental stages (Beukema et al., 2009). Although adult females produced more eggs after a colder winter, this could only explain a small proportion (7%) of the increase in subsequent recruit densities (Honkoop et al., 1998). Therefore, processes acting after the egg stage must have contributed more decisively to the observed relationship between winter temperatures and recruitment.

Phillipart et al. (2003) indicated that elevated temperatures upset the reproductive strategy that was finely-tuned to the most optimal environmental conditions. Most importantly, temperature changes affected the synchronisation of spawning time with the phytoplankton bloom and the settlement of juvenile shrimps (*Crangon crangon*) on tidal flats (the main predator of juvenile *Macoma*). Indeed, Beukema and Dekker (2005) noted that the high near-shore flats in the Wadden Sea showed invariably low shrimp biomass values and appeared to serve as a refuge for postlarval *Macoma* in years of high predation pressure. Only in this coastal part of Balgzand was no decline in bivalve recruitment found. Inter-annual variability in recruitment (in response to increased winter temperature) was one of the main factors responsible for variations in *Macoma* production within this system (Dekker and Beukema, 2007).

4.3 Migration

- Increasing temperature limits *Macoma* juvenile migration

Macoma juveniles undertake post-settlement migration by drifting on their byssus threads from one area to another. Floating behaviour in *Macoma* spat is stimulated by low water temperatures, which may be brought about by the increased viscosity of colder water (resulting in lower sinking rates and greater transportation), combined with the increased stimulus to float (Beukema and Dekker, 2003).

In the tidal streams of the Wadden Sea, Hiddink and Wolff (2002) caught fewer spat in plankton nets in warmer than average winters than in cold winters. Migratory abilities are important components of benthic species' ability to tolerate environmental stress. Motile species can mitigate increased environmental stress by moving away from the immediate area. Adult *Macoma* are relatively sessile within sediments and unlikely to be able to actively avoid increased environmental temperatures. The effect of a temperature-driven reduction in juvenile migration may be more pronounced in species with low adult mobility, such as *Macoma*, and may have consequences for local population dynamics.