ECOLOGICAL AND EVOLUTIONARY THERMAL PHYSIOLOGY OF MANGROVE GASTROPODS IN THE CONTEXT OF GLOBAL CHANGE

NURSALWA BAHARUDDIN

Ph.D. BIOLOGY

UNIVERSITI BRUNEI DARUSSALAM

2016

ECOLOGICAL AND EVOLUTIONARY THERMAL PHYSIOLOGY OF MANGROVE GASTROPODS IN THE CONTEXT OF GLOBAL CHANGE

A thesis submitted in total fulfilment of the requirements for the degree of

Doctor of Philosophy in Biology

at the Universiti Brunei Darussalam

Brunei Darussalam

By:

Nursalwa Baharuddin

M. Sc. (Hons) Canterbury New Zealand

B. App. Sc. (Hons) Kolej Universiti Sains dan Teknologi Malaysia

March 2016

To my father (Haji Baharuddin Jana)
and my mother (Hajjah Norkiah Abdul Rahman)
for the support that I needed to build a dream to chase after.

Pulau Bedukang Dec 2014

In every direction you will see the apparently endless wall of mangrove,
unvarying in color, unvarying in form, unvarying in height,
save from perspective ~ Mary Kingsley (1862 – 1900)

TABLE OF CONTENTS

Page

ABSTRACT

Animals and communities respond to global change, particularly to climate warming, which is a foremost phenomenon that impacts directly on biological systems. Ectothermic animals are considered susceptible to this change because their body temperature and physiological performance varies acutely with environmental conditions. A primary goal of this thesis is to contribute empirical data important to the build of a theoretical framework for ectothermic response to climate warming, which are distinctly lacking for major taxonomic groups and regions, such as tropical gastropods.

This thesis investigates tropical mangrove gastropods as a model study system to explore the vulnerability of biological systems to climate warming. Studies are based on gastropod physiological performance, acclimation, and behaviour in relation to body and environmental temperature. Under this framework, theories that tropical ectotherms are vulnerable to climate change because they live close to their thermal limits and are limited in acclimatory capacity are explored. This is because observation is based primarily on insect and lizard models, thus little is known or is underexplored for other highly diverse systems such as tropical gastropods.

The first two chapters consider the underlying influence of evolution on thermal tolerance in mangrove gastropods. The question on whether habitats, body size and phylogenies (species level) of these gastropods affect physiological performance is investigated. The results suggest that habitat and species have strong relationships with thermal tolerance, however poorly with body sizes. Secondly, whether ecological transitions of gastropods with narrow lineages across thermally-discrete habitats affected adaptation or phylogenetic conservatism is observable through thermal tolerance is explored. It was found that gastropods that colonized mangroves exhibited marginally lower upper lethal temperature (ULT) than their rocky shore counterparts. Thermal tolerance was also found to be highly conserved in the phylogeny, which is in agreement with studies on upper lethal temperatures of terrestrial ectotherms. Thirdly, gastropods' resilience to climate warming was also tested by assessing thermal safety margins (TSM). The results show that the TSM is broadened in

mangrove forest by inhabiting snails, resulting in the potential to tolerate substantial increases in temperature, which contradicts the general prediction for tropical ectotherms.

In the two chapters that follow, the evolution of thermal acclimation according to the ability of organisms to vary their physiological performance and tolerance during their lifetime is investigated. Whether high shore intertidal gastropods such as littorinids (Littorinidae) at tropical mangrove and rocky shore habitats are able to acclimate thermal tolerance under short versus long term treatments is explored. The results suggest that the ability to acclimate upper thermal tolerance limits might not be possible in these littorinids. Secondly, whether tropical ectotherms acclimate at aerial and/or aquatic climes is investigated. This is tested by acclimating *Indothais gradata* (common whelk gastropod that occupies different habitats within tropical intertidal zones) at aerial and/or aquatic climes. The results suggested that *Indothais gradata* acclimated neither at aerial nor aquatic climes. Warming tolerance analysis suggested that *I. gradata* from the rock habitat has the lowest warming tolerance of those tested, just 2 – 3°C before performance drops to fatal levels, compared to 7 – 8°C and 13 – 14°C in those from tree and mud habitats respectively.

The last two chapters consider behavioural thermoregulation as a means of escaping thermal stress, or an avoidance to climate warming. The question is to understand the general thermoregulatory behaviour (turning temperature) and choice of resting temperatures of mangrove snails (littorinids and neritids) under laboratory-controlled conditions. The results suggest that littorinid species had at least 5-6°C higher in turning (T_{turn}) and settling (T_{settle}) temperatures compared to neritid snails. The final chapter aims to investigate the effect of habitat use on climate warming vulnerability of the tropical high-shore snail, *Echinolittorina malaccana*, which aestivates in sun-exposed or shaded habitats. The results suggested that through behavioural selection of cool, shaded overhangs or crevices, high-shore *Echinolittorina* snails, adapted for resting in the sun, vastly improve their "warming tolerance", which is the thermal range between the environmental temperature and incipient lethal temperature.

Thus, the vulnerability of mangrove snails to high temperatures associated with future climate warming could be moderated by the availability of shaded habitat, making existing climate warming predictions more complex than previously realised.

ABSTRAK

Haiwan dan komuniti bertindak balas terhadap perubahan global, terutamanya pemanasan iklim yang memberikan kesan secara langsung ke atas sistem biologi. Haiwan ektotermik dianggap terdedah kepada perubahan ini kerana suhu badan dan prestasi fisiologi yang bergantung kepada perubahan suhu persekitaran. Matlamat utama tesis ini adalah untuk menyumbang kepada data empirikal yang penting dalam haiwan ektotermik terhadap pemanasan iklim, yang jelas kekurangan dalam taksonomi dan serantau seperti gastropod tropika.

Tesis ini mengkaji gastropod bakau tropika sebagai sistem model kajian untuk meneroka kelemahan sistem biologi kepada pemanasan iklim. Kajian adalah berdasarkan kepada prestasi fisiologi gastropod, penyesuaian diri, dan tingkah laku yang berkaitan dengan badan dan suhu alam sekitar. Di bawah rangka kerja ini, teori ektotermik tropika yang terdedah kepada perubahan iklim kerana mereka mendiami kawasan berhampiran dengan had terma dan terhad dalam kapasiti menyesuaikan diri telah diterokai. Ini adalah kerana pemerhatian berdasarkan pada model serangga dan cicak terutamanya, maka pengetahuan yang sedikit atau kurang diteroka untuk sistem yang lain seperti gastropod bakau tropika.

Dua bab yang pertama mempertimbangkan pengaruh asas evolusi pada toleransi haba dalam gastropod bakau. Persoalan sama ada habitat, saiz badan atau filogeni (di peringkat spesies) gastropod ini mempengaruhi prestasi fisiologi disiasat. Keputusan menunjukkan bahawa habitat dan spesies mempunyai hubungan yang kukuh dengan toleransi haba, walau bagaimanapun hubungan yang lemah dengan saiz badan. Kedua, sama ada peralihan ekologi gastropod dengan keturunan yang melalui habitat panas dan diskret serta adaptasi atau konservasi filogenetik diterokai. Keputusan mendapati bahawa keturunan gastropod yang menduduki hutan bakau mempunyai suhu yang rendah dalam had atas toleransi haba berbanding gastropod yang menduduki pantai berbatu. Toleransi haba juga didapati sangat terpelihara dalam filogeni, yang sejajar dengan had atas toleransi haba haiwan ektotermik daratan. Ketiga, daya tahan gastropod kepada pemanasan iklim juga telah diuji dengan menilai margin keselamatan haba. Keputusan menunjukkan bahawa margin keselamatan haba

diperluas dalam siput yang menduduki hutan bakau, menyebabkan potensi untuk bertolak ansur dengan peningkatan suhu yang ketara bercanggah dengan ramalan umum haiwan ektotermik tropika.

Dalam dua bab yang diikuti, evolusi penyesuaian diri terhadap haba mengikut keupayaan organisma untuk mengubah prestasi fisiologi mereka dan toleransi semasa hayat disiasat. Sama ada gastropod yang menduduki pasang surut tinggi seperti littorinid (Littorinidae) di hutan bakau tropika dan habitat pantai berbatu dapat menyesuaikan diri pada toleransi haba di bawah jangka masa pendek atau akut berbanding jangka masa panjang diterokai. Keputusan menunjukkan bahawa keupayaan untuk menyesuaikan diri pada had atas toleransi haba mungkin tidak sesuai dalam littorinid. Kedua, sama ada haiwan ektotermik tropika menyesuaikan diri pada persekitaran suhu udara atau suhu akuatik disiasat. Ini telah diuji melalui *Indothais gradata* (gastropod yang menduduki habitat yang berbeza dalam zon pasang surut tropika) di dalam persekitaran suhu udara atau suhu akuatik. Keputusan mencadangkan bahawa *Indothais gradata* tidak menyesuaikan diri sama ada pada persekitaran suhu udara mahupun suhu akuatik. Analisis toleransi haba mencadangkan bahawa *I. gradata* dari habitat batu-batuan mempunyai toleransi haba yang rendah iaitu sebanyak 2 – 3°C sebelum keupayaan organisma jatuh ke paras kematian, berbanding 7 – 8°C dan 13 – 14°C yang menduduki habitat di pokok – pokok dan berlumpur.

Dua bab yang terakhir mempertimbangkan tingkah laku termoregulasi sebagai cara melepaskan diri dari tekanan haba, atau mengelakkan diri dari pemanasan iklim. Persoalannya adalah untuk memahami tingkah laku umum iaitu suhu berpaling dan suhu berehat oleh siput bakau (littorinid dan neritid) di bawah keadaan makmal yang terkawal. Keputusan menunjukkan bahawa spesies littorinid mempunyai sekurang-kurangnya 5-6°C lebih tinggi dalam suhu berpaling dan suhu berehat berbanding siput neritid. Bab terakhir bertujuan untuk mengkaji kesan penggunaan habitat oleh siput yang menduduki pasang surut tinggi, *Echinolittorina malaccana* yang dorman dibawah suhu melampau kepada matahari atau pun terlindung. Keputusan mencadangkan bahawa pilihan tingkah laku siput *Echinolittorina malaccana* yang

dorman apabila terdedah kepada suhu melampau matahari, jika sebaliknya menduduki habitat yang sejuk atau berteduh di rekahan batu dapat meningkatkan toleransi pemanasan iaitu julat haba diantara suhu persekitaran dan suhu had atas toleransi haba.

Oleh itu, kelemahan siput bakau kepada suhu yang tinggi berkaitan dengan pemanasan iklim pada masa hadapan akan berkurangan dengan adanya habitat yang teduh, maka membuatkan ramalan pemanasan iklim yang sedia ada tentang haiwan ektotermik tropika lebih kompleks daripada sebelumnya.