



Metabolic and oxidative stress responses of the jellyfish *Cassiopea* to pollution in the Gulf of Aqaba, Jordan

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ABSTRACT

Physiological responses of jellyfish to pollution are virtually overlooked. We measured the activity of two glycolytic enzymes (pyruvate kinase (PK) and lactate dehydrogenase (LDH)), lipid peroxidation (LPO), protein and chlorophyll *a* content in the jellyfish *Cassiopea* sp. from polluted and reference sites along the Gulf of Aqaba, Jordan. In jellyfish from polluted sites, low PK/LDH ratios and high LDH activity clarify their reliance on anaerobic metabolism. PK and LDH were positively correlated in the jellyfish. While medusae from polluted sites showed no signs of oxidative stress damage, protein content was significantly lower. This might suggest protein utilization for energy production needed for maintenance. Unchanged LPO in polluted sites indicates the ability of jellyfish to keep reactive oxygen species under control. Overall these results suggest that the jellyfish seems to tolerate the current levels of pollution at the studied sites and they might be anaerobically poised to live at such habitats.

1. Introduction

Scyphozoan jellyfishes are generally robust and noxious short-lived animals. They are known to tolerate wide ranges of environmental conditions and pollutants. At present, many pelagic jellyfish are increasing massively worldwide and forming noxious blooms (Arai, 2001; Graham, 2001; Mills, 2001; Purcell, 2005). Jellyfish grow rapidly and die *en masse*, releasing massive amounts of nutrients into the water column due to decomposition of their dead bodies (Pitt et al., 2009). They can change fish community structure and reduce fish stocks, competing with fishes for the same planktonic prey; furthermore they are able to predate on fish larvae (Breitburg et al., 1997; Mills, 2001). Economically, the negative impacts of jellyfish blooms on fisheries and tourism are of higher concern for society. For example, while *Nemopilema nomurai* blooms caused millions of dollars loss in fisheries around China and Japan in the past decade (Robinson et al., 2014), other jellyfish invasions in the Mediterranean Sea caused 1.8–6.2 million € annually due to beach closures (Ghermandi et al., 2015). The scyphozoan jellyfish *Cassiopea* leads an epibenthic life style. The jellyfish is alternatively called “the mangrove jellyfish” or the “zooxanthellate jellyfish”. Unlike most other scyphozoans, *Cassiopea* exhibits an intimate mutualistic symbiosis with photosynthetic dinoflagellate

endosymbionts (i.e., zooxanthellae; Hofmann and Kremer, 1981). The jellyfish could benefit of 5–10% of net algal photosynthate being translocated to its tissues *in vivo*, mainly in the form of glycerol and glucose (Hofmann and Kremer, 1981). *Cassiopea* spp., are widely distributed in tropical and subtropical shallow coastal marine habitats (Gohar and Eisawy, 1960; Holland et al., 2004; Niggel and Wild, 2010; Welsh et al., 2009; Stoner et al., 2011, 2014). In some reef habitats, *Cassiopea* is a key organism leading an essential role in nutrient recycling (Jantzen et al., 2010; Niggel et al., 2010); however, little attention has been paid to its role in jellyfish blooms.

Global warming and anthropogenic activities (e.g. eutrophication and coastal constructions) are proposed as the main drivers of jellyfish blooms (Arai, 2001; Mills, 2001; Purcell, 2005). Because of their proximity to main cities, coastal systems are usually subjected to a wide array of pollutant inputs from effluents associated with industrial, agricultural and domestic activities. Heavy metals are of major concern among these pollutants. *Cassiopea* was found to actively regulate the concentration of some metals (e.g., lithium), while accumulates other metals (e.g. Cu, Mn, Cd, Zn) up to 200 fold their concentration in ambient seawater (Templeman and Kingsford, 2010, 2012). Others metals (e.g., Ca, Mg and Sr) were kept in balance with the ambient environment and reflected ambient seawater concentration of these

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metals (Templeman and Kingsford, 2010, 2012). In mollusks, crustaceans and other marine invertebrates, the ability to regulate the intracellular metal concentrations and accumulation of excess metals in nontoxic forms attributes to their tolerance to high tissue concentrations of metals (Rainbow, 2002). Further, while jellyfish may accumulate higher concentrations of metals than those of their ambient environment, it may be that those metals are not metabolically available and therefore the toxicity of those metals may be less than it seems (Rainbow, 2002).

Reactive oxygen species (ROS) formation due to metal exposure could induce oxidative stress in animal tissues; this might induce cellular damage (Zhang et al., 2010). ROS mediated lipid peroxidation (LPO) is one mechanism of metal exposure toxicity and is one of the main signs of experiencing oxidative stress mediated cellular damage (Knight and Voorhees, 1990). Transition metals (e.g. as cadmium (Cd), copper (Cu) and lead (Pb)) were found to induce ROS formation and LPO (Knight and Voorhees, 1990). In another mechanism of metal toxicity, Cd for example could inhibit the mitochondrial electron transport system (ETS) enzymes, resulting in more ROS formation and less ATP synthesis (Livingstone, 2001). Furthermore, even low concentrations of Cd might result in uncoupled mitochondrial respiration and less efficient energy production (Jacobs et al., 1956). In decapod crustaceans, heavy metal exposure was associated with decreased oxygen consumption (MO_2) rates (Barbieri, 2009; Barbieri et al., 2013). On the other hand, oyster exposure to heavy metal (i.e., Cd) suppressed the anaerobic metabolism (Ivanina et al., 2010). Therefore, inducing oxidative stress, impairment of aerobic/anaerobic metabolism and mitochondrial functions, are common mechanisms of metal toxicity which result in cellular and organismal energy imbalance.

Stress represents an extra sink for energy. Reallocation of cellular energy to maintenance and keeping cellular homeostasis comes at the expense of the energy available for other cellular activities such as growth and reproduction (Gambill and Peck, 2014). Normally, animals sustain their energy demand through aerobic metabolism; however, under stressful conditions when energy demands are exaggerated, the anaerobic energy metabolism becomes essential.

In animal physiology, onset of anaerobiosis is a well-known sign of elevated energy demand beyond aerobic potential. At this stage, when aerobic scope declines severely, transition to anaerobic metabolism becomes essential to sustain cellular energy demands (Pörtner, 2002). In oyster, it was found that transition to anaerobiosis is a sensitive biomarker of energetic stress induced by high temperature and Cd exposure (Bagwe et al., 2015). The activity of glycolytic enzymes can also correlate with anaerobic capacity and is often used as a proxy for measuring anaerobiosis (Hochachka et al., 1983). Pyruvate kinase (PK) and lactate dehydrogenase (LDH) are two universal glycolytic rate controlling enzymes in most animals. While PK, one of the main rate controlling enzymes in glycolysis, sits at the crossroad directing glucose carbon toward biosynthesis or into glycolysis (Mazurek et al., 2002), LDH, the main enzyme sitting at the crossroad between aerobic and anaerobic metabolisms, is well known to be increased under conditions of increased cellular energy demand. Moreover, LDH correlates well with anaerobic capacities and therefore is commonly used as a proxy of anaerobiosis (Hochachka et al., 1983).

In the Gulf of Aqaba, Jordan, *Cassiopea* sp., is a key epibenthic organisms in reef habitats playing roles in food webs by fueling the coral reefs with their released organic matter (Niggl et al., 2010). Furthermore, Niggl and Wild (2010) have observed its increased occurrence over years. Field and experimental studies on *Cassiopea* sp., from the Great Barrier Reef have shown that the jellyfish is able to bioconcentrate metals within its tissues above the ambient seawater concentrations (Templeman and Kingsford, 2010, 2012; Epstein et al., 2016). Moreover, it is considered invasive (Holland et al., 2004) and exotic (Özbek and Öztürk, 2015) in many coastal marine habitats, including the Hawaiian Islands and the Mediterranean Sea (Holland et al., 2004; Özbek and Öztürk, 2015). The reason behind this successful habitat

extension, however, is still unclear. Stoner et al. (2011, 2016) have recently shown that *Cassiopea* medusae were more abundant and attained larger sizes in human-impacted marine coastal habitats in The Bahamas. The authors, however, did not provide any mechanistic explanations in physiological terms. Aljbou et al. (2017) could show in a laboratory study that *Cassiopea* sp., seems to acclimate well at 32 °C, gain body mass and reduce the aerobic energy consumption. The authors have drawn their conclusion based on cellular respiration (ETS) and oxygen consumption (MO_2) measurements. They concluded that *Cassiopea* medusae are more tolerant to heat than cold temperatures. The lack of research on physiological responses of jellyfish to pollution limits our ability to explain the observed association of jellyfish with anthropogenic activities. Interestingly, and to the best of our knowledge, no studies are available on physiological responses of the medusoid *Cassiopea* to pollution and climatic change induced disturbances except for the aforementioned paper of Aljbou et al. (2017).

This is the first study on *Cassiopea* that investigates the subcellular physiological responses (e.g., in term of cellular glycolytic (PK, LDH) potential and oxidative stress damage in term of LPO) to pollution. Since organisms have certain confined amounts of energy available at any given time, increasing energy consumption in maintaining cellular homeostasis will be at the expense of other cellular activities such as growth and reproduction (Gambill and Peck, 2014). Therefore, we asked the questions: How does pollution status (e.g., heavy metal pollution) of benthic habitat affect *Cassiopea*'s glycolytic potential and anaerobic metabolism? Do *Cassiopea* medusae experience oxidative stress-induced damage under the defined conditions of pollution in the selected site? In order to answer these questions, we have measured the activities of two main glycolytic enzymes (PK and LDH), malondialdehyde content (MDA, a proxy to assess LPO), and both protein and chlorophyll *a* (Chla) content in *Cassiopea* sp. The jellyfish medusae were collected from four environmentally different sites along the coastal line of the Gulf of Aqaba, Jordan. This study aims to provide a better understanding of the association between jellyfish and anthropogenic activities by assessing the physiological performance of *Cassiopea* in response to coastal pollution.

2. Materials and methods

2.1. Study areas

The Gulf of Aqaba (GoA) is a narrow (2–25 km wide), deep (max. Depth 1820 m) and long (180 Km) most northern extension of the Red Sea. It is surrounded by dry desert mountains, no riverine inputs and only a negligible runoff. GoA is the only access of Jordan to the sea. The whole Jordanian coastal system access to the GoA is 26 km long and is heavily exploited for both industrial and touristic business. In this study we chose four sites along the Jordanian coastal line to sample *Cassiopea* medusae. While the Phosphate Loading Berth (PLB) and the Industrial Area (IA) are locally well known polluted sites, the Marine Science Station (MSS) and Coral Garden (CG) are considered to be marine reserved areas (Fig. 1). Our choice of the polluted sites, PLB and IA, was based on literature review and in situ observations acquired from prior knowledge. While both PLB and IA are known to be polluted, especially with the heavy metal cadmium (Al-Najjar et al., 2011; Al-Rousan et al., 2016), they differ mainly in the sedimentation rate, which is very high in PLB compared to the other sites (Badran and Al-Zibdah, 2005; Al-Rousan et al., 2016). Compared to the other sites, the PLB has the highest metal pollution loading index (PLI), followed by IA (Al-Najjar et al., 2011). PLB has the finest sediments grain size, dominated by clay resulting from the deposition of large amounts of phosphate powder during the shipment processes (Badran and Al-Zibdah, 2005; Al-Najjar et al., 2011), while the MSS, CG and IA have sandy texture resulting from the washing out of the fine sediment particles in this area (Al-Najjar et al., 2011). In conclusion and for the purpose of this study we refer hereafter to PLB and IA as polluted sites and we mean that they

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