Fishery Biology and Ecology of the Marine Snail, Turbo militaris

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Seinor, K. (2025). Fishery Biology and Ecology of the Marine Snail, Turbo militaris [Southern Cross University]. https://doi.org/10.25918/thesis.462

FISHERY BIOLOGY AND ECOLOGY OF THE MARINE SNAIL, *TURBO MILITARIS*

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FISHERY BIOLOGY AND ECOLOGY OF THE MARINE SNAIL, *TURBO MILITARIS*

A thesis submitted in fulfilment of the requirements for the degree of Doctor of Philosophy

22nd February 2025

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DECLARATION

I certify that the work presented in this thesis is, to the best of my knowledge and belief, original, except as acknowledged in the text, and that the material has not been submitted, either in whole or in part, for a degree at this or any other university.

I acknowledge that I have read and understood the University's rules, requirements, procedures and policy relating to my higher degree research award and to my thesis.

I certify that I have complied with the rules, requirements, procedures and policy of the University.

Kate Maree Seinor

22nd February 2025

Southern Cross University

ACKNOWLEDGEMENT OF COUNTRY

I acknowledge the traditional custodians of the lands on which I live and work. I pay my respects to the Elders past, present, and emerging.

I am deeply grateful to live on Gumbaynggir Country, where the coastal beauty of the region inspires my passion and connection to the ocean. I am grateful to conduct this research on Bundjalung Country, Gumbaynggir Country, Worimi Country and Yaegl Country and am thankful to the traditional people of these lands.

Gugumbal (turban snail), the key focus to this research is a traditional resource harvested by First Nations Australians. I recognise the connection to community, the land and water by Indigenous Australians and respect their significant role as the first resource managers.

This acknowledgment is made in recognition of the enduring role of Indigenous Australians in managing the land and sea, and the significance of traditional knowledge and caring for community.

ABSTRACT

Demands for the ocean's resources have risen alongside expanding populations, underscoring the need for improved management. A sound understanding of a target species' biology and ecology is pivotal to effective fisheries management. However, research is often limited in small-scale fisheries and for invertebrates. *Turbo militaris* is a large rocky-reef gastropod endemic to the east coast of Australia across ~ 8° of latitude. *Turbo militaris* is harvested by cultural, recreational and commercial fisheries for its high-quality meat and large size. Efforts to manage *T. militaris* stocks are currently hampered by data deficiency, especially regarding life-history. Consequently, this work aims to increase the knowledge base on *T. militaris*, thereby providing a valuable case study for informing other gastropod fisheries. A shell-drilling and gonad-biopsy procedure was developed as a non-lethal method for reproductive sampling in *T. militaris*. Reproductive periodicity in *T. militaris* was assessed at two locations spatially separated by ~3° of latitude, using gonadosomatic index measures and oocytes obtained using the drill-biopsy method*. T. militaris* showed prolonged reproductive activity, with peak ripeness in warmer months and spawning over multiple events, mainly in winter. Reproductive timing was asynchronous between locations and linked to environmental variables such as sea surface temperature. A mark-recapture study was conducted to assess the mobility and growth of *T. militaris* at subtropical and temperate locations along eastern Australia. Movement patterns were similar across rocky shores; displacement distances were localised and non-directional, with limited upshore-to-downshore mixing. These findings suggest that harvested intertidal populations are not readily replenished, and unsuitable habitats may inhibit snail movement confining adult snails to each rocky shore. Thus, heavy harvesting may considerably impact local populations, especially for snails in shallow areas, while deeper habitats may be safeguarded due to limited accessibility. *Turbo militaris* grows rapidly and can live up to 10 years. Growth varies latitudinally, with temperate snails growing faster, attaining a larger average size, having higher natural mortality and a shorter lifespan than subtropical snails. This indicates a potentially higher turnover for the temperate populations and thus a greater resilience to stress, whereas the subtropical snails may be more susceptible to overfishing or other environmental impacts due to slower recovery. Sexual maturity was attained by temperate snails in less than one year and within two years for subtropical snails, allowing approximately 1.5 years for temperate snails and 4.4 years for subtropical snails to

reproduce prior to entering the fishery. Therefore, current minimum size limits offer suitable protection across the fishery to ensure population replenishment. Should further management be required, decreased bag limits or total allowable catch for commercial fisheries may be necessary, especially in subtropical regions. Furthermore, due to limited adult movement and extended, asynchronous reproduction, spatial protection in favourable habitats would be suitable for reducing harvesting impacts and safeguarding existing adult populations. This research has substantially enhanced our knowledge on the biology and ecology of *T. militaris*. Turban snails are ecologically important and are valuable fisheries resources with cultural significance. By addressing data deficiencies on *T. militaris*, this research provides empirical data that supports the management of this important, spatially restricted species.

ACKNOWLEDGEMENTS

My profound appreciation goes to my supervisors, Prof. Kirsten Benkendorff, Prof. Steven W. Purcell, Prof. Stephen D. A. Smith, and Dr. Hamish Malcolm. Thank you for supporting and guiding me, for your invaluable help with fieldwork, lab work and analysis, for insightful and thorough feedback and for providing me with additional opportunities. You have each inspired me and helped me develop into the scientist I am today, and I will carry your wisdom into my future endeavours. This PhD wouldn't have been possible without you all, and I couldn't have asked for a better team; thank you.

I greatly appreciate the traditional owners of the lands on which this work occurred. Special thanks to the NTSCORP and Yaegl Traditional Owners Aboriginal Corporation for granting permission to research on Yaegl Country. Thank you to Uncle Ferlin Laurie for assisting with fieldwork at Diggers Camp. Thank you to New South Wales (NSW) Marine Parks for permitting fieldwork in the Solitary Islands Marine Park and the Port Stephens – Great Lakes Marine Park. I greatly thank the funding bodies mentioned below for supporting research and conference costs and the Australian Government Research Training Program Scholarship.

Special thanks to Dr. Hamish Malcolm and the team at Marine Ecosystems, NSW Department of Primary Industries and Regional Development, for the industry internship opportunity. Thanks to Dr. Robert Creese for guidance and support, assistance in the field, and expertise in fisheries research and management. Thanks to Dr. Andy Davis, external panel member for the Confirmation of Candidature and In-Candidature Review, whose insightful feedback helped shape this work.

Thank you to the technical team and administration staff at the National Marine Science Centre for their support, facilities and technical assistance. Thanks to Dr. Danny Bucher, Prof. Symon Dworjanyn and Dr. Karina Hall for lending equipment. Thanks to Dr. Peta Schofield for generously sectioning the opercula samples. Thanks to Gary Hamer for sharing knowledge on tagging and growth studies and generously providing samples and fieldwork support. To the PhD candidates at the National Marine Science Centre, thank you for sharing this journey with me and for your support through the good times and the challenges. I wish you all the best.

Thank you to all the volunteers who generously gave their time and efforts to help with fieldwork and lab work, including Rin Adachi, Mikaela Abayakoon-Stanborough, Kayla Baker, Nyomi Bodley, Katelyn Broadfoot, Zoe Butcherine, Simone Gardiner, Scott Graham, Gary Hammer, Sam Hawke, Kendal Houghton, Katie Kelly, Naomi Mesic-Kruse, Natasha Orange, Toneya Smith and Lilly Sydenham. Special thanks to my #1 fieldwork buddy, my father, Douglas Seinor. The fieldwork at Port Stephens wouldn't have been possible without your help. Thanks for your enthusiasm for my research and for always being keen to jump in the water!

My greatest appreciation to my family and friends for their love and support. Thank you to my partner Scotty Graham for being my biggest supporter. Scotty, I am grateful for your devoted help in the field, for your words of encouragement, and for sharing all the highs and lows of this journey; I love you. Finally, to my son Oliver Graham, you have shown me the most incredible strength and growth, not just in your own remarkable journey thus far, but in myself too. I love you, and I hope to inspire you to dream big, my little one.

PERMITS

This research was conducted under a Scientific Collection Permit from Section 37 of the Fisheries Management Act 1994 (Permit No: P14/0014-2.0). The work in the Solitary Islands Marine Park and Port Stephens – Great Lakes Marine Park was conducted under the authorisation of NSW Marine Park Permits (Permit No: MEAA21/109 & MEAA24/27). NTSCORP and Yaegl Traditional Owners Aboriginal Corporation granted permission to work on Yaegl Country.

FUNDING

I, Kate Seinor, received financial support from the Australian Government Research Training Program Scholarship. The project was supported by postgraduate-associated funding ($9,000) through the Faculty of Science and Engineering, Southern Cross University.

The Malacological Society of Australasia (MSA) awarded an early researcher grant, providing funding of $2,500 towards research-related costs for Chapters 2 to 5. The MSA funded attendance at the Molluscs Conference, 2022, where work from Chapter 3 was presented.

The NSW Department of Primary Industries and Regional Development, Recreational Fishing Saltwater Trust awarded research funding of $8,000 for research-related costs towards Chapters 3 to 5.

The Australian Marine Sciences Association (AMSA), NSW division, granted a conference travel award. This award supported attendance at the AMSA – NZMSS (New Zealand Marine Sciences Society) 2024 Conference, where the work from Chapter 5 was presented.

The Australian Society for Fish Biology (ASFB) granted the John Glover travel award to support attendance at the ASFB Conference, 2024, where work from Chapter 4 was presented.

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DISCLAIMERS

I, Kate Seinor, declare that Chapters 2, 3 and 4 of this thesis have been published in peer-reviewed journals. Chapter 5 is in preparation for submission to a peer-reviewed journal. These chapters have been modified per university guidelines for inclusion in the thesis.

I, the candidate, am the lead author of all chapters in the thesis and the resulting publications. I led the conception, data collection, analysis and writing of these works.

Statements of co-authorship outlining the details of each author's contributions to the publications are included in Appendix F.

Environmental data for Chapters 3, 4 and 5 were sourced using E.U. Copernicus Marine Environment Monitoring Service Information; 10.48670/moi-00165, 10.48670/moi-00017, 10.48670/moi-00016, 10.48670/moi-00015, 10.48670/mds-00321

Remotely sensed topographic and bathymetric data for Chapter 4 were derived from Lidar Aerial Survey data sourced from Geoscience Australia (2021).

Signed by the candidate:	Confirmed by principal supervisor:
Date:14/11/2024	Date: 5/11/2024
Kate Maree Seinor	**Prof. Kirsten Benkendorff**

PUBLISHED WORK IN THE THESIS

Chapter 2: **Seinor, K**., & Benkendorff, K. (2023). Shell drilling and gonad biopsies provide a rapid, non-lethal method for *in-situ* assessment of reproductive periodicity in Turbinidae. *Journal of Molluscan Studies, 89(2)*: e012. doi:10.1093/mollus/eyad012

Chapter 3: **Seinor, K**., Purcell, S. W., Malcolm, H., Smith, S. D. A., & Benkendorff, K. (2023). Extended and spatially asynchronous reproductive periodicity in a harvested, warm-temperate rocky-reef gastropod (Turbinidae). *Fisheries Oceanography, 33(1)*: e12653. doi:10.1111/fog.12653

Chapter 4: **Seinor, K**., Purcell, S. W., Malcolm, H., Creese, R. G., & Smith, S. D. A. (2025). Long-term mobility of a harvested, rocky-reef gastropod. *Fisheries Management and Ecology*, e12794. doi:10.1111/fme.12794

OTHER PUBLICATIONS

Nimbs, M., Champion, C., Lobos, S. E., Malcolm, H. A., Miller, A. D., **Seinor, K**., Smith, S. D. A., Knott, N., Wheeler, D., & Colemen, M. A. (2023). Genomic analyses indicate resilience of a commercially and culturally important marine gastropod snail to climate change. *PeerJ. 11(3)*: e16498. doi:10.7717/peerj.16498

Smith, S. D. A., Mohring, M. B., Rule, M. J., **Seinor K**., Schultz. A., & Malcolm, H. A. Morphological variation of *Turbo militaris* in northern NSW, Australia, with implications for management of harvesting. *Draft manuscript, 2022.*

Malcolm, H. A., Smith, S. D. A., **Seinor, K**., Shultz, A., Creese, B., Strehling, N. Monitoring the abundance and size of large molluscs on intertidal rocky shores in northern NSW. *Preliminary report to Department of Primary Industries and Regional Development, 2022.*

ASFB Conference, 2024 – Full presentation (Chapter 4)
Snails pace: nomadic movement of a harvested rocky shore gastropod. **Seinor, K**., Purcell, S. W., Malcolm, H., Creese, R. G. & Smith, S. D. A.

AMSA – NZMSS Conference, 2024 – Full presentation (Chapter 5)
Growth varies between subtropical and temperate populations of the harvested Australian turbinid, *Turbo militaris.* **Seinor, K**., Malcolm, H., Benkendorff, K., Smith, S. D. A., Creese, R. G., & Purcell, S. W.

Solitary Islands Aquarium, Marine Discovery Series, 2024 – Public lecture
She studies sea shells by the sea shore. **Seinor, K.**

MSA, Molluscs Conference, 2022 – Full presentation (Chapter 3)
Reproductive periodicity of the large Australian turbinid, *Turbo militaris.* **Seinor, K**., Purcell, S. W., Malcolm, H., Smith, S. D. A., & Benkendorff, K.

Southern Cross University, RISE (Researching Information Technology, Science and Engineering) Conference, 2021 – Full presentation (highly commended) (Chapter 1)
A novel, non-lethal technique for sampling the reproductive cycle in marine turbinids. **Seinor, K**., & Benkendorff, K.

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LIST OF ABBREVIATIONS

AIC	Akaike Information Criterion
AMSA	Australian Marine Sciences Association
ANOVA	Analysis of Variance
ASFB	Australian Society for Fish Biology
BEST	best estimate
CDFW	California Department of Fish and Wildlife
CMEMS	Copernicus Marine Environment Monitoring Service
DAFF	Department of Agriculture, Fisheries and Forestry
DBLM	Distance Based Linear Model
DCCEEW	Department of Climate Change, Energy, the Environment and Water
DPI	Department of Primary Industries
DPIRD	Department of Primary Industries and Regional Development
EAC	East Australian Current
ESRI	Environmental Systems Research Institute
FAACC	formalin, acetic acid, calcium chloride dehydrate and ultrapure water
FAO	Food and Agriculture Organization of the United Nations
G	gonad
GDg	gonad and digestive gland
GIS	Geographic Information System
GPS	Global Positioning System
GSI	gonadosomatic index
IUCN	International Union for Conservation of Nature
K	Brody growth co-efficient
L_∞	asymptotic size

LA ICP-MS	-	Laser Ablation Inductively-Coupled-Mass-Spectrometry
LED	-	light emitting diode
LM_{50}	-	size at first maturity
LMMA	-	Locally-Managed Marine Area Network
M	-	natural mortality
MOS	-	modal oocyte size
MSA	-	Malacological Society of Australasia
NMSC	-	National Marine Science Centre
NSW	-	New South Wales
PERMANOVA	-	Permutational Multivariate Analysis of Variance
PIRSA	-	Department of Primary Industries and Regions, South Australia
RISE	-	Researching Information Technology, Science and Engineering
SIMP	-	Solitary Islands Marine Park
SPC	-	South Pacific Commission
SUTS	-	sea urchin and turban snail
T_{max}	-	longevity
WoRMS	-	World Register of Marine Species

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CHAPTER 1.

INTRODUCTION

Over the last several decades, demands on the ocean's resources have risen dramatically, consequential to expanding human populations and the attraction of coastal living (Anderson et al., 2011). Population growth is predicted to continue to rise over the coming decades (Gerland et al., 2014), thus escalating food consumption, including seafood (Teixeira & Silva, 2023). Marine resources are essential to future food security, improved human nutrition and coastal livelihoods (Cohen et al., 2019; Golden et al., 2021; Maire et al., 2021). Seafood provides a pivotal source of global protein and micronutrient intake (Golden et al., 2016; Guillen et al., 2019; Golden et al., 2021; Tacon, 2022). The consumption of seafood is promoted as a healthy option compared to other agricultural meat choices (Tacon, 2022). However, ethical choice of seafood should prioritise stocks that are assessed, sustainable and effectively managed (Teixeira & Silva, 2023).

Heavy harvesting of marine resources and the predicted impacts of future ocean climate conditions pose serious threats to marine ecosystems and fishery stocks (Anderson et al., 2011; Andréfouët et al., 2014). Increased pressure on the ocean’s resources has increased the proportion of stocks harvested above sustainable levels (Teixeira & Silva, 2023), with over 37% of global seafood stocks currently overfished (FAO, 2024). Overharvesting can lead to stock depletions and overexploitation, which present dire consequences to future human nutrition and food security, especially in coastal communities of developing countries (Golden et al., 2016; Maire et al., 2021). As demands on common marine resources increase, alternatives become increasingly popular, with new underutilized resources promoted to supplement overfished stocks (Leiva & Castilla, 2002; Anderson et al., 2011). There is an urgency to effectively manage all marine resources to mitigate threats to exploited stocks so they can be sustained into the future.

1.1 Gastropod fisheries

Harvesting on rocky shores has been practised for thousands of years; however, harvesting of rocky shore invertebrates has dramatically increased over the last several decades (Anderson et al., 2011; FAO, 2024). The rocky shore is home to many invertebrates, including gastropods harvested by subsistence, recreational and commercial fisheries (Anderson et al., 2011; Santhanam, 2018). Marine molluscs represent some of the most valuable invertebrate fisheries, contributing to around 7% of global commercial fishery production (Leiva & Castilla, 2002; FAO, 2021). Of the phylum Mollusca, the class Gastropoda accommodates around 3% of the global catch (Leiva & Castilla, 2002; FAO, 2021), with around 300 species of marine gastropods harvested commercially worldwide (Santhanam, 2018).

Gastropods are an increasingly popular source of seafood harvested globally (Anderson et al., 2011). Marine gastropods provide high-quality meat and are considered a delicacy in some countries, such as France, Japan, Korea and China (Santhanam, 2018). In addition, the shells of many marine gastropods are of high economic value (e.g., from Haliotidae, Strombidae, Conidae, Trochidae and Turbinidae), sought after for their ornamental beauty or their nacreous mother-of-pearl material (Nayar & Appukuttan, 1983; Murakoshi et al., 1993; Hickman, 1998; Andréfouët et al., 2014; Santhanam, 2018). Marine gastropods are also used for medicinal purposes, dye production, and the aquarium trade (Benkendorff et al., 2015; Schnierer & Egan, 2016; Ahmad et al., 2018).

1.2 Turban snail fisheries

Turban snails are gastropods of the family Turbinidae (subclass: Vetigastropoda, Order: Trochida) and are primarily sought after for human consumption for their high-quality meat (Weidland et al., 1998; Santhanam, 2018). Turban snails offer a quality protein source (Romolo et al., 2021) that is high in essential micronutrients and polyunsaturated fats, with a good omega-three to six fatty acid ratio and low in saturated fats (Ab Lah et al., 2017b; Ab Lah et al., 2018). Turban snails may provide a suitable option for substituting other overexploited fisheries. For instance, turbinid meat offers an alternative option to depleted stocks of abalone (Davis et al., 2005; Anderson et al., 2011; Ab Lah et al., 2017b). Harvesting is expected to increase for turbinids, which may already be under stress from other environmental pressures (Zacharias & Kushner, 2006; Cooling & Smith, 2015).

1.2.1 Commercial fisheries

Turbinidae fisheries are responsible for around 4% of global commercial gastropod fisheries production (FAO, 2021). Turban snail commercial fisheries occur in many countries, with popular commercially harvested species including *Turbo cornutus, T. marmoratus* and

Megastraea undosa (Figure 1.1). Japan and South Korea lead global commercial turban snail production from landings of the highest-yielding species, *T. cornutus* (Leiva & Castilla, 2002; FAO, 2021). *Turbo cornutus* is distributed throughout South and Southeast Asia off the coasts of Japan, South Korea and Malaysia (Figure 1.1). Commercial fishing of *T. cornutus* dates back to the 1950s when landings yielded around 4,000 t annually (FAO, 2021). Commercial fishing of *T. cornutus* increased from the mid-1960s until the mid-20th century; landings have been relatively stable since, varying from around 8,000 to 10,000 t annually (FAO, 2021). Peak landings of *T. cornutus*, yielding around 20,000 t, occurred in 1973, 1998 and 2003 (FAO, 2021).

Turbo marmoratus is the largest snail of the genus *Turbo* (Reeve, 1848) and is one of the most widespread, with an extensive native and introduced distribution throughout the Indo–Pacific and Asia–Pacific (Devambes, 1961; Nayar & Appukuttan, 1983; Murakoshi et al., 1993; Andréfouët et al., 2014) (Figure 1.1). *Turbo marmoratus* is harvested commercially and for subsistence, for both its meat and shell. The mother-of-pearl shell of *T. marmoratus* (and other turban snails) is valued in the button-making, shell craft and jewellery-making industries (Nayar & Appukuttan, 1983; Yamaguchi, 1992; Murakoshi et al., 1993; Andréfouët et al., 2014). Substantial commercial landings of *T. marmoratus* were reported through the 1980s (800-1000 t per year), but after that, the fishery experienced a dramatic decline (Nayar & Appukuttan, 1983), which continued through the 1990s and 2000s (Murakoshi et al., 1993; Anderson et al., 2011; Andréfouët et al., 2014). As *T. marmoratus* stocks have already been heavily depleted through overfishing (Murakoshi et al., 1993; Komatsu et al., 1995; Andréfouët et al., 2014), regeneration efforts, through translocation and reseeding, have been implemented to re-establish a sustainable fishery for (Andréfouët et al., 2014).

Figure 1.1. Turban snail fishery species throughout the world. Shading depicts approximate distributions. Turban snail images are proportional to actual size.

In the United States and Mexico, *M. undosa* fisheries (Figure 1.1) operate as substitute fisheries for overfished abalone stocks (Zacharias & Kushner, 2006; Martone & Micheli, 2012). *Megastraea undosa* meat is processed into an abalone-like product, termed 'wavalone' (a reflection of the common name, wavy turban snail) (Taniguchi & Rogers-Bennett, 2001). Commercial fishing of *M. undosa* dates back to the early 1990s at less than 10 t annually; landings peaked in the late 1990s, yielding over 30 t and, thereafter, reduced to around 10 t annually (Taniguchi & Rogers-Bennett, 2001). Little data is available on the current landings or sustainability of *M. undosa* fisheries.

In Australia, common species of turbinids targeted by commercial fishing include *T. militaris, T. marmoratus, Lunella torquata* and *L. undulata* (Figure 1.1). Until the last two decades, commercial catch primarily comprised *T. marmoratus,* targeted in the northern parts of the continent, and *L. undulata*, which has been exploited in Tasmania since the 1980s (Keane et al., 2014; DCCEEW, 2018b). Landings of *L. undulata* in Tasmania steadily increased through the early 1900s and have since varied between 13 and 35 t, averaging 22 t per year (Keane et al., 2014). A commercial *L. undulata* fishery has operated in South Australia since 2000 as part of the South Australia Miscellaneous Fishery (DCCEEW, 2018b; PIRSA, 2024a). Harvest of *L. undulata* in South Australia increased in the first decade and has since remained low, with catch primarily sold domestically (DCCEEW, 2018b). The commercial *L. undulata* fisheries in South Australia and Tasmania are classified as sustainable and effectively managed (Keane et al., 2014; DCCEEW, 2018b). There is potential to expand the *L. undulata* fishery by increasing catch in unexploited areas (Keane et al., 2014).

Australian species, *T. militaris*, *L. torquata* and *L. undulata,* are commercially harvested in the combined sea urchin and turban snail (SUTS) commercial restricted licence fishery in New South Wales (NSW) (Rowling et al., 2010; DCCEEW, 2018a; NSW DPI, 2018b). Harvesting turban snails in the SUTS fishery is permitted throughout NSW waters in compliance with commercial exclusion zones and marine park zoning (DCCEEW, 2018a; NSW DPI, 2024). Harvesting of turban snails in the SUTS fishery was relatively low during the early 1900s, yielding less than 1.5 t annually and increased during the late 1900s (Rowling et al., 2010). In 2004, harvest peaked at just over 21 t; subsequent rises in yield occurred during 2006–2007, 2016–2017 and 2020–2022 (Chick, 2023) (Figure 1.2). Commercial harvest has averaged around 5 to 6 t annually in recent decades (Chick, 2023) (Figure 1.2). Before 2009, landings were not reported to the species level; reporting after 2009 indicates that the catch composition is mostly *T. militaris* (Chick, 2023) (Figure 1.2). The number of active fishers harvesting turban snails in the SUTS fishery has generally increased since 2000 (Chick, 2023) (Figure 1.2). Fishing for turban snails is considered low-impact and environmentally responsible due to the non-destructive harvesting method of hand collection (DCCEEW, 2018a; Chick, 2023). The exploitation status of turban snail stocks in the SUTS fishery is considered ‘undefined’ due to the limited available information on stock status (Rowling et al., 2010; Stewart et al., 2015).

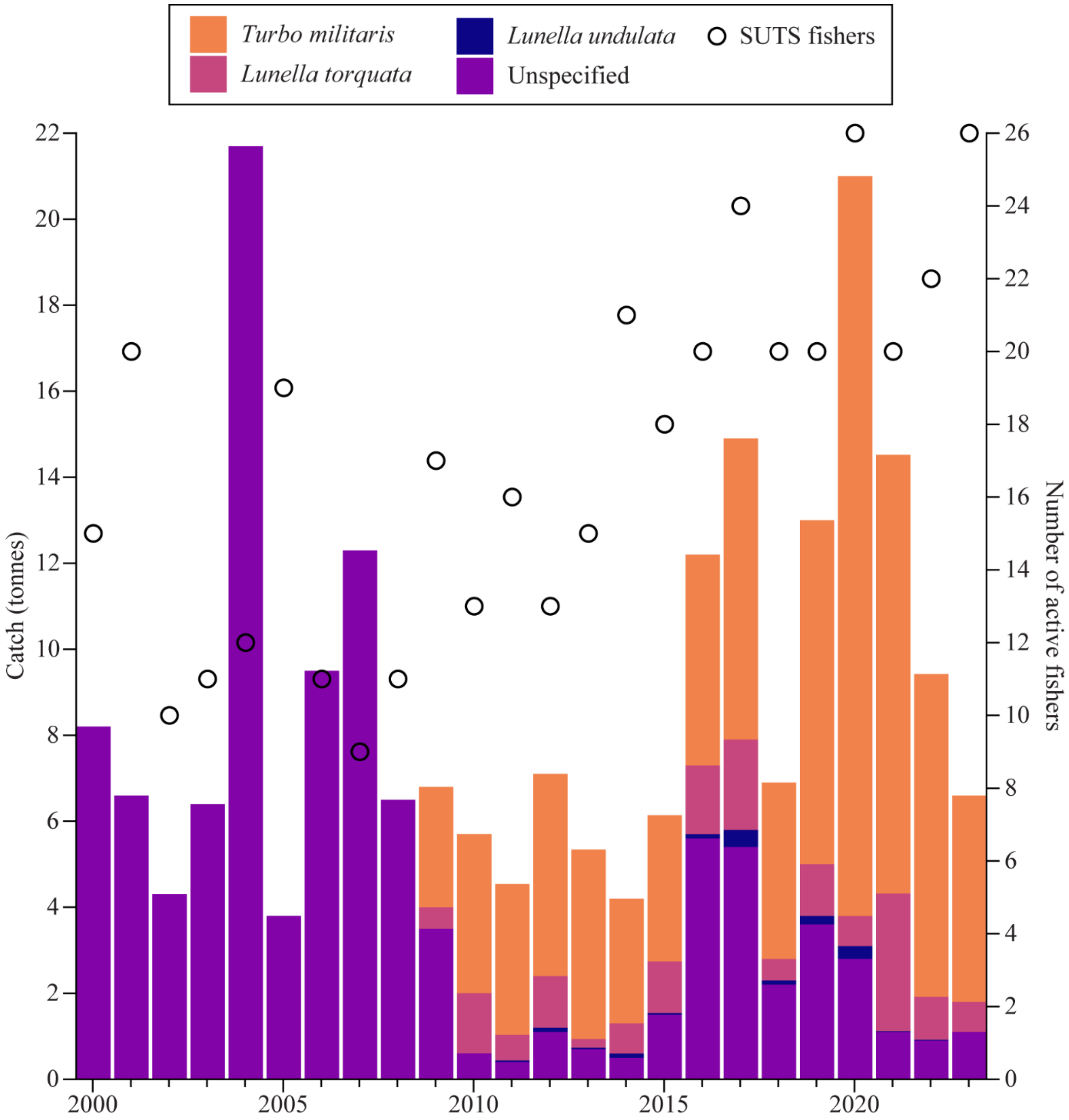


Figure 1.2. Catch (t) of turban snails and the number of active fishers (targeting turban snails) in the sea urchin and turban snail (SUTS) combined fishery in Australia. (Data: Chick, 2023).

1.2.2 Traditional and artisanal fisheries

Subsistence fisheries are essential for food security and income for developing countries, especially through the islands of the South Pacific, Indo–Pacific and Asia–Pacific (Salas et al., 2007; Purcell & Pomeroy, 2015; Cohen et al., 2019; Rousseau et al., 2019). Species targeted by subsistence fishers may be abundant in some remote places and, therefore, are highly valuable resources to the communities that harvest them (Holguin Quiñones & Michel-Morfin, 2006). Traditional and artisanal turbinid fisheries include *T. funiculosus* in Mexico (Holguin Quiñones & Michel-Morfin, 2006), *T. sarmaticus* in South Africa (McLachlan & Lombard, 1980, 1981; Bruton et al., 1991; Lasiak, 1991; Proudfoot et al., 2006), *L. coronata* throughout the Indo–Pacific, Arabian Peninsula and East Asia and *L. smaragda* in New Zealand (Figure 1.1).

Marine resources, including molluscs, have major economic, nutritional and cultural value for First Nations People (Faulkner, 2000; Henry & Lyle, 2003; Arrawarra Sharing Culture, 2009; Santhanam, 2018; PIRSA, 2024b). Traditional fisheries provide essential sources of protein and nutrients for many coastal communities. Traditional fishing represents a connection to Country for Indigenous Australians and is important for ceremonial and social values (Faulkner, 2000; Arrawarra Sharing Culture, 2009; Trân et al., 2016; PIRSA, 2024b). Evidence of traditional harvesting of marine gastropods, including turbinids, is found throughout coastal middens (Horwitz et al., 1991; Lasiak, 1992; McGrath et al., 2015; Sherwood, 2018; Cohen et al., 2019). In Australia, *T. militaris*, *L. torquata* and *L. undulata* are recognised as traditional resources for Indigenous Australians (Arrawarra Sharing Culture, 2009; PIRSA, 2024b). Turban snails are a valued cultural food resource; traditionally, the animal is cooked on the fire, by boiling or in hot coals (Arrawarra Sharing Culture, 2009). Turban snail shells are also valuable as they can be fashioned into sharp objects such as needles, cutting instruments or fishing hooks (Arrawarra Sharing Culture, 2009).

1.2.3 Recreational fisheries

Recreational fishing is an important pastime in Australia, with around one-fifth of the population engaging in fishing activities at least once yearly (Henry & Lyle, 2003; Moore et al., 2023; Murphy et al., 2023). The rocky shore provides an accessible habitat for recreational fishers to collect marine invertebrates with little effort, skill, or gear. Turban snails are a relatively easy-to-catch source of protein as they are large-sized compared to most other intertidal invertebrates, often occur in high densities and have low mobility (compared to fish) (McLachlan & Lombard, 1980; Bruton et al., 1991; Pulfrich & Branch, 2002; Holguin Quiñones & Michel-Morfin, 2006; Wernberg et al., 2008; Cooling & Smith, 2015; Ab Lah et al., 2017b). Turbinids are recreationally collected for food, and for bait by anglers (McLachlan & Lombard, 1980; Bruton et al., 1991; Pulfrich & Branch, 2002). In Australia, turban snails commonly targeted for recreational harvesting include *T. marmoratus, T. militaris, L. torquata* and *L. undulata* (NSW DPI, 2023; PIRSA, 2024b; The State of Queensland, 2024; The State of Victoria, 2024). Recreational harvesting is highly prevalent in NSW, where *T. militaris* and *L. torquata* are primary targets. While fishers can shallow dive for turban snails, harvesting pressure is highest on intertidal rocky platforms.

Defining the scale of non-commercial fisheries presents inherent challenges, especially in remote areas, as the catch is generally unreported and consumed locally (Schnierer & Egan, 2016). Recreational fishers' catch may be substantial due to the large number of participants for some species (Henry & Lyle, 2003). Limited scientific studies are conducted on small-scale fisheries species compared to those from larger fisheries (Rousseau et al., 2019), and catch data are hard to reliably document and often limited (DCCEEW, 2018b; Chick, 2023). In Australia, the quantity of recreational catch of turban snails is undefined. In NSW, non-commercial harvest is suggested to be of a similar magnitude to commercial harvesting (Rowling et al., 2010; DCCEEW, 2018a). In South Australia, despite the limited data to assess the stock's potential, the non-commercial harvest of *L. undulata* is considered negligible (DCCEEW, 2018b), perhaps due to the restriction on intertidal collection (Table 1.1). Nevertheless, non-commercial harvesting is predicted to rise with expanding populations, particularly with an influx of seasonal agricultural workers in some coastal locations, such as the NSW mid-north coast (Cooling & Smith, 2015). Thus, future unregulated or mismanaged recreational harvesting could negatively affect marine ecosystems and threaten fisheries sustainability through overexploitation.

Turban snail populations are currently being monitored on rocky shores in the Solitary Islands Marine Park (SIMP) by the Department of Primary Industries and Regional Development (DPIRD) (project led by Dr. Hamish Malcolm and Prof. Stephen Smith). Preliminary results suggest that turban snail populations may be depleted at some locations which are accessible and are subjected to heavy recreational harvesting pressure (Malcolm et al., unpublished data). Intertidal recreational harvest may be higher in subtropical populations (e.g., SIMP) due to the influx of transient agricultural workers (i.e., pickers from Asia and the Pacific) who may commonly supplement their protein from ocean resources (pers. comm. Prof Stephen Smith). During the fieldwork, groups of harvesters were often observed on rocky shores; given the per-person bag limit (20 snails), the presence of multiple harvesters has the potential to rapidly deplete local populations (Cooling & Smith, 2015).

1.3 Fisheries management and research inputs

Increasing demands on marine resources, and the ongoing and projected impacts of climate change highlight the growing need for conservation and sustainable management of marine species. Sustainable fisheries management aims to manage harvests, protect habitats and ensure resources can be utilized into the future (Henry & Jarne, 2007). Management tools can be categorised into input and output controls that specify how, where and when fishing can occur (Bellido et al., 2020). Input controls, such as licencing, gear specifications and spatial and temporal protection measures (i.e., sanctuary zones or closed fishing seasons) conserve stock by limiting the fishing effort (Pope, 2002; Henry & Lyle, 2003; Bellido et al., 2020). Input controls have the advantages of being implemented prior to fishing activity and are simple to quantify (Bellido et al., 2020). Output controls regulate the outgoings of a fishery by setting limits on the size or amount taken from a resource by implementing size limits, bag limits and total allowable catch (Pope, 2002; Henry & Lyle, 2003; Bellido et al., 2020). Regulatory measures for Australian turban snails vary by state fishery; these include size and bag limits, spatial measures, licencing and commercial zoning, and total allowable catch (Table 1.1).

1.3.1 Input controls

Licencing is a common input control implemented in most fisheries in Australia (Table 1.1). Commercial licencing is mandatory for all commercial turban snail fisheries in Australia (Table 1.1), with a restricted number of licences limiting harvest by controlling the number of permitted operators within the fishery. In Australia, the SUTS fishery is limited to 37 operators; many licence holders also hold endorsements in other fisheries (NSW DPI, 2018b). Licencing is also common in recreational fisheries, where fishers (excluding pensioners, children and First Nations People) must hold a paid licence to legally collect any animals (Table 1.1). Yet recreational licence fees are small, are uncapped on number of fishers, and catch reporting is not required. Recreational fishing may substantially impact stock as effort is difficult to define or regulate.

Table 1.1. Australian turbinid fisheries and management regulations.

State	Fishery	Species	Regulations	Source
New South Wales	Sea Urchin Turban Snail Fishery (commercial)	*Turbo militaris* *Lunella torquata* *Lunella undulata*	Limited commercial licences Spatial closures through marine park zoning, aquatic reserves and commercial exclusion zones Size limit: minimum 75 mm shell width	(NSW DPI, 2018b)
	Recreational	*Turbo militaris* *Lunella torquata* *Lunella undulata*	Mandatory recreational fishing license Spatial closures through marine park zoning and aquatic reserves Size limit: minimum 75 mm shell width (*T. militaris* and *L. undulata*) Bag limit: 20 individuals	(NSW DPI, 2023)
Victoria	Recreational	*Lunella torquata* *Lunella undulata*	Mandatory recreational fishing license Spatial closures through Marine National Parks and Sanctuaries Habitat closure, prohibiting collecting invertebrates on intertidal reefs Bag limit: 5L of whole combined molluscs Bag limit: 1L of shucked combined molluscs	(The State of Victoria, 2024)
Tasmania	Periwinkle Fishery of Tasmania (commercial)	*Lunella undulata*	Commercial licencing Commercial zones and total allowable catch Size limit: minimum 45 mm shell width	(Tasmanian Government)

	Recreational	*Lunella undulata*	Mandatory recreational sea fishing license Spatial closures through marine reserves Size limit: minimum 45 mm shell width Bag limit: 100 individuals	(Tasmanian Government)
South Australia	South Australia Miscellaneous Fishery (commercial)	*Lunella torquata* *Lunella undulata*	Limited commercial licences Spatial closures through marine park zoning and aquatic reserves Individual fisher total allowable catch Fishing method restricted to diving	(PIRSA, 2017)
	Recreational	*Lunella torquata* *Lunella undulata*	Habitat closure, prohibiting collecting invertebrates on intertidal reefs	(PIRSA, 2018)
Queensland	Recreational	*Turbo marmoratus* *Turbo militaris*	Spatial closures through marine park zoning and no-take zones Size limit: 280g (*T. marmoratus*) Bag limit: 20 individuals (*T. marmoratus*) Bag limit: 30 individuals (combined molluscs and gastropods)	(The State of Queensland, 2024)

Spatial management is commonly used in the marine estate to manage fisheries (Gill et al., 2024). Marine reserves provide conservation outcomes through refuge areas, which promote ecosystem health, protect biomass, and enhance species diversity, abundance and size (Lester et al., 2009; Gill et al., 2024). Spatial measures are common in Australia and are achieved through marine park zoning and aquatic reserves, providing sanctuary or no-take zones where all collecting is prohibited (Table 1.1). Spatial protection measures are an effective means to safeguard populations of benthic invertebrates such as turban snails from harvesting, where greater abundances can be found in sanctuary zones (pers. comm. Dr. Hamish Malcolm; Pulfrich & Branch, 2002). Commercial fishing zones allow commercial harvesting in permitted areas (Table 1.1). Spatial management creates a network of areas where activities are prohibited and collecting and type of fishing gear is regulated, providing access to stakeholders and refuge for biota (Leiva & Castilla, 2002; Rowling et al., 2010; NSW DPI, 2018c).

Temporal management stipulates the timing of the year in which fishing can and cannot occur, which involves closed and open harvesting seasons. Seasonal closures can be designed to protect adults from harvesting during their reproductive spawning season (Chang, 2002 as cited in Lee et al, 2014; Ward & Davis, 2002; Martone & Micheli, 2012). Seasonal closures are uncommon in turbinid fisheries, and there are no seasonal closures for turban snail fisheries in Australia. Temporal regulations occur in *M. undosa* fisheries in Mexico (Gluyas-Millán et al., 1999; Martone & Micheli, 2012; SPC, 2022) and *T. marmoratus* fisheries in French Polynesia (SPC, 2022); however, the suitability or effectiveness of these management regimes is not documented. Seasonal closures for harvesting *T. cornutus* are designed to protect the population during their spawning season (Chang, 2002 as cited in Lee et al, 2014). However, seasonal closures for *T. cornutus* may offer disparate protection across the fishery as the timing of spawning has since been shown to be asynchronous among locations (Lee et al., 2014).

1.3.2 Output controls

Catch limits are designed to support sustainable fishing strategies (Gluyas-Millán et al., 1999). Bag limits refer to the number of animals one person is legally allowed to collect daily. Bag limits may offer benefits to slow moving animals, such as turban snails, due to their potential limited capability for adults to replenish heavily harvested areas. Individual bag limits are a common output control in non-commercial turbinid fisheries (Bruton et al., 1991; Cooling & Smith, 2015; NSW DPI, 2018a) (Table 1.1). In commercial fisheries, total allowable catch for operators or the entire fishery is common, such as for *T. marmoratus* (Andréfouët et al., 2014) and *M. undosa* (Martone & Micheli, 2012) and some Australian fisheries (Table 1.1).

Size limits are a common output control in fisheries management, that specify the minimum or maximum legal size that animals can be collected. Individuals must be measured before collection to comply with regulations. In some fisheries, measurement devices are freely available (Figure 1.3). Minimum size limits aim to ensure that animals have had the chance to reproduce before being collected, whereas maximum size limits aim to enhance a population's breeding potential by protecting highly fecund larger individuals. In turban snail fisheries, maximum size limits are not typical and are only regulated for the large green snail, *T. marmoratus,* maximum size limits apply in some locations (SPC, 2022). Minimum size limits are much more common in turbinid fisheries (Nayar & Appukuttan, 1983; Bruton et al., 1991; Gluyas-Millán et al., 1999; Pulfrich & Branch, 2002; Andréfouët et al., 2014; NSW DPI, 2018a). Minimum size limits are compulsory for Australian turban snail fisheries, *T. militaris* and *L. torquata* in NSW, *L. undulata* in Tasmania and *T. marmoratus* in Queensland (Table 1.1).

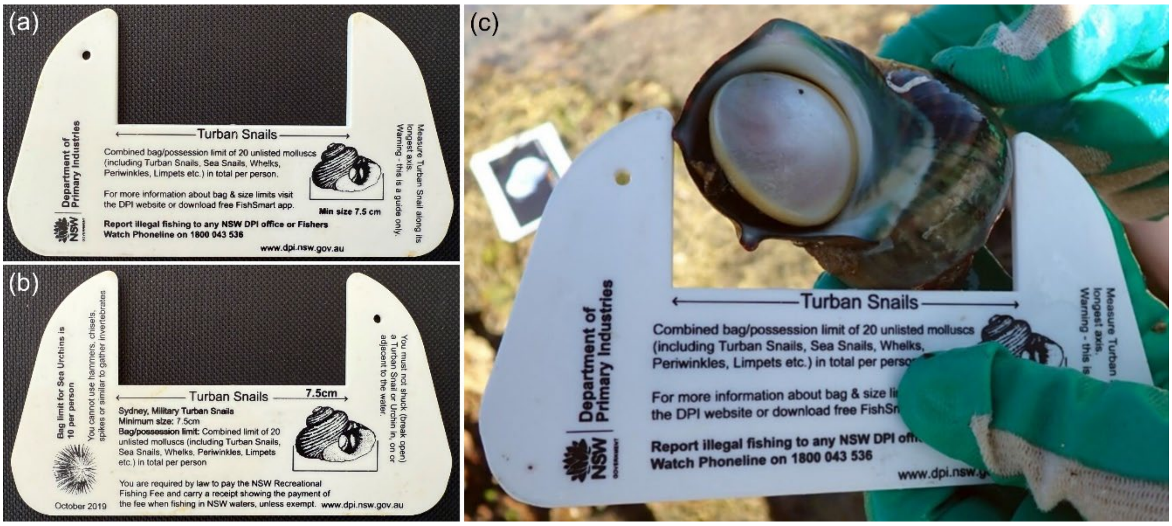


Figure 1.3. A turban snail legal length measuring device from New South Wales, Department of Primary Industries and Regional Development (photos: Professor Stephen D. A. Smith) (a, b). Snails must not be able to pass through the gap to be legally collected. An individual of *Turbo militaris* measured with the measuring device (c). Note: The

presence of a spine, a morphological trait of some turban snails, results in this individual being of legal size.

1.3.3 Knowledge to inform effective management

Knowledge on a target species is pivotal for building population models, comprehensive assessments of harvested stocks and guiding informed decision-making to effectively manage harvested species (Henry & Lyle, 2003; Anderson et al., 2011; NSW DPI, 2021). Essential information includes a sound understanding of the target species' functional biology and ecology (Leiva & Castilla, 2002; FAO, 2024), including reproductive biology and periodicity, size at maturity, fecundity, age and growth, and aspects of species ecology (Perry et al., 1999; Leiva & Castilla, 2002; Henry & Lyle, 2003; Martone & Micheli, 2012; FAO, 2020; NSW DPI, 2021). Consideration of the variability in life-history traits over spatial and temporal gradients is essential for the evaluation and refinement of management regulations across geographical ranges. This will help ensure that management regulations are not misinformed across broader scale fisheries (Martone & Micheli, 2012; Lee et al., 2014). Furthermore, this information is important in understanding the potential impacts of future climate change on fisheries, such as fisheries resilience, distributional shifts and ecological changes.

Understanding the population dynamics and standing stock of harvested populations is vital for fisheries management (Lasiak, 1991; Smith et al., 2006; Cooling & Smith, 2015). The lack of this information makes total allowable catch and zoning planning challenging to define (Pulfrich & Branch, 2002). Ecological knowledge, such as species habitat preferences, movements and population connectivity, is important for designing spatial protection measures, such as sanctuary zones (Smoothey, 2013). Understanding species ecology is especially relevant for species harvested on rocky shores, as cross-shore connectivity of adult populations may facilitate replenishment of harvested stocks from adjacent unfished populations (Bruton et al., 1991; Proudfoot, 2006; Keane et al., 2014; Cooling & Smith, 2015).

Information on life-history provides essential knowledge underpinning management regulations to promote sustainability (Ponder et al., 2020). Reproductive seasonality of the target species may inform seasonal closures, as these can be implemented on the basis of protecting adults during peak spawning seasons (Chang, 2002 as cited in Lee et al., 2014;

Martone & Micheli, 2012). Knowledge of reproductive biology can provide information for size and bag limits by identifying recruitment and stock replenishment potentials (Leiva & Castilla, 2002; DCCEEW, 2018b). Biologically appropriate size limits are based on information on the size at sexual maturity, fecundity and reproductive seasonality (Devambes, 1961; Martone & Micheli, 2012; DCCEEW, 2018b). Suitable limits should allow individuals to reproduce at least once or twice before entering the fishery (Keane et al., 2014). Research on growth rate, age and longevity can informs fisheries management strategies (such as bag limits) because they provide insights for estimating maximum sustainable yield (Bourgeois et al., 1997; Pulfrich & Branch, 2002; Ramesh et al., 2010; Andréfouët et al., 2014).

Fisheries regulations should be based on adequate scientific data, to guide decision-making (Cochrane, 2002; Bellido et al., 2020). However, scientific studies may be deficient for small-scale invertebrate fisheries where research attention is limited (Rousseau et al., 2019). Studies on turbinids date back over 40 years. However, there are still considerable gaps in our knowledge of this family, especially in small-scale or remote fisheries (Bruton et al., 1991; Holguin Quiñones & Michel-Morfin, 2006; Proudfoot et al., 2006), and basic information about many turbinid species is limited in the scientific literature (Table 1.2). These knowledge gaps highlight the need for relevant research to support the sustainable management of turbinid fisheries. For stocks that lack relevant information, a conservative approach to fisheries management should be adopted to prevent overexploitation until stocks can be fully assessed and management practices better informed.

Table 1.2. The number of papers based on searches in the Web of Science (Clarivate Analytics, 2024) database using “Turbinidae” and “turban snail” and the listed search terms. The total number of papers listed for Turbinidae were screened to represent the number of studies for each listed species. An asterisk indicates a truncation search operator.

		Turbo							***Lunella***				***Megastraea***
	Turbinidae	*Turbo militaris*	*Turbo cornutus*	*Turbo sarmaticus*	*Turbo funiculosus*	*Turbo marmoratus*	*Turbo sazae*	*Turbo setosus*	*Lunella torquata*	*Lunella undulata*	*Lunella smaragda*	*Lunella coronata*	*Megastraea undosa*
fisheries management	**65**	3	4	3	1	1			3	1		3	7
climate change	**15**	3		1			2			2			
population dynamics	**36**	1	3	1	1				2	2		2	4
reprod* OR spawning OR fecundity	**43**	3	1	3		2			4	2	1	2	5
life-history OR larval OR maturity	**35**	1	4	1					2		1	1	3
movement OR mobility OR displacement	**14**	1	1							1		1	1
growth OR age	**71**	1	4	1			1	1	5	3			6
habitat OR macroalgae OR herbivor*	**84**	1	6	5		1	2		4	3		3	4

1.4 Biology and ecology of turban snails

1.4.1 Taxonomy and diversity

Gastropods are among the most speciose class of the phylum Mollusca, occurring across terrestrial, freshwater and marine habitats (Kay et al., 1998). Gastropods from the order Trochida occur in a large array of marine environments; in Australia, they are a dominant component of rocky shores assemblages (Hickman, 1998). Turban snails are herbivorous gastropods from the family Turbinidae (Figure 1.4). Turban snails are found worldwide, currently with, 274 accepted species from 25 genera (WoRMS Editorial Board, 2024). Snails from the family Turbinidae can be found at various latitudes and depths worldwide but are highly diverse throughout shallow subtropical and warm-temperate waters (Beechey, 2005). Turban snails of the genus *Turbo* occur primarily in warm waters (Figure 1.1), confined to more tropical locations than other genera (Reeve, 1848).

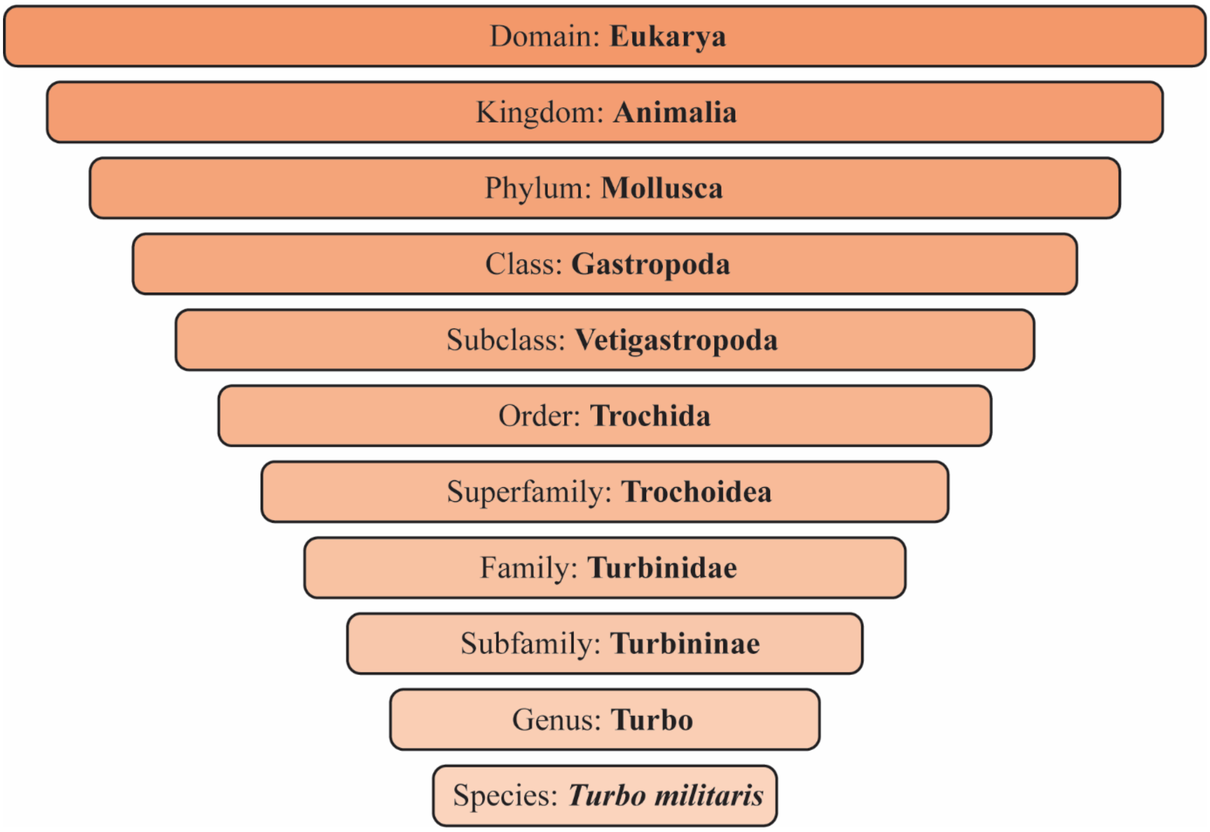


Figure 1.4. Taxonomic diagram for the turban snail *Turbo militaris*.

1.4.2 Morphology

Turban snails have a hard shell that supports and protects the soft-bodied animal. The shells are turbinate or helicoid where whorls are laid down successively around a central columella (Figure 1.5) (Reeve, 1848). The hard shell is secreted from the mantle epithelium and calcium glands in calcium carbonate layers as aragonite or calcite (Kay et al., 1998). The inside of the shell is a pearly nacre, which is often quite iridescent (Reeve, 1848). An organic layer, the periostracum, is generally present, which provides an outer layer of the shell (Kay et al., 1998). In some species, the shell has protuberances as bumps or spines. The protuberances of *T. coronatus* vary between localities due to either intragenerational selection or phenotypic plasticity, most likely the latter (Kurihara et al., 2006).

Turban snails possess a markedly calcified operculum attached to the opercula disc dorsally located on the foot (Fretter et al., 1998). The operculum sits inside the shell when the animal is emerged, and when the animal retracts into the shell, the operculum seals the aperture closed (the shell opening) (Fretter et al., 1998) (Figure 1.5). The operculum is secreted by the opercular lobe and grows simultaneously with the shell. There are different operculum forms in Turbinidae, specific to different species; the coiling patterns are usually multispiral or paucispiral, the shape is usually oval to almost circular, and the surface ranges from smooth to strongly sculptured (Reeve, 1848; Weidland et al., 1998).

Gastropods are asymmetrical and generally whorl in a dextral spiral (right-handed or clockwise as seen from the apex) (Kay et al., 1998). Internal anatomical features can be grouped into the lower foot and the higher visceral mass (Figure 1.5). The lower part protrudes when the animal emerges from the shell and interacts with the environment for feeding and locomotion (Fretter et al., 1998; Kay et al., 1998). The strong muscular foot is used to attach the animal to the substrate and undulates for forward movement. The lower part also comprises the head, which houses the feeding and sensory organs, including the eyes, cephalic tentacles, mantle papillae and snout with a mouth and a radula, a toothed muscular structure used for feeding (Fretter et al., 1998; Hickman, 1998; Kay et al., 1998).

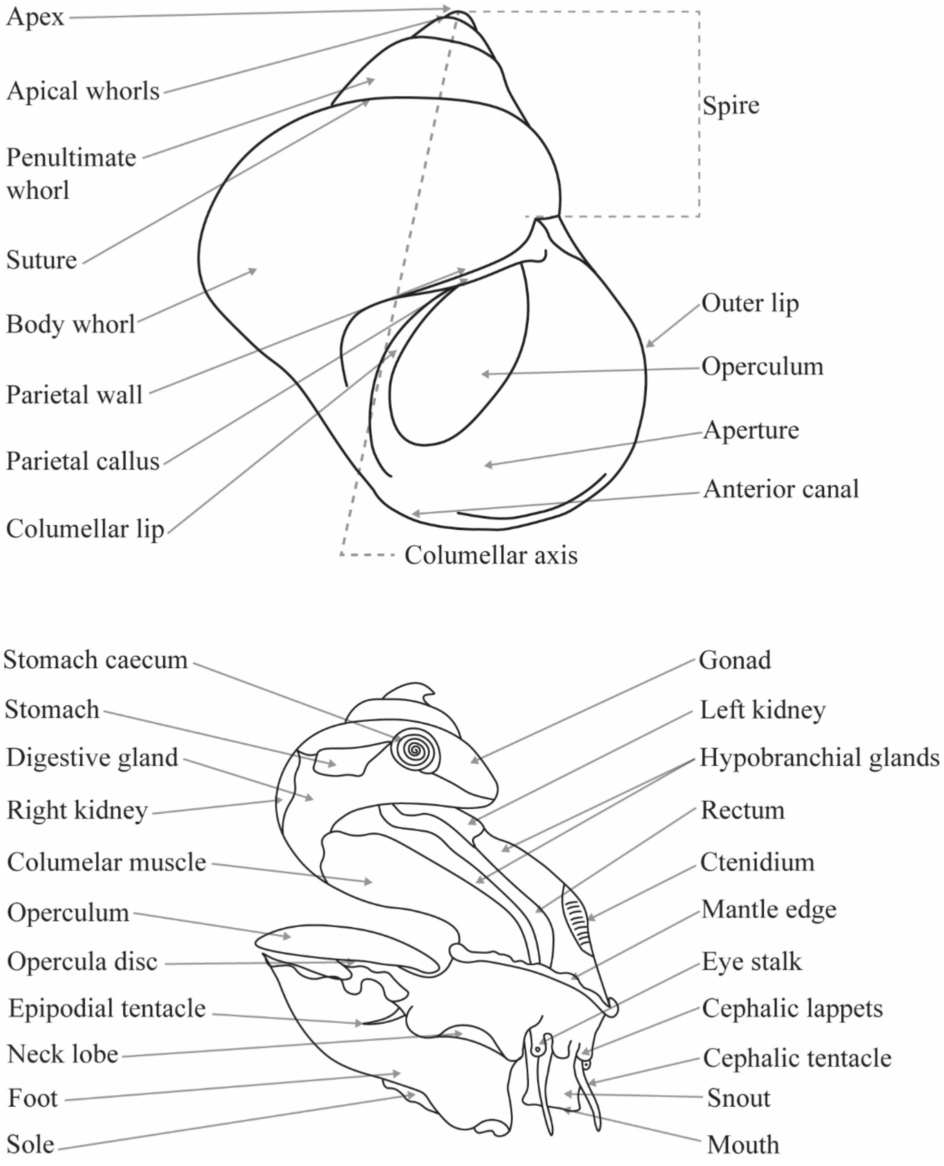


Figure 1.5. External and internal anatomy of a turban snail, reflective of *Turbo militaris*. Internal anatomy adapted from Fretter et al. (1998) and Hickman (1998); some organs are not illustrated.

A strong columellar muscle attaches the animal to the shell columella, which contracts to move, emerge, and retract the animal (Fretter et al., 1998). The visceral mass bears the columellar muscle and the internal organs responsible for digestion, reproduction and circulation (Kay et al., 1998). The mantle cavity contains the ctentidium (feather-like gills), osphradium (a sensory organ to detect water chemical changes), a central contractile heart, kidneys, stomach organs, rectum, mucous-producing hypobranchial gland, and a central nervous system encompassing five brain structures (Fretter et al., 1998; Kay et al., 1998).

Prosobranch gastropods are primarily dioecious, possessing a single gonad which is closely associated with the digestive gland and fills most of the coils from the penultimate whorl to the apex (Fretter et al., 1998; Kay et al., 1998).

1.4.3 Life-history

Turbinids undergo continuous gametogenesis with peak spawning events and vitellogenesis shortly after spawning (Underwood, 1974; Joll, 1980; Lasiak, 1986; Hickman, 1998; Ward & Davis, 2002). Spawning in turbinids occurs with a broadcast strategy and external fertilisation (Grange, 1976a; Komatsu et al., 1995; Fretter et al., 1998). The larvae are generally lecithotrophic with a short planktonic period of three to five days (Grange, 1976a; Andréfouët et al., 2014) and some up to 10 days (Lasiak, 1986; Salas-Garza et al., 2009). Reproductive fecundity has not been widely reported for turbinids, and there is no research on the reproductive potential of any Australian species. Research from other countries indicates that larger turbinids are more highly fecund than smaller species, and fecundity is positively correlated with animal size (within species) (Komatsu et al., 1995; Ramesh et al., 2010; Martone & Micheli, 2012).

Spawning seasonality and duration are diverse, occurring over short periods or extended seasons, most turbinids have a cycle of annual reproduction (Lasiak, 1986; Komatsu et al., 1995; Lee, 2000; Matoto et al., 2002; Guzmán Del Próo et al., 2003; Salas-Garza et al., 2009; Ramesh et al., 2010; Afsar et al., 2013). However, some turbinids spawn over multiple annual events (Underwood, 1974; Kay et al., 1998). Australian turbinids *L. undulata, L. torquata* and *T. intercostalis* exhibit multiple, close events or a prolonged breeding season with peak activity generally in the warmer months (Underwood, 1974; Joll, 1980; Ab Lah et al., 2019). However, *L. torquata* has also been shown to spawn twice a year, in autumn to winter and spring to summer in southern NSW, with asynchronous events between spatially separate populations (Ward & Davis, 2002). Until now, there have been no studies on reproduction in the key Australian fisheries species, *T. militaris.*

Size at sexual maturity in turbinids is generally greater in larger species. Larger turbinids generally reach maturity around just under half their maximum size (Yamaguchi, 1988; Lasiak, 1991; Martone & Micheli, 2012; Andréfouët et al., 2014). For Australian turbinids, *L. torquata* and *T. intercostalis* gonad development was observed at shell heights between 15 mm and 22 mm (Joll, 1980). This size is similar to maturity in the medium sized New

Zealand species, *L. smaragda* which reach maturity as small as 15 mm shell diameter (Walsby, 1977). The smaller South African species, *T. brunneus* reached maturity at a size between 23 mm and 27 mm, which is similar to the smaller Australian turbinid *L. undulata*. Sexual maturity in *L. undulata* was reached at shell heights between 23 mm and 32 mm in Tasmania, where snails at lower latitudes had a smaller size at maturity than those in the cooler waters of higher latitudes (Keane et al., 2014). In contrast, for the northern hemisphere species, *M. undosa* (in Mexico), females reached sexual maturity at a smaller size in higher latitudes than those in warmer lower latitudes (Martone & Micheli, 2012).

Turbinids are long-lived with a moderate to fast growth rate (Bruton et al., 1991; McClanahan, 2002). Turban snails have a logarithmic growth pattern, where smaller individuals have faster growth and obtain a greater yearly growth increment than larger individuals (Bruton et al., 1991; Ramesh et al., 2009; Keane et al., 2014). The growth of Australian turbinids has been the focus of a limited number of studies (Keane et al., 2014; Kienzle et al., 2022) and, until now, none have considered growth in *T. militaris*. For the Australian species, *L. undulata*, growth rate varied over latitudinally separate populations in Tasmania, where growth was faster at higher latitudes, and snails had a greater maximum size (Keane et al., 2014). Spatial variability in growth may be due to algal productivity; for example, the subtropical species *M. undosa* (in Mexico) has a higher growth rate in upwelling areas, compared to less productive areas (Martone & Micheli, 2012).

1.4.4 Distribution and ecology

Turban snails are exclusively marine (Hickman, 1998). The highest diversity of turban snails occurs in shallow subtropical and temperate waters (Hickman, 1998), but they can be found in various latitudes and depths worldwide (Beechey, 2005). Turbinids mainly inhabit rocky shores and shallow subtidal waters (Bruton et al., 1991; Holguin Quiñones & Michel-Morfin, 2006; Proudfoot, 2006) and are often highly abundant in the intertidal zone (Pulfrich & Branch, 2002; pers. obs.). Australian turbinids are common in the lower littoral zone and shallow subtidal waters (Worthington & Fairweather, 1989; Hickman, 1998; Ettinger-Epstein & Kingsford, 2008; Smoothey, 2013).

The distribution of turban snails can be patchy as they are often restricted by the presence of suitable habitat (Smoothey, 2013). Turban snails prefer reefs with consolidated benthos and high habitat complexity, with the presence of cracks, holes and crevices important for shelter (Ettinger-Epstein & Kingsford, 2008; Wernberg et al., 2008; Smoothey, 2013). Turban snails tend not to be found in barren or sandy regions or areas with low complexity (Ettinger-Epstein & Kingsford, 2008; Smoothey, 2013). Australian turbinids are closely associated with biogenically structured habitats (Wernberg et al., 2008; Smoothey, 2013). As generalist herbivores, they are found in areas with a high abundance of algae, such as crustose coralline algae, turfing algae, green algae (including *Ulva* spp.) and canopy-forming algae, such as *Ecklonia radiata* or *Sargassum* spp. (Worthington & Fairweather, 1989; Wernberg et al., 2008; Smoothey, 2013). The preferred habitat of *T. militaris* includes structures formed by aggregations of the polychaete worm *Idanthyrsus pennatus* (Cooling & Smith, 2015), the solitary ascidian, *Pyura stolonifera* or the brown alga, *Hormosira banksii* (pers. obs.).

As turbinids occur across intertidal and subtidal habitats, movement between zones could be important in buffering harvested stocks in the intertidal zone (Walsby, 1977; Lasiak, 1991; Cooling & Smith, 2015; Hayakawa et al., 2018) assuming the animals can readily move between the zones. A study on *L. smaragda* assessed movements through monthly population assessments and found that vertical (especially down-shore) movement was much greater than lateral movements (Walsby, 1977). However, the connection between intertidal and subtidal populations of turbinids is not well understood.

In turbinids, a high degree of connectivity is facilitated by the larval phase, connecting distant populations and promoting genetic connectivity (Nimbs et al., 2023). Adult turban snails are less mobile (Ettinger-Epstein & Kingsford, 2008; Yeo et al., 2024), with locomotion facilitated by the muscular contraction of the foot in waves (Fretter et al., 1998; Kay et al., 1998). Gastropods in the order Trochida are generally negatively phototactic, primarily active at night and sheltering during the daytime (Fretter et al., 1998). In a thermal tolerance laboratory study, *L. undulata* and *T. militaris* demonstrated higher activity at night and movements restricted to a preferred thermal range (Ab Lah et al., 2017a). Movements have been shown to be mediated by size for some turban snails, where larger sized *L. torquata* have greater movements than smaller individuals (Ettinger-Epstein & Kingsford, 2008). Furthermore, larger individuals of *L. smaragda* and *M. undosa* move down-shore and tend to occupy deeper waters than smaller snails (Walsby, 1977; Taniguchi & Rogers-Bennett, 2001). In contrast, smaller individuals of *L. undulata*, *L. torquata* and *T. cornutus* tend to remain in sheltered habitats and have lower mobility (Worthington & Fairweather, 1989; Smoothey, 2013; Hayakawa et al., 2018).

Turbinids are a conspicuous component of reef platforms, often clustering and occurring in high densities (Holguin Quiñones & Michel-Morfin, 2006; Wernberg et al., 2008). They are among the most abundant herbivores on Australian intertidal lower rocky shores, and consequently are expected to influence community structure (Hickman, 1998; Wernberg et al., 2008). Turbinids are an important prey food source for predatory sea snails (i.e., whelks – *Dicathais orbita*), sea turtles, large fish and octopus (Hickman, 1998; SPC & LMMA Network, 2021). As generalist, opportunistic herbivores that often occur in high densities, turban snails can play a functional role in their ecosystems by facilitating nutrient flow (Worthington & Fairweather, 1989; Hickman, 1998; Wernberg et al., 2008). Heavy grazing has a top-down influence on algal cover and, depending on density and rate of grazing, can substantially influence the abundance and distribution of macroalgae (Worthington & Fairweather, 1989; Wernberg et al., 2008; Martone & Micheli, 2012). Additionally, turban snails can be useful in research as indicators of ecosystem health, environmental change, and as bio-accumulators of environmental trace elements (Ab Lah et al., 2018).

1.5 The study species: *Turbo militaris*

Turbo militaris (Reeve, 1848) is a large turbinid gastropod (Family: Turbinidae). *Turbo militaris* can attain large sizes of up to 130 mm shell height (pers. obs.). The shell has a ventricose shape (bulging in the lower region of the shell) with smooth whorls that slant around the spire and is imperforated (closed umbilicus) (Reeve, 1848). The external shell is a faun colour with a distinct pattern of maroon lines and blotches (Figure 1.6a); the columella edge exhibits a blue-grey colour, and the interior is nacreous (Reeve, 1848). The shell is often encrusted with epifaunal growth from crustose coralline algae, turfing algae or polychaete worms. The morphology of the shell ranges from smooth to spiny; the extent of protuberances ranges from incipient bumps to prominent open-fronted spines (Figure 1.6b). An individual can have up to five rows of spines, and individuals of any size can exhibit any number or extent of spines (Smith et al., 2007). The calcified operculum of *T. militaris* is round and smooth, with a paucispiral formation and an eccentric nucleus (Figure 1.6c).

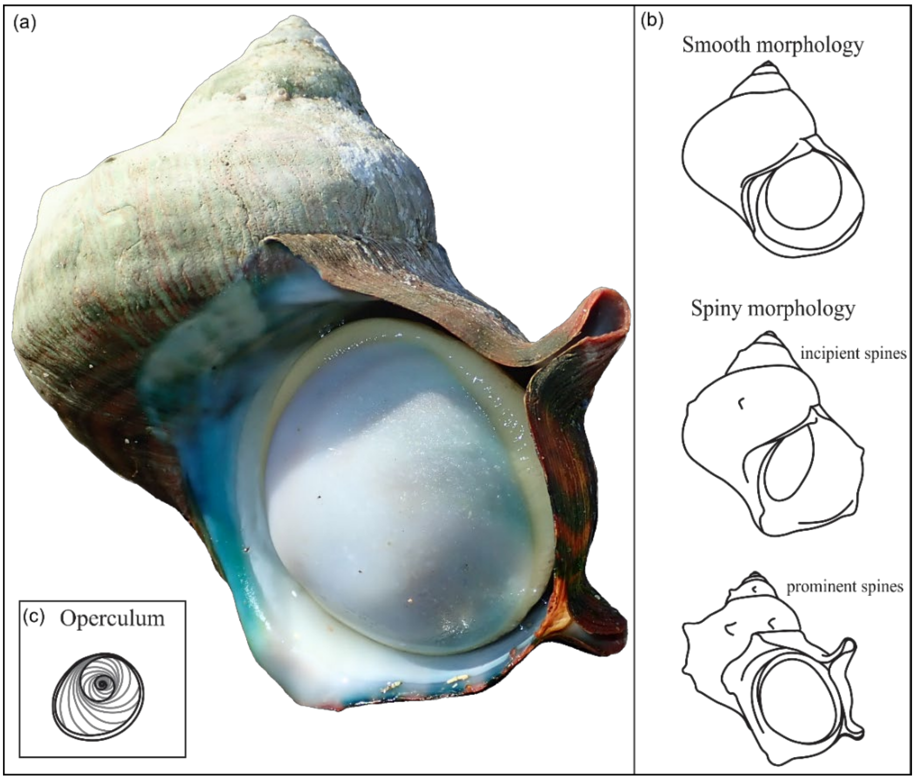


Figure 1.6. Illustration of *Turbo militaris* (a), shell morphology (smooth and spiny) (b), and operculum (depicted from the underside) (c).

Turbo militaris is endemic to the east coast of Australia, inhabiting the eulittoral and infralittoral zones on rocky shores and shallow rocky reefs up to around 20 m water depth. The current distribution of *T. militaris* extends across approximately 8° of latitude from southern Queensland to southern NSW (Beechey, 2005; Atlas of Living Australia, 2023; GBIF.org, 2025; iNaturalist, 2025) (Figure 1.7). Over the last few decades, *T. militaris* has undergone a poleward range extension over the last several decades (Beechey, 2005; Atlas of Living Australia, 2023; Nimbs et al., 2023) (Figure 1.7). Prior to the 1970s, *T. militaris* was common in northern NSW but sparse around Sydney (33.8° S) (pers. comm. Dr. Phil Coleman). By the early 2000s, *T. militaris* was described as common around Sydney, with some sightings as far south as Wollongong (34.4° S) (Beechey, 2005). Currently, *T. militaris* is common around Sydney (pers. comm. Dr. Gary Hamer) and on the NSW south coast as far as Jervis Bay (35.2° S) (pers. comm. Dr. Nathan Knott and Dr. Jeremy Day). Further on the south coast, *T. militaris* are rare (GBIF.org, 2025), with the southernmost sighting of one individual in Guerilla Bay in 2011 (35.8° S) (iNaturalist, 2025).

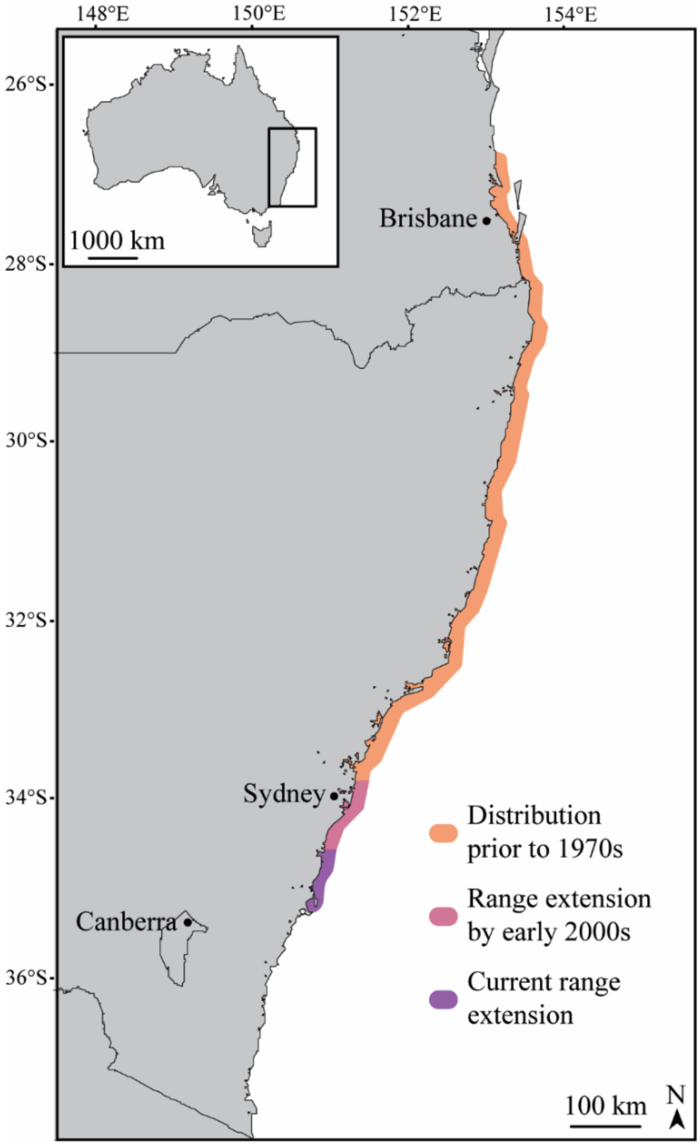


Figure 1.7. Distribution of *Turbo militaris* from southern Queensland to southern New South Wales. Shading denotes approximate distribution and poleward range extension.

The warm poleward flowing East Australian Current (EAC) strongly influences oceanographic conditions and coastal ecosystems along Australia's east coast (Ridgway & Hill, 2014; Pattiaratchi & Siji, 2020; Phillips et al., 2022). The EAC has strengthened and extended poleward over the last several decades and is predicted to intensify in future climate conditions (Ridgway & Hill, 2014). Thus, the Australian south-east coast is considered a global warming hotspot (Hobday & Pecl, 2013). The preferred water temperature of *T. militaris* is 22 °C (Ab Lah et al., 2017a), which is expected to be increasingly exceeded within its range on the east coast of Australia. Thus, *T. militaris* is an example of a species impacted by climate change (Ab Lah et al., 2017a).

1.6 Thesis aims and structure

1.6.1 Rationale

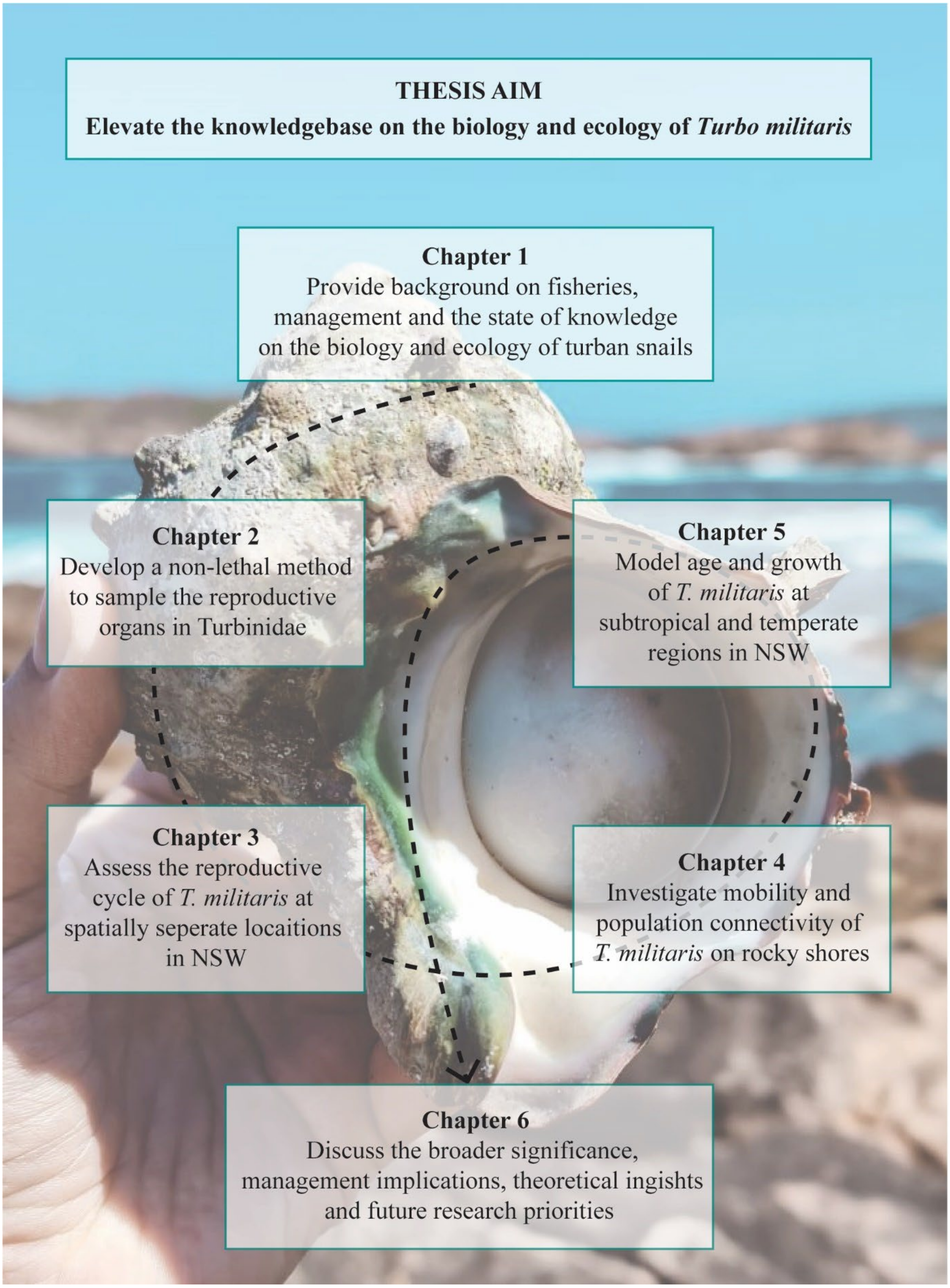
Despite the importance of turbinids traditionally, environmentally, and as fisheries resources, they have been the focus of very little scientific research to date, especially life-history studies (Table 1.2). Of the harvested Australian turbinids, *T. militaris* is highly targeted due to its large size, often accessible habitat, ease of collection and quality for human consumption (Ab Lah et al., 2017b), yet is one of the least represented throughout the literature. Studies on *T. militaris* are limited to genomics (Nimbs et al., 2023), thermal tolerance (Ab Lah et al., 2017a; Mamo et al., 2019), nutritional quality (Ab Lah et al., 2017b; Ab Lah et al., 2018), regional population characteristics and harvesting impacts (in the Solitary Islands Marine Park) (Mohring, 2007; Cooling & Smith, 2015). However, critical knowledge gaps remain including an understanding of reproduction, maturity, growth, longevity and movements. The limited information to inform sustainable management, the potential for overharvesting and the cultural and fisheries significance of *T. militaris* provides a strong rationale for this research.

1.6.2 Aim

This thesis aims to address current knowledge gaps on the biology and ecology of the recreationally, commercially, and culturally harvested turban snail, *T. militaris* (Figure 1.8). Specifically, this work aims to provide empirical data on reproduction, mobility, age and growth and size at maturity. Given that the fishery spans over 8° of latitude in a climate change hotspot, this research aims to offer insights into the spatial variability in life-history traits for turbinids over latitudinally separate locations. Overall, this thesis aims to elevate our knowledge of *T. militaris* and provide information that could inform effective fisheries management decisions and facilitate the transition of this species from data-deficient to scientifically managed.

1.6.3 Structure

The thesis consists of an introductory chapter, four data chapters and a general discussion chapter (Figure 1.8). The overarching aim will be addressed through the aims and objectives of each chapter.



THESIS AIM
Elevate the knowledgebase on the biology and ecology of *Turbo militaris*

Chapter 1
Provide background on fisheries, management and the state of knowledge on the biology and ecology of turban snails

Chapter 2
Develop a non-lethal method to sample the reproductive organs in Turbinidae

Chapter 3
Assess the reproductive cycle of *T. militaris* at spatially seperate locaitions in NSW

Chapter 4
Investigate mobility and population connectivity of *T. militaris* on rocky shores

Chapter 5
Model age and growth of *T. militaris* at subtropical and temperate regions in NSW

Chapter 6
Discuss the broader significance, management implications, theoretical ingights and future research priorities

Figure 1.8. Conceptual diagram outlining the aims and structure of the thesis: Fishery biology and ecology of the marine snail, *Turbo militaris*.

Chapter 1: *Introduction*

Chapter 1 aims to outline the knowledge gaps and provide a rationale for the research. The objectives of Chapter 1 are to provide background information on turbinid fisheries, common and current management regulations in turbinid fisheries and the kinds of information required for building effective management strategies; review the current state of knowledge on the biology and ecology of turban snails; and provide background information on the study species.

Chapter 2: *Data chapter: Shell drilling and gonad biopsies provide a rapid, non-lethal method for in-situ assessment of reproductive periodicity in a turbinid gastropod*

Chapter 2 aims to develop and test a method for non-lethal sampling of the reproductive organs in turban snails with the goal of applying this to study reproductive periodicity in *T. militaris.* The objectives of Chapter 2 are to: develop a shell drilling and gonad biopsy method; validate the method as non-lethal in the laboratory; optimise the placement of the biopsy; develop a technique for storing oocytes for applicability in the field; and trial the technique on *T. militaris* in the field.

Chapter 3: *Data chapter: Extended and spatially asynchronous reproductive periodicity in a harvested, warm-temperate rocky-reef gastropod (Turbinidae)*

Chapter 3 aims to investigate the reproductive timing of *T. militaris* at spatially separate locations in NSW. The objectives of Chapter 3 are to: apply the non-lethal gonad biopsy method (from Chapter 2) alongside traditional methods of gonadosomatic index to determine spawning timing, comparing the results of the two methods; determine if spawning is synchronous between males and females; determine if reproductive timing is synchronous at two spatially different locations in NSW; and, investigate potential environmental variables driving reproductive periodicity.

Chapter 4: *Data chapter: Long-term mobility of a harvested, rocky-reef gastropod*

Chapter 4 aims to provide insights into the mobility of *T. militaris* and the extent of population connectivity on intertidal rocky shores and shallow reefs in NSW. The objectives of Chapter 4 are to: determine whether *T. militaris* migrates between intertidal and subtidal zones; quantify the extent of population mixing on rocky shores; compare the movement patterns over different locations; and, determine if there are differences in displacement rate, directional movement or elevational change associated with animal size or shell morphology.

Chapter 5: *Data chapter: Spatial variation in age and growth of a harvested, subtropical to warm-temperate marine gastropod*

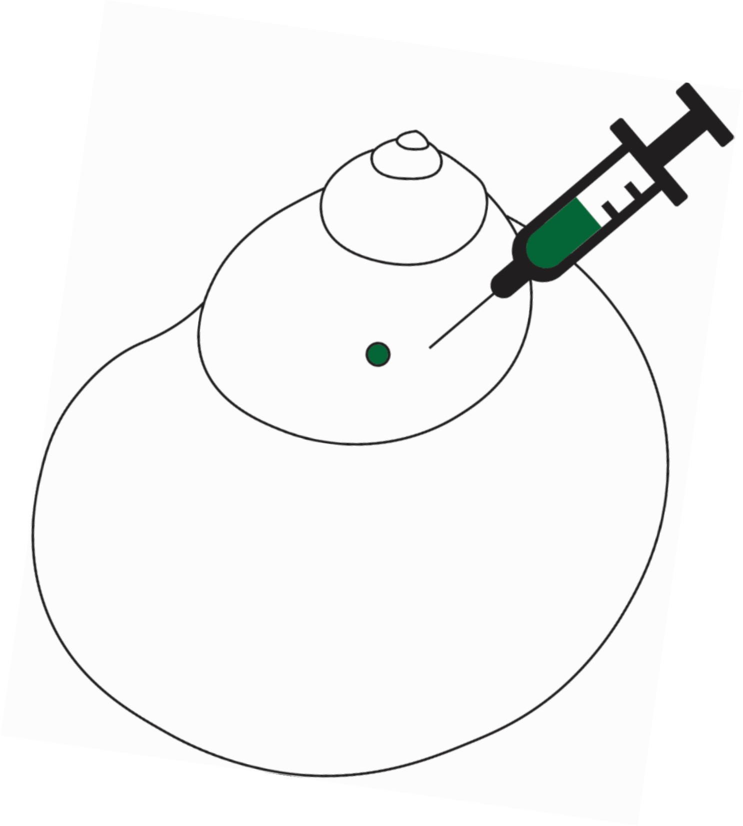
Chapter 5 aims to assess the age and growth of *T. militaris* in subtropical and warm-temperate regions in NSW. The objectives of Chapter 5 are to: assess growth rate across a range of size classes; develop age-and-growth models and make comparisons between subtropical and temperate populations; establish size at sexual maturity and estimate age; determine age at legal harvesting size; and, infer longevity and natural mortality.

Chapter 6: *General Discussion*

Chapter 6 synthesizes the findings from previous data chapters, including latitudinal trends in life-history traits and discusses the broader significance of the project. Chapter 6 connects the research outcomes to fisheries management, provides insights for turban snail fisheries in changing climate conditions and discusses priorities for future research.

CHAPTER 2.

SHELL DRILLING AND GONAD BIOPSIES PROVIDE A RAPID, NON-LETHAL METHOD FOR *IN-SITU* ASSESSMENT OF REPRODUCTIVE PERIODICITY IN A TURBINID GASTROPOD



Chapter 2 has been modified as per university guidelines from the published paper:

Seinor, K., & Benkendorff, K. (2023). Shell drilling and gonad biopsies provide a rapid, non-lethal method for *in-situ* assessment of reproductive periodicity in Turbinidae. *Journal of Molluscan Studies, 89(2)*: e012. doi:10.1093/mollus/eyad012

Abstract

Reproductive data on marine molluscs is imperative for informing conservation and management strategies. Most methods for assessing reproductive periodicity are lethal, which could be unfavourable for fragile populations. This study aimed to trial a non-lethal, drill-biopsy technique for assessing the reproductive cycle in the turbinid gastropod, *Turbo militaris*. This technique was tested in the laboratory, where a small hole was drilled into the shell, from where a biopsy of the gonad was taken. The procedures resulted in zero mortalities and rapid recovery of the animals when returned to seawater. Sex was identified by viewing the gonad colour through the shell hole and confirmed by viewing gametes from a biopsy. Preservation of the female biopsy was investigated, with buffered Formalin found to be the most suitable solution. The drill-biopsy method was also tested in the field; five (out of six) recaptured *T. militaris* had repaired the shell hole after six weeks and two were recaptured on multiple occasions up to the end of this study, 10 months later. The size-frequency distributions of oocytes from female biopsies suggested an increase in mode size over two months with a shift towards a higher number of larger oocytes, supporting the practicality of this non-lethal approach to evaluate reproductive periodicity and sex determination. Non-lethal sampling is recommended for broad-scale studies and populations under stress; methods, such as the drill-biopsy technique, facilitate reproductive sampling without detriment to the target populations.

2.1 Introduction

Seafood makes an essential contribution to global food security, constituting 20% of the average per capita intake of animal protein for billions of people (Guillen et al., 2019; Hicks et al., 2019). However, the world's ocean resources are under threat due to overexploitation, with over 34% of the global seafood stocks currently overfished (FAO, 2020). Therefore, new sustainable options for under-utilized seafood species need to be considered. Marine gastropods are an increasingly important component to seafood, with many species targeted for commercial wild harvest and aquaculture (Leiva & Castilla, 2002; Anderson et al., 2011; FAO, 2021) (Table 2.1). Turbinids make up ~4.3% of gastropod fisheries (FAO, 2021) and are also produced by aquaculture in the Pacific Islands (Table 2.1) (FAO, 2022). Turbinids are also commonly harvested by recreational fishers on rocky shores and shallow reefs around the world (Pulfrich & Branch, 2002; Martone & Micheli, 2012; Keane et al., 2014; Lee et al., 2014; Cooling & Smith, 2015). This highlights the need to protect and manage stocks.

For effective conservation or fisheries management, a good understanding of the functional biology of the target species is essential (Leiva & Castilla, 2002; FAO, 2020). Research on reproduction is important for understanding a species' life-history, including gametogenesis, parental investment, reproductive periodicity, reproductive synchrony, fecundity, age at maturity, sex ratios and population structure (Hughes, 1986; Ponder et al., 2020). There are significant gaps in knowledge on the reproduction of the many gastropods that are harvested in small-scale commercial fisheries (Table 2.1) or recreationally. Relatively few scientific papers have investigated aspects of Turbinidae reproduction, including the reproductive cycle, spawning or sex determination (Table 2.1). Only six studies have assessed the reproductive cycle or spawning in some turbinids, such as *Lunella torquata*, *L. undulata*, *L. coronata*, *Turbo intercostalis* and *T. sarmaticus* (Table 2.1) (Underwood, 1974; Joll, 1980; Foster, 1997; Ward & Davis, 2002; Afsar et al., 2013; Ab Lah et al., 2019). However, no studies have been done using non-lethal techniques and there is no previous work on the reproductive cycle of the study species, the turban snail *T. militaris* (Reeve, 1848).

Table 2.1. Summary of the main commercially harvested gastropod families.

	Muricidae	Trochidae	Volutidae	Buccinidae	Littorinidae	**Turbinidae**	Strombidae	Haliotidae
No. Species	2,440	1,176	7,87	501	303	**254**	234	106
Fisheries harvest (t)	25,890	45	14,337	702	504	**7,698**	28,775	5,088
% of Fisheries (FAO)	14.3%	0.02%	7.9%	7.0%	0.28%	**4.3%**	15.9%	2.8%
Aquaculture harvest (t)	241,234	-	-	-	-	**2**	1	203,379
Aquaculture value (US$ 1000)	268,493	-	-	-	-	**6**	5	2,257,649
Search Term	**Number of hits**							
Family	999	313	127	306	576	**192**	208	1,781
Reprod*	274	49 (28)	44 (30)	83 (45)	150 (47)	**29 (13)**	67 (47)	377
“Reproductive Cycle”	40 (26)	3 (1)	15 (7)	10 (5)	2 (1)	**8 (4)**	5 (3)	16 (9)
Spawning	53 (39)	13 (10)	16 (9)	15 (9)	16 (11)	**15 (6)**	25 (20)	96 (64)
“Sex determination” OR “sex identification”	3 (1)	0	0	1 (1)	2 (2)	**0**	1 (1)	8 (7)

The number of (accepted) species (no. species), is sourced from WoRMS Editorial Board 2022 (WoRMS Editorial Board, 2024). The fisheries and aquaculture statistics, sourced from FAO (2021), are based on 2019 production, with percent of fisheries harvested from a total of 180,466 t, with the remaining taxa unidentified. The number of hits is based on searches in the Web of Science (Clarivate Analytics, 2024) database using the family name and the other listed search terms. The numbers in brackets are screened for relevant hits based on studies on reproduction in species within the target family only. An asterisk indicates a truncation search operator.

Reproductive studies on gastropods using conventional methods generally involve the sacrifice of the study organisms to access and sample the reproductive organs. Histological methods are common (Joll, 1980; Lasiak, 1986; Afsar et al., 2013) as they elucidate reproductive structures on a cellular level. However, once the process of gametogenesis has been comprehensively assessed for a species or genus, continuing to apply invasive approaches (e.g., histology) may be unnecessary to obtain the core information required for fisheries management. Another common approach for the assessment of reproductive cycles in turbinids involves measuring or staging oocytes or taking weights and measurements of the whole gonad for condition and reproductive indices, such as the gonadosomatic index (Komatsu et al., 1995; Ward & Davis, 2002; Ab Lah et al., 2019). These studies are useful for determining the spawning cycle and optimal seasons for fisheries harvest but, to date, have also required destructive harvesting.

Studies of reproductive periodicity generally demand high numbers of individuals from the same populations, with repeated collections over time, resulting in many animals being sacrificed. For example, Ward and Davis (2002) studied the reproductive cycle of *L. torquata*, which involved collecting 18–30 *T. militaris* every three to seven weeks at three different locations; this resulted in the sacrifice of over 1,200 *L. torquata*. A similar study by Ab Lah et al. (2019) sacrificed 137 *L. undulata* over 14 months (6–10 individuals collected per month) from one location in New South Wales (NSW), Australia to assess the reproductive cycle and nutritional quality. Sacrificing animals for research could adversely impact local populations, especially those already subject to harvesting depletions, populations with limited recruitment potential, species vulnerable to other stressors or endangered and threatened species (Berg et al., 1995; Svärdh, 2003; Tsakiris et al., 2016). Scientific collections may be small compared to large quantities of commercial harvests, however, depending on the spatial scale, such numbers might impact a population if research is concentrated in one location. For rare, endangered, vulnerable or data deficient species, scientific collections could pose serious threats to populations. Non-destructive methods should be favoured, and there should be a priority for research and development of these techniques, especially for larger-scale studies and monitoring purposes. However, these techniques must be developed and validated before application.

Non-lethal techniques have been successfully used in previous studies on various molluscs, including biopsy methods for extraction of foot, mantle and body wall tissues (Berg et al., 1995; Naimo et al., 1998; Haskell & Pan, 2010; Khor et al., 2013). An increasingly popular method for non-lethal reproductive research involves using hypodermic needles and syringes to obtain gonad material. A gonad biopsy method was developed for non-lethal sex identification in limpets (Wright & Lindberg, 1979) and has since been utilized (Le Quesne & Hawkins, 2006; Guallart et al., 2013; Guallart et al., 2020). The gonad biopsy method has been succcessful in obtaining sperm from limpets suitable for fertilization (Guallart et al., 2020) and to obtain viable gametes from abalone for interspecific fertilization (Visser-Roux, 2011). The gonad biopsy technique has also been applied to bivalve species to assess gonad condition, obtain gametes, evaluate female gravidity and identify castrating parasites (Bradley, 1984; Acosta-Salmón & Southgate, 2004; Lee, 2010; Tsakiris et al., 2016; Beaver et al., 2019; Brian & Aldridge, 2020).

Turbinids and many other harvested marine gastropods, such as trochids, muricids, strombids, volutes, buccinid whelks and littorinds (Table 2.1), possess a thick, protective outer shell that encases the reproductive organs (Santhanam, 2018). This shell can hinder the applicability of the direct biopsy method due to the difficulty associated with accessing the gonad (Dobson & Lee, 1994). For instance, in a study on the muricid gastropod *Thaisella chocolata* a gonad biopsy was used to obtain gametes and identify sex, although only after first cracking the shell open to access the reproductive organs (Mattos & Romero, 2016). In contrast, to identify the sex of the teguilid gastropod *Rochia nilotica* non-lethally, Dobson and Lee (1994) developed a 'window' technique that involved shaving back shell layers. The 'window' technique has been successfully used in subsequent studies to sex *R. nilotica* (Dobson, 1997; Gimin & Lee, 1997; Lee & Toelihere, 1997). Similarly, shell drilling has been successfully used to create a permanent hole in oysters without killing the animal (Veitch, 1974) and in mussels to extract live tissue samples, albeit with some lethal and sublethal effects (Svärdh, 2003). Methods of shell drilling (such as the 'window' technique) could be used to overcome the limitation of the protective outer shell to the gonad biopsy procedure; however, the two techniques have seldom been evaluated.

Turbo militaris (Reeve, 1848) is characterized by a thick, whorled shell and calcified operculum, which together protect the soft-bodied animal (Beechey, 2005; Santhanam, 2018). The head and muscular foot are located at the base of the shell and the gonad and digestive gland coil up the apex of the shell. Turbinids are dioecious, with no external sexual dimorphism (Joll, 1980; Lasiak, 1986; Komatsu et al., 1995; Afsar et al., 2013); sex is distinguishable in the mature gonad, where the male gonad is cream-to-white in colour and the female gonad is dark green (Joll, 1980; Ward & Davis, 2002). Whilst the early life-history of *T. militaris* is widely unknown, turbinids have been described as broadcast spawners with external fertilization (Grange, 1976b; Komatsu et al., 1995; Afsar et al., 2013; Andréfouët et al., 2014).

The objective of this study was to investigate a potential non-lethal method for reproductive research in gastropod molluscs. Specifically, we aimed to optimize a non-lethal technique that could be used for assessing the reproductive periodicity of *T. militaris* in the field. We developed a method for shell drilling and gonad biopsy (hereafter referred to as the drill-biopsy technique) in the laboratory. We tested the null hypothesis that the drill-biopsy technique is lethal in *T. militaris*. Then, we compared oocyte sizes throughout the gonad to optimize biopsy placement and test methods for preserving biopsy samples. Lastly, we tested the drill-biopsy technique in the field over two months, aiming to obtain data suitable for oocyte size-frequency graphs and then opportunistically monitored some drilled individuals for shell repair and survival over 10 months.

2.2 Methods

2.2.1 Experimental design

Twenty-five individuals of *T. militaris* within a size range of 70–90 mm shell height were collected in March 2021 from the rock platform at Woody Head (29.4° S, 153.2° E), NSW, Australia. Whilst size at maturity is unknown for this species, from personal observations animals over 60 mm were mature; therefore, our target size class was chosen to encompass a moderately narrow range to reduce inter-individual variation, whilst ensuring all animals were mature. The individuals of *T. militaris* were placed in a bucket with aerated seawater and transported to the National Marine Science Centre (NMSC), Coffs Harbour, Australia within two hours of collection. At the NMSC, *T. militaris* were placed in aquaria with continual flow-through seawater and allowed to acclimatize for 10 days. The estimated water flow rate throughout the experiment was 1l/min, and the incoming water temperature range was 22.97–25.61 °C. Following the acclimatization period, a small, numbered tag was glued to each shell using cyanoacrylate glue. The snails were randomly assigned to one of four treatment groups: 1, unmanipulated control (*n* = 5); 2, shell drilling (*n* = 5); 3, shell drilling and gonad biopsy (*n* = 10); and 4, shell drilling, gonad biopsy and the shell hole sealed (*n* = 5). Irrespective of the treatment group, all *T. militaris* were subject to the same amount of time out of the aquaria.

2.2.2 Drill-biopsy technique

A small hole was drilled into the shell of each treatment (snail groups 2–4) using a hand-held, battery-operated rotary tool (Ozito 3.6V Lithium-Ion Cordless Rotary Tool) fitted with a 2-mm diamond point head. Each shell was placed with the aperture facing down, and the hole was drilled into the middle of the second largest body whorl (Figure 2.1a). Preliminary investigations determined that this location is directly above the middle of the gonad. Sex was identified through the shell hole by examining the colour of the gonad, which is green in females and creamy white in males.

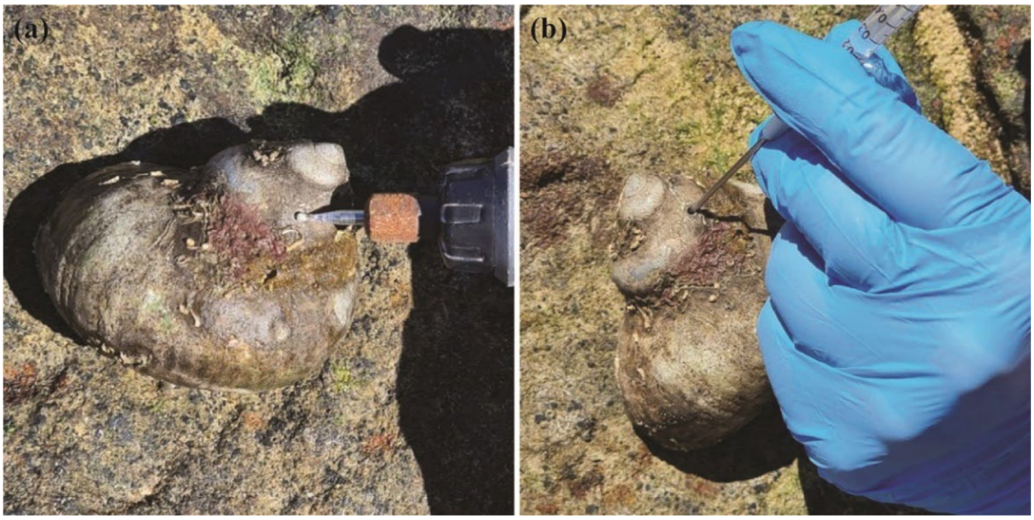


Figure 2.1. Field photographs of the drill-biopsy procedure performed on an animal of *Turbo militaris* (shell height ~80 mm), shell drilling (a) and gonad biopsy (b).

A biopsy of the gonad was taken from each individual in groups 3 and 4 using a 16-gauge hypodermic needle fitted to a 1 ml syringe. Firstly, 500 µl of filtered seawater was drawn into the syringe and the needle was inserted carefully through the shell hole and into the gonad (Figure 2.1b). Gonad material was extracted by pulling the syringe plunger up, moving the needle slightly and retaining tension on the plunger during removal; these techniques aided in the extraction of the highly viscous gonad material (as in, Wright & Lindberg, 1979; Brian & Aldridge, 2020). A new needle and syringe were used for each individual. The shell holes in individuals in group 4 were sealed by applying a small amount of marine safe, underwater epoxy putty (AquaStik Epoxy Putty, Stone Grey) over the hole.

2.2.3 Monitoring

All *T. militaris* were returned to aquaria within approximately 15 minutes and monitored for 16 days. Monitoring inspections occurred daily and involved observations of movement, foot adhesion, dormant behaviour and death. The *T. militaris* fed *ad libitum* on algae fouling the aquaria glass and miscellaneous macroalgae added to the tank. After 16 days in aquaria, the shell holes in all replicate snails in groups 2 and 3 were examined to see if the animal had repaired the shell hole. Individuals in group 4 were checked to see if the epoxy putty remained fixed to the shell.

2.2.4 Additional biopsy studies

The contents of each biopsy were smeared onto glass slides and viewed with an inverted microscope (Nikon Eclipse Ts2). To confirm the sex, we viewed the male gametes under 400 x magnification and the female samples under 40 x magnification. Because of the time required to transport the samples from the field to the laboratory, where oocytes could be viewed with a microscope, we tested several solutions to preserve the female biopsy. We preserved samples for two days in ethanol (70%) and in ethanol (70%) / glycerol (1%) solution. Neither solution was adopted for subsequent use; the oocytes dehydrated and became distorted in ethanol and clumped together considerably in the ethanol / glycerol solution, resulting in their being difficult to view and unreliable for measurements.

Biopsies from three female *T. militaris* were used to test preservation in 10% buffered formalin (formalin 4%, acetic acid 5%, calcium chloride dihydrate 1.3% and ultrapure water 89.7%; FAACC). The fresh biopsies were immediately placed in a six-well plate and random photomicrographs of 20 oocytes in each sample were taken using a camera (MIcrome 20 Pro) fitted to the inverted microscope. These represented a control group for initial oocyte size in seawater (SW). The maximum handling time prior to preservation was 20 min. Each biopsy was then transferred into microcentrifuge tubes containing 1 ml of FAACC and stored at room temperature. Photomicrographs were taken of 20 oocytes in each sample after one (F1), two (F2) and three (F3) days of preservation in FAACC. The diameter of photographed oocytes was measured to the nearest 1 µm using the image analysis software package ImageJ v. 1.53k (Schneider et al., 2012).

To assess whether the biopsy taken from the middle of the second largest body whorl was representative of the whole gonad, we sacrificed three female *T. militaris*. These snails were dissected and the gonad was sectioned into thirds (as in, Komatsu et al., 1995). Oocytes were collected using a scalpel blade from the top (T) and bottom (B) regions and from the middle region of the inner (centre of the gonad; IM) and outer (outer edge of the gonad; OM) areas. Each sample was placed in a six-well plate containing filtered seawater, up to 50 oocytes in each sample were photographed with the microscope, and the diameter was measured using ImageJ .

2.2.5 Field trial

In June and July 2021, the drill-biopsy technique was tested in the field at Big Rocky, Port Stephens (32.8° S, 152.1° E), NSW, Australia. Twenty individuals of *T. militaris* within a size range of 60–90 mm shell height were collected from the low intertidal to shallow subtidal zones on each sampling occasion. The size range was selected to ensure only mature individuals were collected. The snails were brought to a suitable area on the shore for the drill-biopsy procedure. Once six females were identified and biopsied, no more *T. militaris* were drilled; the remaining unmanipulated snails were returned to their habitats. The biopsies were transferred directly from the syringes into (pre-prepared) microcentrifuge tubes containing 1 ml of FAACC. The shell holes in those biopsied and any sexed (drilled only) were sealed with a small amount of epoxy putty, and the snails were released to their initial collection location. The biopsies were transported to the NMSC, photomicrographs were taken of at least 50 oocytes (where present) in each sample, and the oocyte diameter was measured using ImageJ. In June, one biopsy was found to have no oocytes and in July, one biopsy had only one small oocyte; these samples were discounted from further analyses.

During the second month of field trials (July), the six biopsied *T. militaris* were tagged with two small, numbered tags (Hallprint Glue-on Shellfish Tags) glued to the shell using cyanoacrylate glue (Selleys QuickFIX Supa Glue non-drip gel) before being returned to their collection location. This location was visited after ~ six weeks and periodically thereafter for up to 10 months, with the intent to recapture the biopsied *T. militaris*. Upon recapture, the shell was examined for evidence of the drill-biopsy technique.

2.2.6 Statistical analyses

Data visualisation and statistical analyses were performed in RStudio v. 4.1.2 (RStudio Team, 2020; R Core Team, 2021). Data were assessed for normality and homogeneity of variance using Q-Q plots and Levene's tests; parametric assumptions were accepted for the oocyte region data and the field trial data. Nested analysis of variance (ANOVA) was used to test for significant differences in the mean oocyte size among the different regions of the gonad (T, B, IM and OM), with individual as a random factor; a Tukey post hoc test was performed where ANOVA returned a statistically significant *p*-value. Nested ANOVA was used to test for significant differences in mean oocyte size between the two field trial months, with individual as a random factor. Stacked oocyte size-frequency graphs were constructed for the two-month field trial, and each month's mean and mode oocyte size were calculated. A two-sample Kolmogorov–Smirnov test was used to compare the distribution of the oocyte size-frequency graphs from the field trial. Levene's tests for the oocyte preservation data revealed heteroscedasticity, and data transformations did not improve the homogeneity of variance. Therefore, a Kruskal–Wallis ANOVA was performed on the oocyte preservation data to test for significant differences in the mean oocyte size among the fresh (SW) and preserved (F1, F2 and F3) samples. Significance was accepted in all tests where $p \leq 0.05$.

2.3 Results

2.3.1 Monitoring and survival

All *T. militaris* were deemed fit prior to the procedures; each individual was attached to the aquarium glass or another shell. The drill-biopsy method was rapid, taking less than five minutes for each individual and appeared to have no immediate negative effect on the snails. There were no mortalities during the procedures, and all snails displayed normal behaviours (re-attachment) immediately after being returned to the aquaria. During the monitoring period, on some occasions, the snails were actively moving; this behaviour was observed across all treatment groups, and there were no signs of dormant behaviour (foot unattachment with the animal protruding from the shell) from any individuals. Upon completion of the 16-day monitoring period, all *T. militaris* had survived. The shell holes in snails from groups 2 and 3 remained open (had not self-repaired), and the putty remained fixed to the shells of those in group 4.

2.3.2 Drill-biopsy technique

The shell drilling procedure was straightforward and rapid; some shells were thicker than others, requiring more force on the rotary tool. However, care must be taken when applying pressure to avoid puncturing the soft animal underneath. Two animals were accidentally punctured in our laboratory trial, although no mortality was observed. Sex was reliably identified by observing the colour of the gonad through the drill hole (Figure 2.2a,b). Occasionally shell dust obstructed viewing of the gonad through the hole, and we observed that the light-coloured shell material could be mistakenly identified as the male gonad. We found that periodically rinsing the shell during drilling and afterwards helped to wash away loose shell material. We also found that gently pushing on the opercula moved the animal closer against the shell, making the gonad easier to identify. Gametes were present in all biopsy samples. The male and female biopsy samples were different: the male biopsy appeared to be a cloudy cream colour, whereas the female biopsy had dark green oocytes visible to the naked eye. When viewed with a microscope, mobile sperm were observed in the male samples (Figure 2.2c) and oocytes were observed in the female samples (Figure 2.2d).

2.3.3 Oocyte analysis

Using the drill-biopsy technique, we obtained oocytes that could be clearly measured with a microscope. In seawater, the oocytes appeared spherical and homogenous, and an outer gelatinous coating was observed encasing most oocytes. After preservation in FAACC, oocytes retained the same characteristics as the seawater samples (Figure 2.2e). The mean oocyte size from the samples in SW was 224 µm (± 1.6 µm SE), and the mean oocyte size after preservation in FAACC was 228 µm (± 1.9 µm SE) after one day (F1), 222 µm (± 2.2 µm SE) after two days (F2) and 223 µm (± 2.9 µm SE) after three days (F3). There was no significant difference in mean oocyte size measured in SW or after preservation in FAACC (F1, F2 and F3: $p = 0.361$).

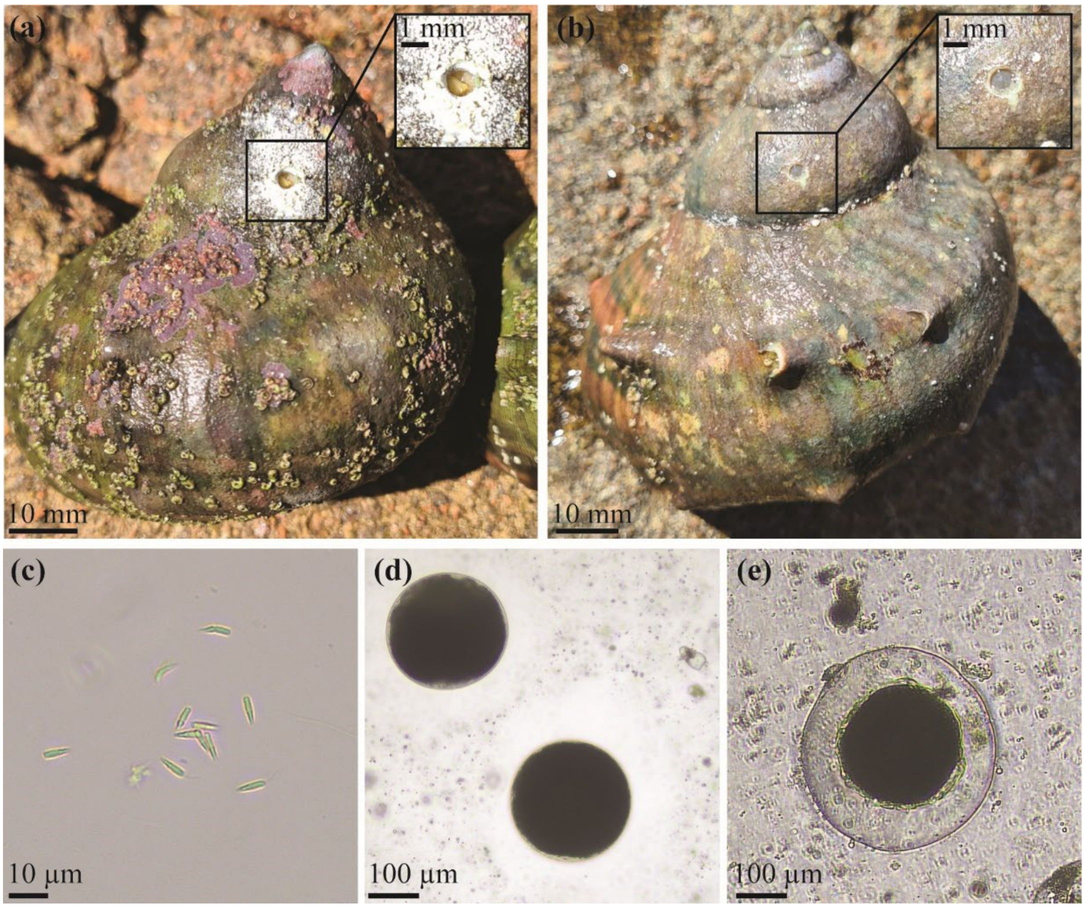


Figure 2.2. Photographs from the shell drilling and gonad biopsy procedures of *Turbo militaris*. Male gonad viewed through the shell hole (a); the insert depicts a close-up view of the drill hole. Female gonad viewed through the shell hole (b); the insert depicts a close-up view of the drill hole. Photomicrograph of the male biopsy in seawater (c). Photomicrograph of the female biopsy in seawater (d). Photomicrograph of the female biopsy after two days preserved in 10% buffered formalin (e).

Analysis of samples taken from the different regions of the gonad revealed that oocytes in the lower region were significantly larger than in all of the other regions (p <0.05) (Figure 2.3). There were no significant differences in oocyte size between the top, middle inner and middle outer regions (p >0.05) (Figure 2.3). Nested ANOVA revealed a significant effect from the random factor, individual (p <0.05). However, in the middle gonad region, the modal population was generally consistent beween individuals. There appeared to be more variability in the lower region, wheraeas in the upper region, there was a lower size range in all individuals (Appendix A: Figure A1).

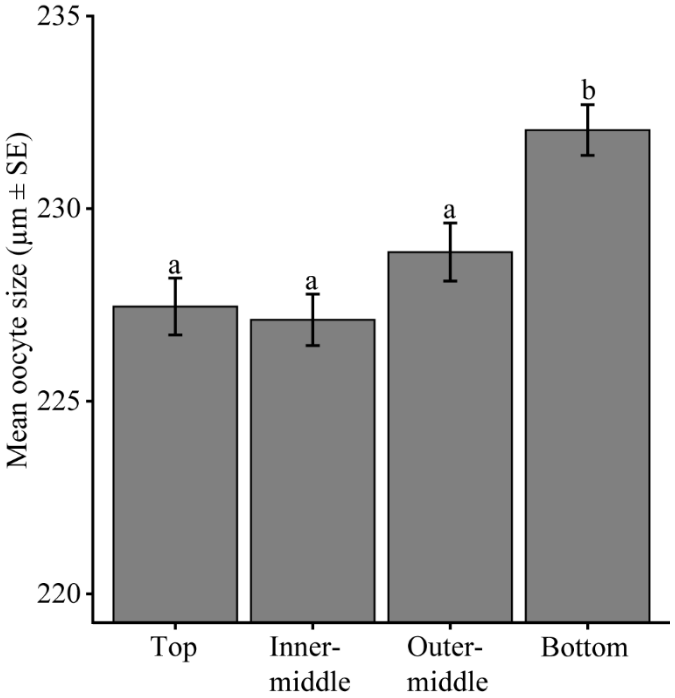


Figure 2.3. Mean size of oocytes removed from different regions of the female gonad of *Turbo militaris* (*n* = 3). The different letters denote statistically different groups as determined by Tukey pairwise comparisons (p <0.05).

2.3.4 Field trial

The drill-biopsy technique was successfully applied in the field; the procedure was rapid, taking under five minutes per individual. The snails were temporarily held in a catch bag in a rock pool before and after the procedure until all sampling was complete. The snails were returned to their collection location within ~30 minutes. From June to July 2021, the mean oocyte size increased from 225 µm (± 1.7 µm SE) to 227 µm (± 1.6 µm SE), and the mode oocyte size increased from 224 to 231 µm (Figure 2.4). There was no significant difference in mean oocyte size between June and July 2021 in the field trial (p = 0.425). However, there was a significant effect from the random factor, individual (p <0.05). Results from a Kolmogorov–Smirnov test show the size-frequency distributions of the oocytes differed significantly between months (p <0.05), with proportionally more larger oocytes in the population in the July samples (Figure 2.4).

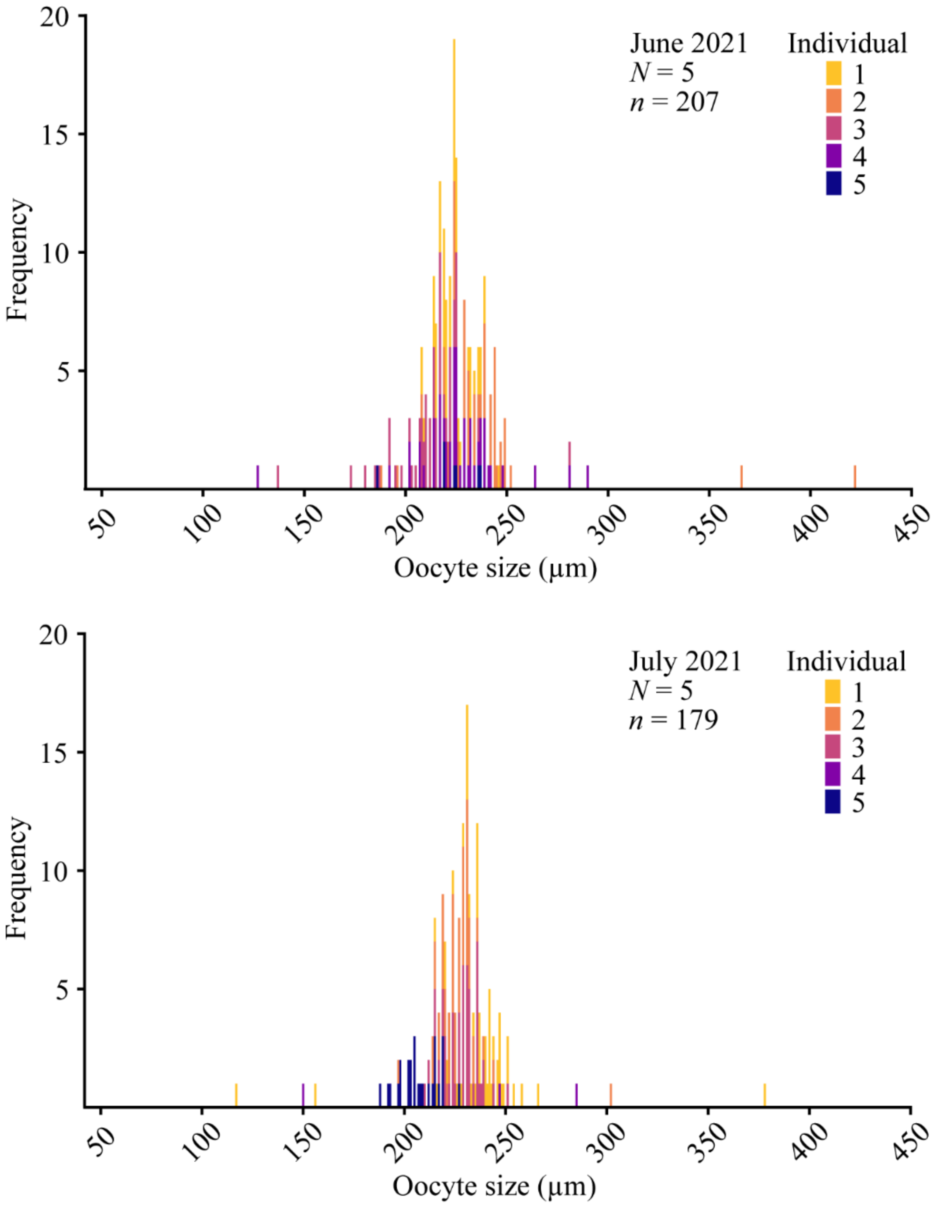


Figure 2.4. Oocyte size frequencies of *Turbo militaris* obtained using the non-lethal drill-biopsy technique in June and July 2021 at Big Rocky, New South Wales, Australia. Mode oocyte size was 224 µm in June 2021 and 231 µm in July 2021. N = number of females, n = number of oocytes used to construct each graph.

Five out of the six *T. militaris* biopsied and tagged in July 2021 were recaptured after 40 days. The recaptured individuals were found close to their original locations (within ~2 m vicinity). All five snails had repaired the shell holes on the inner side and the putty had come off. During later visits to the site, two of the snails were recaptured on multiple occasions within the same vicinity after 16 weeks (112 days), ~30 weeks (208 days) and 42 weeks (294 days). On each recapture occasion, evidence of shell drilling could still be identified;

a depression on the surface of the shell was observed, although it was generally well camouflaged due to epifaunal growth on the shell (Figure 2.5). Each recaptured snail retained the two tags glued to the shell.

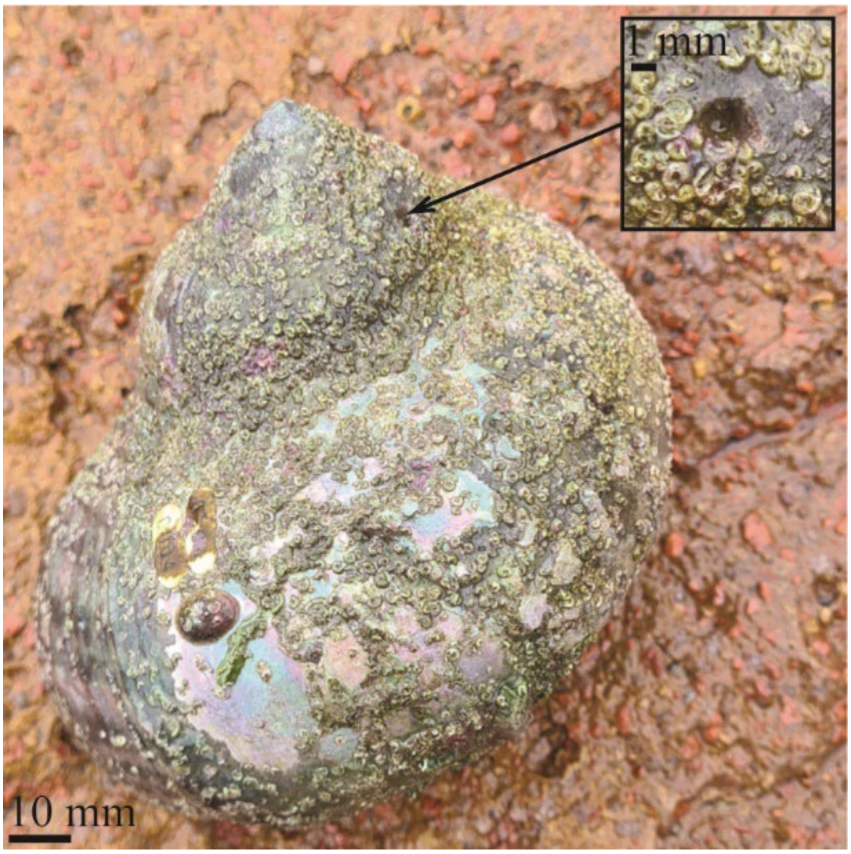


Figure 2.5. Individual of *Turbo militaris* (shell height 86 mm) recaptured after 42 weeks in the field post drill-biopsy. The insert depicts a closeup view of the repaired hole.

2.4 Discussion

This study has successfully applied a non-lethal method involving shell drilling and gonad biopsies to sample the reproductive organs in *T. militaris*. Survival trials in the laboratory resulted in zero mortality, as did subsequent field trials. Other studies using similar techniques on marine molluscs have also reported no mortality, but these were limited to only the gonad biopsy (Acosta-Salmón & Southgate, 2004; Saha & Layzer, 2008; Lee et al., 2010; Visser-Roux, 2011; Guallart et al., 2013; Tsakiris et al., 2016) or the shell drilling procedure alone (Veitch, 1974; Dobson & Lee, 1994). Here we have demonstrated that the two techniques can be used together without any lethal effects on the snails. This procedure provides novel opportunities for non-destructive sex determination and reproductive studies in Turbinidae to facilitate sustainable fisheries management.

Drill-biopsy techniques have potential applications in a broad range of large gastropods currently targeted for fisheries and aquaculture (Table 2.1). However, other studies that have used these two techniques (or similar) together present inconsistent outcomes. For instance, shell drilling and tissue sampling from mussels resulted in no significant mortality when compared to other less invasive treatments (although the mantle mussel was sampled, not the gonad) (Svärdh, 2003). In contrast, studies on the trochid *R. nilotica* demonstrated that death resulted when the gonad was accidentally punctured during shell drilling (Dobson & Lee, 1994). In our study, however, animals that were incidentally punctured during drilling survived. A subsequent study on *R. nilotica* also recorded mortality when eggs were sampled through a hole drilled in the shell (Lee & Toelihere, 1997). Whilst the reason for varying results is unknown, it is important to consider gentle shell drilling and a sterile biopsy. The work on *R. nilotica* used a high-speed, water-cooled diamond saw and a cannula like extraction of material (sterility unknown), whereas conditions used in our study included a small rotation tool and a new sterile needle and syringe for each individual. Additionally, it might be that some species or certain organs are more sensitive than others. Consequently, this method will require careful trials in different species to locate the optimal position for drilling, depth and size of the biopsy and shell sealing *vs* repair mechanisms.

Our observations of live *T. militaris* up to 10 months post procedure in the field confirm that the biopsied individuals can survive for some time after the drill-biopsy procedure. This observation agrees with other studies that have used gonad biopsies on mussels, where no significant mortality was found after one year (Saha & Layzer, 2008) or after two years (Tsakiris et al., 2016). Results and findings from similar studies indicate negligible mid-term impacts when the technique is suitably optimized.

We found that animals displayed no abnormal behaviour immediately after the technique was administered suggesting minimal, if any, short-term disturbance. In this study, we did not quantify sublethal effects, although other studies (on mussels) have considered the sublethal effects of gonad biopsies and found that the method did not affect future reproduction or growth (Saha & Layzer, 2008; Tsakiris et al., 2016; Beaver et al., 2019). For shell drilling, only one study (on mussels) reported on sublethal effects, where drilling holes in the shells resulted in significantly slower growth over a two-month period (Svärdh, 2003). This slower growth could result from additional energy input required to repair the shell hole (Kidneys, 1994 as cited in Svärdh, 2003).

Shell repair in the drilled *T. militaris* did not occur within two weeks in our laboratory trial, suggesting some time is required to recover and build up necessary resources. However, we did observe shell repair after almost six weeks in the field trial, suggesting this process can commence in the short term in natural conditions. Similarly, in drilled shells of *R. nilotica*, a membrane was formed over the hole after two weeks, and within six to eight weeks, calcified layers began to form over the hole (Dobson, 1997). We observed shell repair to have occurred from the inside of the shell, which was also the case for drilled mussels, where shell repair was observed on the inner side two months after holes were drilled (Svärdh, 2003).

Whilst sex could be reliably identified through the drill hole in *T. militaris*, caution must be exercised when sexing based solely on visual examination, as the dark female gonad could easily be mistaken for the digestive gland. Gonad colour can differ between mollusc species (Underwood, 1974) and with respect to reproductive condition (Underwood, 1974; Foster, 1997; Ramesh et al., 2010; Visser-Roux, 2011). In turbinids, the gonad colour is more apparent when the gonad is ripe, whereas after spawning, the male gonad takes on a more brownish-cream colour and the female gonad a brownish-green colour (Robinson, 1992; Foster, 1997; Ramesh et al., 2010). Additionally, studies have found that mature oocytes were present in the ovary of female turbinids year-round, although in low quantities post spawning (Joll, 1980; Lasiak, 1986; Ward & Davis, 2002; Ab Lah et al., 2019). Therefore, especially at times after spawning, the gonad and digestive gland may be more difficult to distinguish from each other. Our biopsies of males and females, however, were distinctly different when viewed with the naked eye, providing further confidence in our approach to sexing the study animals (as in, Le Quesne & Hawkins, 2006; Saha & Layzer, 2008; Lee et al., 2010). Studies aiming to apply this technique to a new species should first consider confirming sex predicted with further examination of the gonad (or a biopsy) with a microscope to ensure the reliability of the technique in correctly identifying the sexes.

We did not find a difference in oocyte size between the inner middle and outer middle regions of the gonad. Therefore, we conclude that there is no requirement for standardizing the depth to which the needle is inserted into the gonad for biopsies of *T. militaris*. However, there was significantly larger oocytes found in the lower portion of the gonad, indicating standardized placement of the biopsy is required, especially for temporal assessments of the reproductive cycle. For *T. militaris*, we recommend targeting the middle gonadal region due to the wide representation of oocyte size and generally consistent modal population between individuals. In contrast to our study, a study on *T. marmoratus* found no difference in oocyte size among different regions of the gonad (Komatsu et al., 1995). These conflicting results highlight the need for preliminary investigations to determine the optimal placement for the biopsy, even for species within the same family. Such preliminary investigations are essential for the successful application of the method so that researchers can consistently and correctly target the most appropriate location for the biopsy (Tsakiris et al., 2016).

Our gonad biopsy method could potentially be successfully applied in reproductive research, as gametes were successfully obtained in both male and female *T. militaris*. Likewise, the gonad biopsy has had general success in obtaining gametes from other marine molluscs (Bradley, 1984; Saha & Layzer, 2008; Tsakiris et al., 2016; Beaver et al., 2019). The oocyte samples we obtained using this technique were suitable for measurements with a microscope as they were clear and remained intact. Using these measurements, we could construct oocyte size-frequency graphs and observe an increase in mode oocyte size and a change in size distribution, with higher numbers of larger oocytes over time. The variation between individuals likely affected the power to detect a mean difference in oocyte size between months. However, for species with continuous or nonsynchronous development, we would expect that after spawning there is a shift in size frequency rather than in mean size. Characteristics of asynchrony within the population could be observed. For example, individual 5 had a smaller mode size and fewer oocytes obtained than most other individuals in July, which may reflect a more recent spawning event; whereas other individuals (e.g., individual 2 in June and individual 1 in July) were likely in a more mature stage with a higher proportion of larger oocytes and greater numbers of oocytes obtained from the biopsy (Figure 2.4). Evaluation of the variation in monthly oocyte size-frequency graphs is widely used to monitor changes in reproductive cycles in marine invertebrates (Matoto et al., 2002; Ward & Davis, 2002; Setyono, 2006; Baillon et al., 2011; Ab Lah et al., 2019). In this study, we have demonstrated that the drill-biopsy technique could potentially be used to observe temporal changes in oocyte size-frequency distributions in *T. militaris* without the need for destructive harvesting.

The drill-biopsy technique was suitable for application in the field; our field trial found the method simple and quick to administer *in-situ.* We found that using hand-held and battery-operated tools meant obtaining equipment was inexpensive, transportation of equipment was simple and the method is potentially well suited for work in remote field locations. Before our field trial, we prepared microcentrifuge tubes with FAACC, so that biopsies could be stored before being transported to the laboratory; we recommend this practice for ease of handling samples (also recommended by, Tsakiris et al., 2016, Brian and Aldridge, 2020). Our results from successive measurements of oocytes fixed in FAACC showed no significant difference in oocyte size from those measured immediately after collection, supporting our recommendation for its use.

The AquaStik epoxy putty we used for sealing the drill holes had no impact on the mortality of the snails in our study, unlike drill holes in mussels sealed with cement (Svärdh, 2003). AquaStik is considered nontoxic to marine life (Ellis & Sharron, 1997; Sypniewski et al., 2016). The putty is promoted for use in aquaria (Sprung & Delbeek, 1997 as cited in Ellis & Sharon, 1997) and is commonly used in other marine studies (Ellis & Sharron, 1997; Harrington et al., 2004; Poray & Carpenter, 2014; Sypniewski et al., 2016). The putty provides a good option for sealing drill holes and use in the field, as it has no impact on survival, has an inconspicuous coloration, cures underwater and is easy and safe to apply. This study did not investigate the survival of animals not sealed in the field, therefore the necessity of using the putty remains unknown. However, we chose to seal the animals on the assumption that sealing the holes would provide an extra barrier against potential predation or infection.

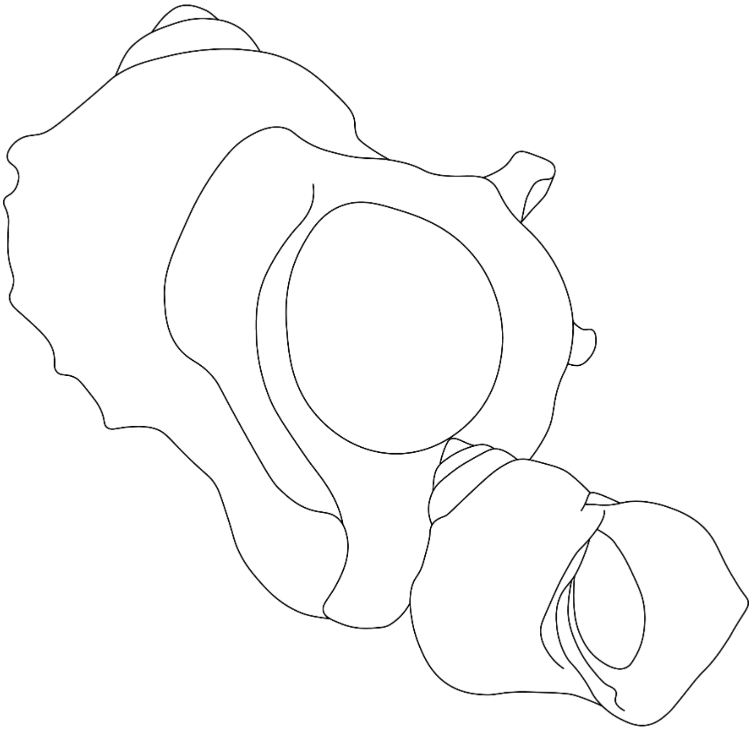
By sampling *in-situ,* the study individuals could be quickly returned to their habitats. The rapid return of individuals can result in minimal handling stress when compared to the more lengthy process of removal from and return to the field. *In-situ* sampling could be especially favourable to mitigate biosecurity concerns associated with the potential transfer of pathogens between sites or between the field and aquaria (DAFF, 2024), and fisheries research permits may prevent animals from being returned from the laboratory or aquaria to the field due to biosecurity regulations. Therefore, field-based methods such as the drill-biopsy technique are advantageous because they are time- and cost-efficient, and suitable for work in remote locations and in cases where biosecurity and research permits prevent the removal and return of study animals.

The drill-biopsy technique has the potential to be adapted to suit other turbinids, such as the harvested Australian species *L. torquata* and *L. undulata* (Rowling et al., 2010; Keane et al., 2014; DCCEEW, 2018b) or key global fisheries species such as *T. cornutus*, *T. marmoratus* or *Megastraea undosa* (Taniguchi & Rogers-Bennett, 2001; Martone & Micheli, 2012; Andréfouët et al., 2014). The drill-biopsy technique could have scope for other reproductive studies, such as research on size at maturity or fecundity. However, preliminary investigations should be considered to ensure that this method is appropriate for the desired application and harmless to the targeted size of animals. Furthermore, this technique could be useful for studies requiring specific sex ratios, such as for induced spawning (as in, Dobson, 1997) and paired breeding for family line establishment. Drill-biopsies could also complement studies requiring the sacrifice of specific sexes (as in, Ward & Davis, 2002; Ab Lah et al., 2019) by targeting key individuals and reducing wasted sacrifices.

Additionally, the drill-biopsy technique could be beneficial for research on molluscs from other families with similar protective shells, for instance, large whelks from the families Muricidae, Strombidae, Tegulidae or Buccinidae (FAO, 2021). Non-destructive sampling is especially advantageous to populations that are critically endangered, vulnerable, near threatened or data deficient. From the IUCN Red List of Threatened Species, a search on marine gastropods yields 46 critically endangered, 50 endangered, 73 vulnerable, 75 near threatened and 133 data deficient species (IUCN, 2022), indicating the potential scope of applicability of this method. This method could also benefit research on species protected under domestic legislation. An example is the giant triton, *Charonia tritonis*, which is under full protection in Queensland, Australia and is currently the subject of research efforts aiming to culture the species for control of the crown of thorns starfish (Motti et al., 2022). The development of non-lethal methods, such as the drill-biopsy technique, will allow researchers to conduct future studies on reproduction in marine gastropods without adverse impacts on targeted populations, albeit with the support of preliminary investigations to determine whether this technique can be applied successfully and reliably to different species.

CHAPTER 3.

EXTENDED AND SPATIALLY ASYNCHRONOUS REPRODUCTIVE PERIODICITY IN A HARVESTED, WARM-TEMPERATE ROCKY-REEF GASTROPOD (TURBINIDAE)



Chapter 3 has been modified as per university guidelines from the published paper:

Seinor, K., Purcell, S. W., Malcolm, H., Smith, S. D. A., & Benkendorff, K. (2023). Extended and spatially asynchronous reproductive periodicity in a harvested, warm-temperate rocky-reef gastropod (Turbinidae). *Fisheries Oceanography, 33(1)*: e12653. doi:10.1111/fog.12653

Abstract

Turban snails are targeted for their high-quality meat and, consequently, are often subjected to heavy harvesting pressure. Managing recreational and small-scale fisheries is challenging, partly due to a lack of biological data underpinning certain regulatory measures. This study aimed to fill current knowledge gaps on the reproductive cycle of the recreationally and culturally harvested Australian turbinid, *Turbo militaris.* The objectives were to investigate the reproductive timing of *T. militaris* in New South Wales (NSW) and identify likely environmental drivers of reproductive periodicity. Oocytes and gonads were sampled from wild animals monthly over 15 months at two sites separated by ~500 km. Analysis of oocyte size frequency and gonadosomatic index revealed that *T. militaris* has a pattern of extended reproduction, which is synchronous between sexes. *Turbo militaris* had the highest mean gonadosomatic index and higher frequency of larger oocytes during the summer months, and spawning appears to have occurred over multiple events, although primarily during winter. Reproductive timing was associated with environmental explanatory variables, including sea surface temperature, wave height, salinity, phytoplankton and nitrate concentration, together accounting for 81% of the variation in oocyte size-frequency and 67% in the gonadosomatic index. Reproductive periodicity was correlated with wave conditions and phytoplankton concentrations inconsistently between sites, indicating that the effect of some environmental conditions may be unpredictable or site-specific. Reproductive timing was asynchronous between two sites in the NSW fishery, posing challenges for designing seasonal fishing closures and community-based harvesting rules. Spatial closures for species with spawning over extended timeframes or spatially asynchronous reproductive cycles are potentially more suitable for achieving fisheries management objectives.

3.1 Introduction

Marine gastropods are an important component of seafood consumption across many cultures; they are targeted by commercial and recreational fisheries, but only a small number of species are produced in aquaculture (Leiva & Castilla, 2002; FAO, 2021). Popular fisheries species include those from the families Muricidae, Strombidae, Haliotidae and Turbinidae (FAO, 2021). Increasing market demand for gastropods compels a need for better fisheries and conservation management (Keane et al., 2014). However, effective fisheries management requires sound biological data such as abundance estimates, ecological interactions, age and growth, distribution and habitat preferences, movement patterns, mortality and reproductive characteristics (Cochrane, 2002; Hoggarth et al., 2006; CDFW, 2018; NSW DPI, 2021).

Knowledge on reproduction is essential for resource management as it: provides insights into life-history traits and population dynamics (Aranda et al., 2003; Vasconcelos et al., 2008); informs ideal harvest timing for optimum meat quality (Ab Lah et al., 2019; Cumplido et al., 2020; Nieto-Vilela et al., 2021); and supports aquaculture development (Mgaya & Mercer, 1994). Data on reproductive timing are critical for planning fishery regulatory measures (e.g., seasonal closures around peak spawning, or full closures) (Chang, 2002 as cited in Lee et al, 2014; Martone & Micheli, 2012; Martins et al., 2011; Stobart et al., 2013). Fishing closures are common regulatory measures for marine invertebrates and have the purpose of limiting over-exploitation for species that can be more exposed to fishers due to reproductive behaviour; or, reducing fishing effort across an entire year (Leiva & Castilla, 2002; Salas et al., 2007; Purcell & Pomeroy, 2015; Boman et al., 2018). Fishing closures might also be set by community-based management systems for traditional reasons (Aswani & Weiant, 2003; Aswani et al., 2015).

Turban snails (Turbinidae) are generalist herbivores that can attain large sizes and dense aggregations (Grange, 1976a; Foster & Hodgson, 1998; Kikutani et al., 2002; Smoothey, 2013; Mazariegos-Villarreal et al., 2017). Turban snails are a popular target for human consumption as they are easily collected using minimal skill or fishing gear and have high-quality meat (Ab Lah et al., 2017b; Romolo et al., 2021). These favourable characteristics can result in high harvesting pressure; however, effective regulation requires biological data, which are often deficient. Whilst some studies have investigated reproduction and early life-history in Turbinidae, knowledge about reproductive timing within this family is limited and requires further research.

Where studied, turbinids are gonochoric, broadcast spawners with external fertilisation and an equal proportion of males and females (Underwood, 1974; Joll, 1980; Komatsu et al., 1995; Matoto et al., 2002; Ramesh et al., 2010; Afsar et al., 2013). Generally, the reproductive cycle in turbinids is bradytictic (i.e., animals gravid over an extended period) and follows an annual pattern with continuous gametogenesis and vitellogenesis occurring shortly after spawning (Underwood, 1974; Joll, 1980; Lasiak, 1986; Ward & Davis, 2002; Ab Lah et al., 2019). The timing of spawning varies among turbinid species. Species from tropical and subtropical regions generally exhibit a single annual spawning event, with activity over the warmer months (Lasiak, 1986; Foster et al., 1999; Lee, 2000; Matoto et al., 2002; Ramesh et al., 2010). Conversely, species at higher latitudes generally display multiple spawning events (Underwood, 1974; Joll, 1980; Ward & Davis, 2002; Freije & Al-Sayed, 2009). In Australia, the limited data on the reproductive timing of Turbinidae suggest prolonged seasonality and multiple spawning events, with timing differing between species and locations. However, these data are based on just five studies of three Australian species: *Turbo intercostalis* and *Lunella torquata* in Western Australia (Joll, 1980), *L. undulata* in Tasmania (Keane et al., 2014) and *L. torquata* and *L. undulata* on the east coast of Australia (Underwood, 1974; Ward & Davis, 2002; Ab Lah et al., 2019).

In New South Wales (NSW), Australia, three turbinids, *L. torquata*, *L. undulata* and *T. militaris,* are targeted for commercial, recreational and cultural harvesting (Arrawarra Sharing Culture, 2009; Cooling & Smith, 2015). *Turbo militaris* (Reeve, 1848) is abundant on rocky shores and shallow rocky reefs from southern Queensland to southern NSW (Beechey, 2005; Atlas of Living Australia, 2023) (Figure 3.1). Despite the abundance of *T. militaris* on rocky shores and the popularity of harvesting, both traditionally and increasingly by transient agricultural workers (NSW DPI, pers. comm.), objective management is hampered by data deficiency. This includes reproductive data as, to date, there have been no studies on the reproductive cycle of *T. militaris*. This research aimed to investigate the reproductive cycle of *T. militaris* using oocyte frequency and gonadosomatic index (GSI) measures. Specifically, we sought to determine whether: *T. militaris* exhibits a single annual spawning event; and, reproductive cycles are synchronous between two geographically separated sites within the fishery. By analysing for relationships with key environmental variables (seawater chemistry and weather), we further aimed to evaluate potential environmental drivers of reproductive periodicity.

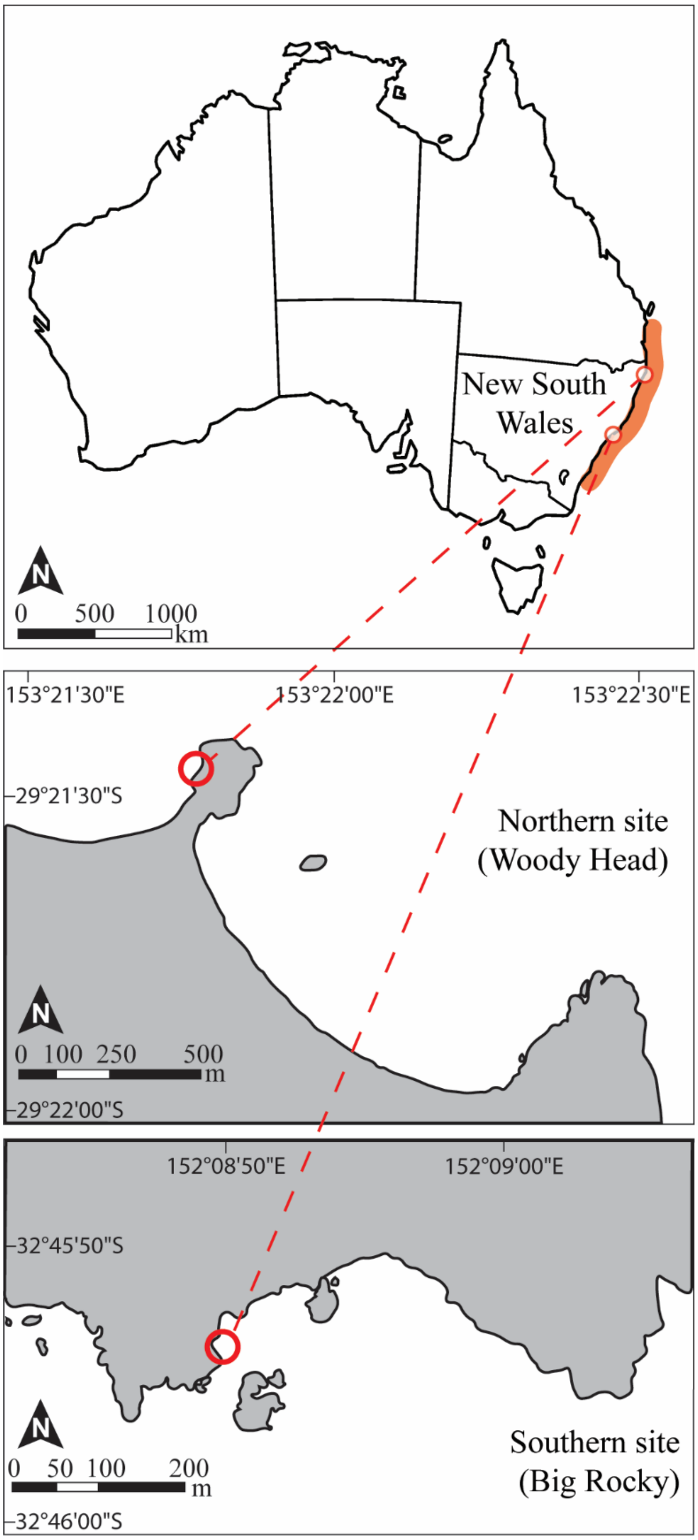


Figure 3.1. The distribution of *Turbo militaris* (orange shading) and the location of the two study sites in New South Wales, Australia.

3.2 Methods

3.2.1 Experimental design

Sampling occurred monthly to assess the reproductive cycle of *T. militaris* at two rocky shore sites in NSW, Australia, separated by 3° of latitude and ~500 km of coastline: Woody Head (29.4° S, 153.4° E), hereafter called northern site, and Big Rocky, Fingal Bay (32.8° S, 152.2° E), hereafter called southern site (Figure 3.1). Data were collected over 15 months, from June 2021 to August 2022. All sampling was undertaken on low tides below approximately 0.5 m during the daytime in calm swell conditions (less than 2 m, depending on direction). Approximately one hour before low tide, turban snails were hand-collected by walking, wading or shallow snorkelling on or adjacent to the rock platform.

On each sampling occasion, up to 20 *T. militaris* within a size range of 60–90 mm shell width were collected and brought to the shore. Preliminary observations indicated turban snails with a shell width >60 mm were mature. According to our hypothesised 1:1 sex ratio, 20 individuals would provide ample replicate females and males for this study. Sex was determined for each turban snail non-lethally by shell drilling and visual examination of the gonad (Seinor & Benkendorff, 2023). Using a non-lethal drill-biopsy technique (Seinor & Benkendorff, 2023), oocyte collection was performed on the first six females encountered in the sample. The subsequent three females, and the first three males, were placed in a bucket with filtered seawater and transported to the laboratory for assessment of GSI. The drill holes in biopsied individuals and those drilled only (sexed but not required) were sealed (Seinor & Benkendorff, 2023); these snails and any remaining snails were returned to their approximate original location.

3.2.2 Oocyte size frequency

Once extracted, the biopsy samples were placed into microcentrifuge tubes containing 500 µL of 10% buffered formalin (formalin 4%, acetic acid 5%, calcium chloride dihydrate 1.3% and ultrapure water 89.7%). These samples ($n = 6$) were transported to the laboratory and transferred into a six-well culture plate. Each sample was viewed with an inverted microscope (Nikon Eclipse Ts2) using 40 x magnification. Photomicrographs of at least 50 oocytes (where present) in each sample were taken at haphazardly chosen locations with a microscope-fitted camera (MIcrome 20 Pro). Oocyte diameter was measured to the nearest

±1 μm from the photographs using digital image software, Image J (version 1.53k) (Schneider et al., 2012).

3.2.3 Gonadosomatic index

The shell of each turban snail was cracked with a hammer and the tissue was separated from the shell and operculum. The visceral coil was trimmed proximal to the gonad and placed in 10% buffered formalin for at least four days. Each visceral coil was placed in a Büchner funnel over a conical flask and thoroughly rinsed with ultrapure water. A 3–4 mm cross-section was cut distal to the stomach caecum (Ab Lah et al., 2019). Each cross-section was photographed, and the gonad area (G) and the gonad and digestive gland area (GDg) were measured using Image J (Schneider et al., 2012). The GSI was calculated as G/GDg × 100.

3.2.4 Environmental variables

Environmental data were sourced from the Copernicus Marine Environment Monitoring Service and the Bureau of Meteorology (https://marine.copernicus.eu/) and included concentration of nitrate and phytoplankton, salinity, pH, primary production, alkalinity, sea surface temperature, significant wave height and rainfall. Marine data were sourced within a 5 km radius of the sampling locations, and rainfall data were sourced from the closest stations to the study site: Yamba Pilot Station (058012) for the northern site and Nelson Bay (061054) for the southern site. A daily average was calculated for each variable with multiple daily records. A weekly average for each variable was calculated for the week prior to sampling (including the sampling day) at both locations. The number of calm days was calculated as the number of days within one week before sampling where the significant height of the sea surface wave was less than 1 m. Sea surface temperature change was calculated as the difference in weekly average temperature between the week prior to sampling and the preceding week. Exploratory data analysis was undertaken using monthly averages of the environmental variables, which produced similar outcomes to the weekly data; therefore, we present only the models using weekly data.

Table 3.1. Environmental variables, sourced from Copernicus Marine Environment Monitoring Service (CMEMS) (https://marine.copernicus.eu/) and Bureau of Meteorology (BOM) (http://www.bom.gov.au/climate/data/).

Code	Description	Units	Source
Alk	Sea water alkalinity expressed as mole equivalent	mol/m3	Global Ocean Biogeochemistry Analysis and Forecast, CMEMS (#001_028)
Calm	Number of days within one week before sampling where the significant height of the sea surface wave was less than 1 m.	days	Global Ocean Waves Analysis and Forecast, CHEMS (#001_027)
NO3	Molar concentration of nitrate in seawater	mmol/m3	Global Ocean Biogeochemistry Analysis and Forecast, CMEMS (#001_028)
pH	Sea water pH reported on total scale	pH	Global Ocean Biogeochemistry Analysis and Forecast, CMEMS (#001_028)
Phy	Molar concentration of phytoplankton expressed as carbon in seawater	mmol/m3	Global Ocean Biogeochemistry Analysis and Forecast, CMEMS (#001_028)
PrProd	Net primary production of biomass expressed as carbon per unit volume in seawater	mg/m3/day	Global Ocean Biogeochemistry Analysis and Forecast, CMEMS (#001_028)
Rain	Daily rainfall	mm	Climate Data Online, BOM. Stations: 061054, 058012
Sal	Sea water salinity	ppt	Global Ocean 1/12° Physics Analysis and Forecast updated Daily, CMEMS (#001_024)
SST	Sea surface foundation temperature	°C	Global Ocean OSTIA Sea Surface Temperature and Sea Ice Analysis, CHEMS (#010_001)
SST. change	Difference in weekly average SST between the week prior to sampling and the preceding week	°C	Global Ocean OSTIA Sea Surface Temperature and Sea Ice Analysis, CHEMS (#010_001)
SWH	Sea surface wave significant height	m	Global Ocean Waves Analysis and Forecast, CHEMS (#001_027)

3.2.5 Statistical analysis

Oocyte size frequency graphs were constructed each month at each site, and modal oocyte size (MOS) was calculated. A Pearson's correlation was used to test the association between female GSI and MOS. A three-factor ANOVA was used to test for significant differences in GSI with sex, month and site as fixed factors. Data were checked for normality using Q-Q plots and a Shapiro-Wilk test; where the data was slightly negatively skewed. A data reflection (each data point is reflected by subtracting the value from the maximum value) and square-root transformation were performed, reducing the skewness. Levene's test indicated homoscedasticity.

Distance Based Linear Models (DBLM) were used to test the relationship between *T. militaris* reproduction parameters and environmental variables. This analysis was applied separately to the GSI (sexes combined) and MOS. Environmental variables were first tested for collinearity, where those with $R > 0.75$ were removed from the analysis. Sea surface temperature, alkalinity and pH were collinear, and exploratory data analysis revealed that retention of sea surface temperature produced the strongest models. The number of calm days was removed due to collinearity with significant wave height. Phytoplankton and primary production were also collinear, therefore, we retained phytoplankton as primary production is derived from the former. DBLM was run using Euclidean distance similarity matrices, and the BEST model was selected using the Akaike Information Criterion (AIC). Statistical significance was accepted where $p \leq 0.05$. Statistical analyses were performed in RStudio (RStudio Team, 2020; R Core Team, 2021) and PRIMER v7 (PRIMER-e, 2017), and graphs were made using RStudio (RStudio Team, 2020; R Core Team, 2021).

3.3 Results

Turban snails were ripening over the austral spring and had high GSI and large MOS around the austral late spring, through summer and early autumn (Figure 3.2 and Figure 3.3). Spawning occurred primarily over late austral autumn to winter, and turban snails were at their most spent condition (low GSI and small MOS) through the austral winter. Other spawning events were apparent throughout the year, during the warmer months, which was evident by a reduction in GSI and decreases in MOS (Figure 3.2 and Figure 3.3). The GSI and oocyte size frequencies therefore show a pattern of extended reproduction for *T.*

militaris. Both the GSI and oocyte size frequency were suitable for evaluating the reproductive cycle of *T. militaris,* as the fluctuation in measures of female GSI and MOS correlated over time ($R^2 = 0.18$, $p = 0.018$).

3.3.1 Oocyte size frequency

The oocyte size frequency graphs show temporal fluctuation in the size distribution of oocytes where, overall, oocytes are larger during the summer and autumn months and smaller during the winter (Figure 3.2). Oocytes were present in all months and, with a few exceptions, there were some very large oocytes (>300 µm) throughout the year. The consistent presence of oocytes in the larger size classes (> 250 µm), even during months where animals were in their most spent condition, is indicative of partial spawning. During the months where, based on size-frequency distributions, a spawning event is likely to have occurred the number of oocytes in the biopsies was often low. The snails appeared in the most spent condition during the middle of winter to early spring 2021 with low MOS and more uniform distribution. Following these months, the oocyte size range was wide, with many presumably new small oocytes (<200 µm) and the MOS generally increased indicative of the ripening of gametes. The snails were mostly in a ripe stage during summer and autumn, with the largest MOS occurring over summer; however, some spawning events may have occurred during these months as decreased MOS occurred at both sites over one month in summer and autumn. In the winter of 2022, the snails were in a spent condition again with low MOS and many smaller oocytes in the biopsies.

3.3.2 Gonadosomatic index

The GSI was relatively consistent between sexes ($p = 0.14$), following similar temporal patterns at both study sites (Figure 3.3), but differed inconsistently between sites across months (interaction $p < 0.01$) and was inconsistent among combinations of site, month and sex (interaction $p = 0.04$). The reproductive cycle at the southern site generally lagged one to two months behind the northern site (Figure 3.3). The GSI was low during the winter of 2021 and 2022. During spring, the GSI increased, with a slight decrease at the northern site in November 2021. The GSI reached the highest overall values over the summer to early autumn period, although there was a substantial decrease and subsequent increase in the GSI during one month in summer. During autumn, the GSI decreased overall, albeit with an increase across both sites in late autumn to early winter. During winter 2022, the GSI decreased and remained low; the overall lowest values for the GSI were during the winter months.

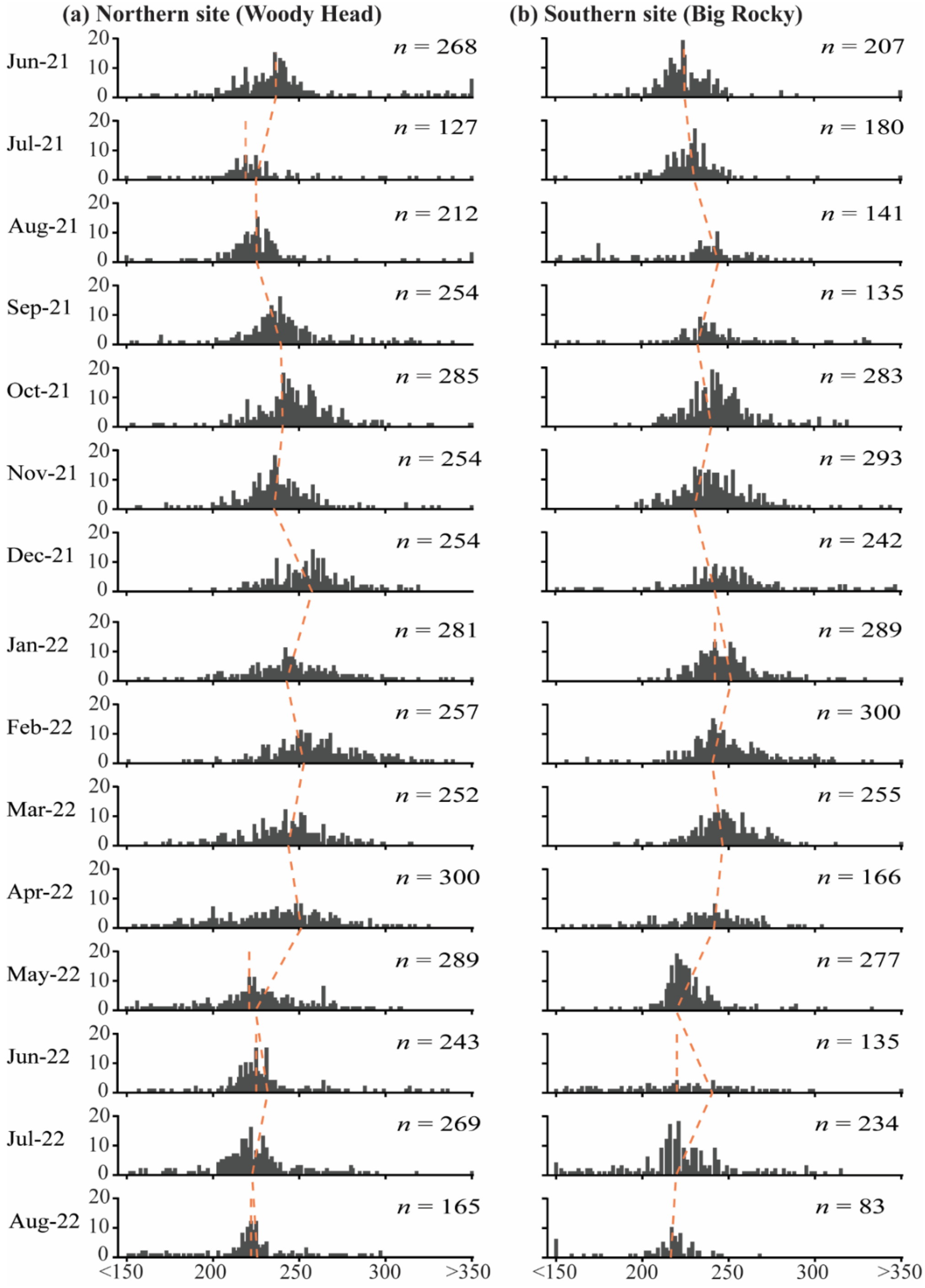


Figure 3.2. Monthly size frequency distributions of oocytes from female *Turbo militaris* (*n* = 6) at the northern site (Woody Head) (a) and the southern site (Big Rocky) (b), New South Wales, Australia. The orange dashed line represents modal oocyte size.

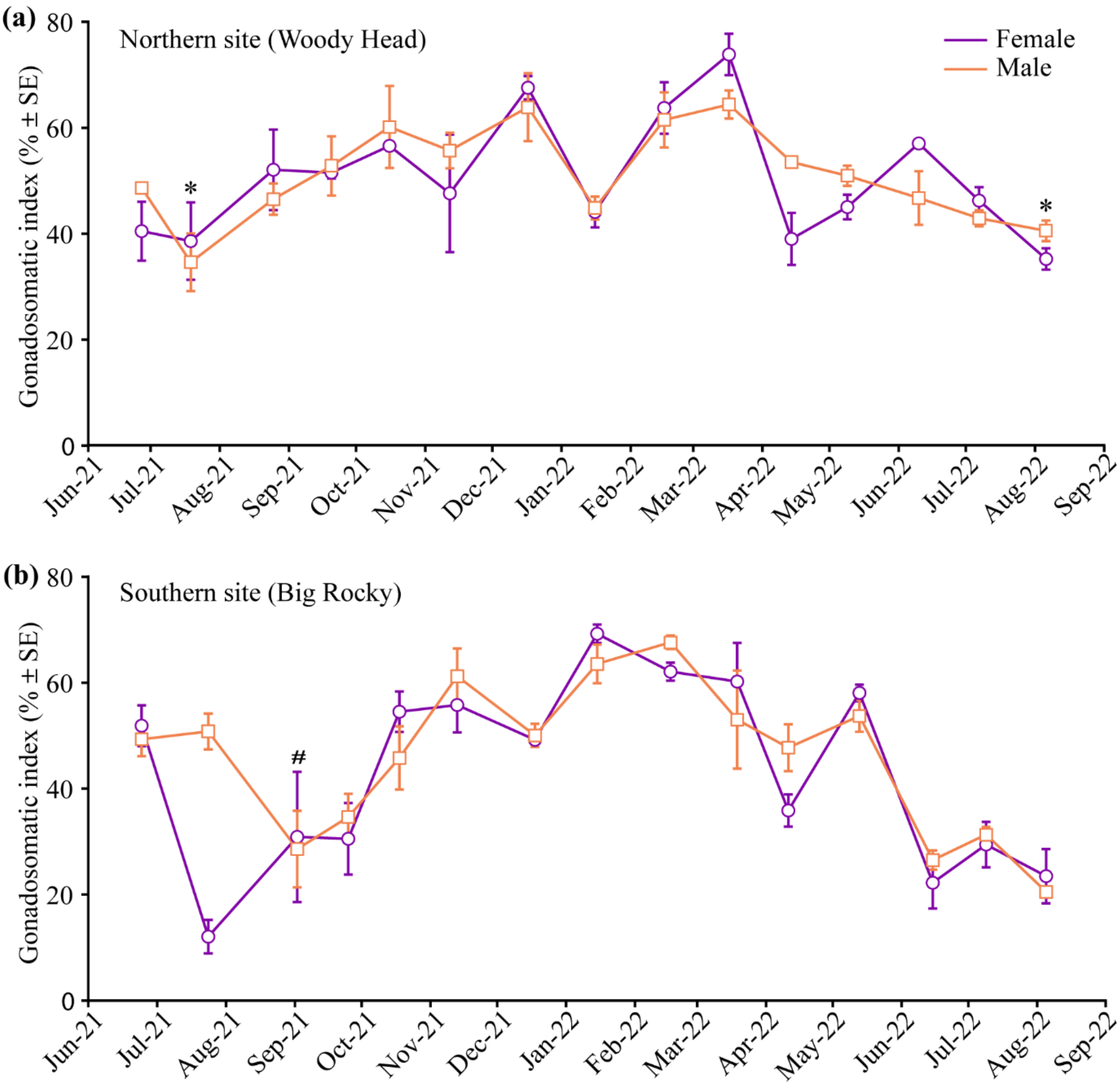


Figure 3.3. Temporal variation in gonadosomatic index of female (*n* = 3) and male (*n* = 3) *Turbo militaris* from the northern site (Woody Head) (a) and the southern site (Big Rocky) (b), New South Wales, Australia. *: *n* = 2 female, 4 male. #: *n* = 2 male, 4 female.

3.3.3 Environmental predictors

As expected, sea surface temperature throughout this study was warmer in the summer–autumn and cooler in the winter–spring. Temperature varied considerably at fine (daily) temporal scales, especially during the summer (Figure 3.4a). Sea surface temperatures were warmer overall at the northern site. Sea conditions were generally rougher over the winter months (more periods of greatest wave heights), although periods of rough seas occurred through late spring to early autumn at the southern site and through summer to early autumn at the northern site (Figure 3.4b). Wave height fluctuated substantially; overall, the northern site was generally calmer than the southern site, where high wave heights were more frequent and of greater magnitude (Figure 3.4b). Salinity fluctuated throughout the year at both sites; however, the lowest salinities were in January and February 2022 (Figure 3.4c). Phytoplankton concentration was generally lower through the cooler months, peaking through spring and summer, whereas nitrate was lower in the warmer months and higher over winter (Figure 3.4d-e).

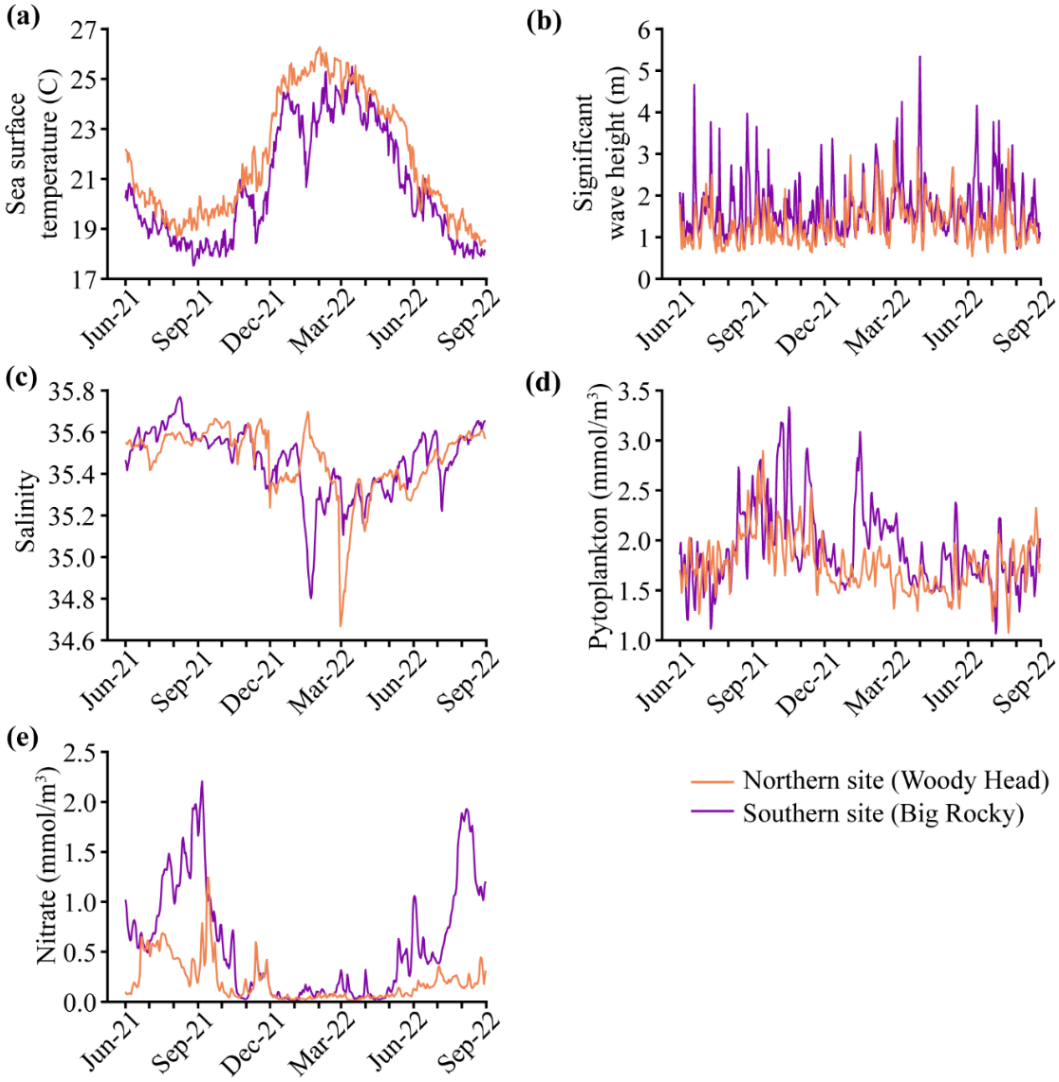


Figure 3.4. Daily fluctuation of environmental variables, sea surface temperature (a), significant wave height (b), salinity (c), phytoplankton concentration (d) and nitrate concentration (e), at two rocky shore sites in New South Wales, Australia, from June 2021 to September 2022.

DBLM analysis revealed significant relationships between variables associated with the reproductive cycle for *T. militaris* and several environmental variables (Table 3.2). The BEST model explained 80.6% of the variation in MOS and comprised a combination of eight variables (Table 3.2). Generally, MOS was larger with warmer temperatures; increased with increasing sea surface temperature; and, generally declined with falling sea water temperatures. At the northern site, MOS was larger with higher wave height and decreased as wave heights became lower. In contrast, at the southern site, MOS was generally larger in calmer conditions and decreased when wave height increased. Larger MOS generally occurred when both salinity and nitrate were lower at both sites, and there was a general increase in MOS when phytoplankton concentrations were highest at the southern site. The BEST models explained 67.1% of the variation in the GSI and involved a combination of six variables (Table 3.2Table 3.2). The GSI generally increased with rising sea surface temperatures and was lower when the sea surface temperature decreased. The GSI generally increased with increasing significant wave height at the northern site; however, at the southern site, the GSI decreased with increasing significant wave height. As salinity and nitrate increased, the GSI generally decreased.

Table 3.2. Outcomes from Distance Based Linear Modelling testing the contribution of various environmental variables (collinear variables removed) obtained for the period one week prior to sampling occasions to the variation among *Turbo militaris* reproduction parameters (gonadosomatic index and modal oocyte size).

Reproduction parameters	**Outcomes**	**Environmental variables**	***R^2***	***RSS***
Modal oocyte size	Marginal tests (p <0.05)	sum, win, SST		
	BEST model 1 variable	win	0.375	2023.9
	BEST model 2 variables	sum, win	0.505	1600.2
	BEST model 3 variables	SST, SST.change, Phy	0.594	1313.2
	BEST overall model	**aut, site, NO_3, Phy, Sal, SST, SST.change, SWH**	**0.806**	**628.5**
Gonadosomatic index	Marginal tests (p <0.05)	sum, win, site, NO_3, Sal, SST, SWH		
	BEST model 1 variable	NO_3	0.399	6538.8
	BEST model 2 variables	win, NO_3	0.493	5516.5
	BEST model 3 variables	win, SST.change, NO_3	0.570	4676.9
	BEST overall model	**aut, win, NO_3, Sal, SST.change, SWH**	**0.671**	**3576.9**
Included variables*	sum, aut, win, spr, site, NO_3, Phy, rain, Sal, SST, SST.change, SWH			

R^2 = proportion
RSS = residual sum of squares
* included variables: sum = summer, aut = autumn, win = winter, spr = spring, site = sampling site, NO_3 = nitrate, Phy = phytoplankton, rain = rainfall, Sal = salinity, SST = sea surface temperature, SST.change = change in weekly SST, SWH = significant wave height.

3.4 Discussion

Turbo militaris has a bradytictic reproductive strategy similar to other turbinids examined in Australia. The long, annual reproductive cycle of *T. militaris* involves peak gonad development over the warmer months, with large oocytes present throughout the year, but the largest oocyte size distribution was during summer-autumn. There were multiple spawning events with evidence of partial spawning at each site within each year, but there was a peak spawning period over the winter. The spawning season appeared to last approximately three to four months during peak activity and one month for other apparent spawning events. Reproductive timing was asynchronous between the study sites but was synchronous within sites between males and females, consistent with a broadcast spawner. The reproductive timing of *T. militaris* was likely driven by a combination of environmental factors, but these could be site-specific and unpredictable.

The reproductive timing of *T. militaris* was asynchronous between sites of 3° latitudinal difference in NSW, and similar to that of another large Australian turbinid, *L. torquata,* on the south coast of NSW. *Lunella torquata* exhibited biannual spawning during autumn to winter and spring to summer (Ward & Davis, 2002). For *L. torquata*, asynchrony in reproductive cycles was found between sites separated by only 15 km (Ward & Davis, 2002). Similarly, for *T. cornutus,* reproductive timing differed by a couple of months between sites of less than 1° latitudinal difference on Jeju Island, South Korea (Lee et al., 2014). In contrast, *L. torquata* displayed a prolonged breeding season with peak summer activity in Perth, Western Australia (Joll, 1980). Other Australian turbinids, *L. undulata* and *T. intercostalis,* were found to spawn mainly over the summer months (Underwood, 1974; Joll, 1980; Keane et al., 2014; Ab Lah et al., 2019). Thus, breeding seasons are diverse within the same gastropod family and can vary for a single species across different populations. Furthermore, as *T. militaris* has undergone a poleward range extension over the last several decades (Beechey, 2005; Atlas of Living Australia, 2023), a shifting distributional range could have implications for planning effective, consistent spatial management for the entire *T. militaris* population. Our results imply that any seasonal regulatory measures, such as seasonal fishing closures based on peak spawning timing, would need to be broad enough (i.e., autumn to winter) to service populations at differing latitudes in the fishery and account for predicted climate change scenarios.

Broadcast spawning species require males and females to have synchronous gametogenic cycles and simultaneous spawning (Grange, 1976b; Afsar et al., 2013), which was the case in our study. Reproductive synchrony between sexes has been demonstrated for other turbinids (Underwood, 1974; Matoto et al., 2002; Ward & Davis, 2002). Oocytes were present in our biopsy samples year-round and often within a wide size range, indicative that *T. militaris* is a partial spawner (Underwood, 1974; Joll, 1980; Ward & Davis, 2002; Freije & Al-Sayed, 2009; Ramesh et al., 2010; Ab Lah et al., 2019). The presence of mature oocytes in the ovary year-round could indicate asynchrony of spawning individuals within populations, rather than a mass spawning event (Joll, 1980; Ward & Davis, 2002; Keane et al., 2014). However, it is evident from this study that female and male *T. militaris* generally develop and spawn simultaneously. Whether turbinids completely spawn-out by the end of the season, or if oocytes are maintained until the next season, is unclear (Joll, 1980). Reproductive success could be optimised if they retain some oocytes (Ramesh et al., 2010).

A combination of environmental factors was correlated with the reproductive timing of *T. militaris*; between-site differences in the temporal fluctuation of temperature and exposure to swell may have contributed to the asynchronicity of reproductive timing in this study. For *T. militaris*, the variation in MOS could be partially explained by sea surface temperature before spawning and the change in sea surface temperature. Our results suggest that sea temperature is likely to be an important factor in the maturation of oocytes or as a cue for spawning events. Sea temperatures are often cited as a primary cue for reproductive timing in marine gastropods (Grange, 1976b; Matoto et al., 2002; Freije & Al-Sayed, 2009; Lee et al., 2014; Boman et al., 2018). Whilst sea temperature has been linked to reproductive timing in some gastropod species, it has been disregarded as the cue for spawning in some other turbinids (Joll, 1980; Ward & Davis, 2002), but could be more crucial in gonad development (Freije & Al-Sayed, 2009). Overall, *T. militaris* appears ripest in periods of warmer water and more spent during periods of cooler water.

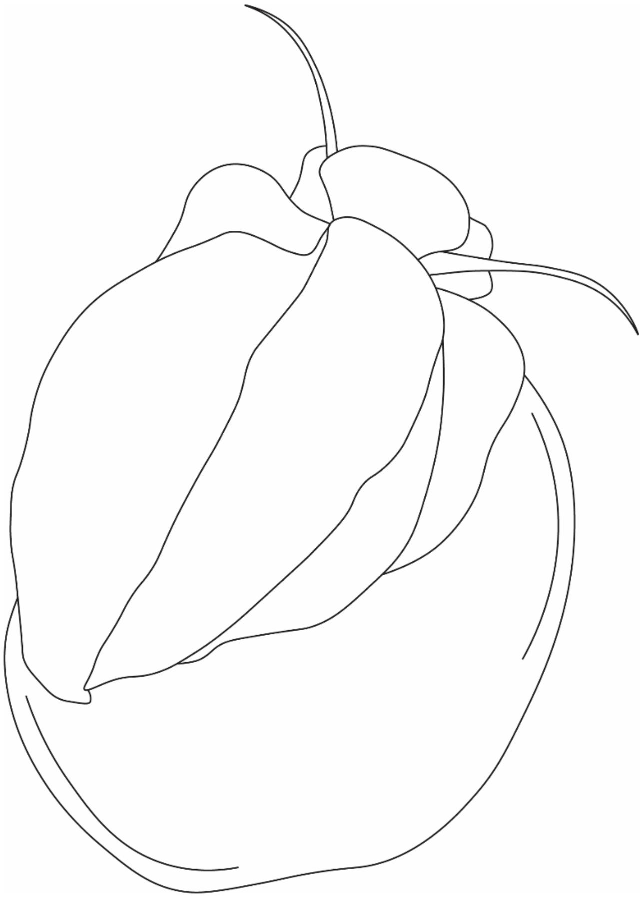
The relationship between wave height and *T. militaris* reproduction parameters was the opposite between sites, which could have resulted in the spatial asynchrony in reproductive cycles. At the northern site, spawning timing was associated with calmer conditions; these conditions offer an advantage for fertilisation success by constraining the dispersal of gametes prior to fertilisation. In contrast, at the southern site, individuals had more spent conditions (with low MOS and low GSI) during rougher seas. Spawning in rough weather (large waves and swell) could be favourable as a population-wide cue for animals to spawn simultaneously or for facilitating population connectivity through larval dispersal (Grange, 1976b). Turbulent water conditions have triggered spawning in turbinid gastropods in aquaculture, by adding new water to aquaria or aerating or agitating water vigorously (Grange, 1976b; Yamaguchi, 1988; Dwiono et al., 2001). Interpreting these results becomes complicated due to the differing site characteristics, resulting in different exposure to swell conditions on these rocky shores (Figure 3.1). The northeastern-extending rock platforms at the northern site provide strong protection on the north-western side from the predominant south-easterly swells; however, this site is more exposed to summer north-easterly wave action. At the southern site (Big Rocky), the south-facing shoreline is not as protected from large south-easterly swells as they are more likely to wrap around into the bay. As our findings imply, wave exposure can have unpredictable, site-specific effects on the reproductive timing of reef gastropods.

Seawater salinity could be influential to the reproductive timing of *T. militaris,* as the temporal fluctuation in reproductive parameters was correlated to salinity. Generally, the turban snails in this study appeared not to be spawning during periods of heavy rainfall and flooding. La Niña influenced periods of heavy rainfall during the study period experienced across NSW over the summer-winter of 2022. Major flood events affected the NSW north coast (Northern Rivers region, including the northern site) in February and March 2022 and the NSW mid-coast (Hunter region, including the southern site) in July 2022. Animals could be stalling spawning during heavy rainfall events due to osmotic risks, which may affect gamete viability and reduce reproductive success (Chim & Tan, 2009; Muraeva et al., 2017; Qin et al., 2020). Reproductive timing could be expected to respond similarly to decreased salinity and high nutrient concentration, as runoff from heavy rainfall and flooding can be associated with elevated nutrient loads. However, further investigation is required to understand these relationships as there may be a lag phase before nutrients efflux from estuaries, and the animals could respond to the increased nutrients in the water. In this study, animals with spent gonads were associated at both sites with high nitrate concentration and, at the southern site, there was a general increase in MOS where phytoplankton increased. Nitrate is important for productivity, however, can be limiting in the ocean (Sigman & Hain, 2012; Moore et al., 2013); higher nitrate levels promote growth of phytoplankton and hence food for larvae. A higher concentration of nutrients and phytoplankton might be an important factor in influencing spawning timing, as adults may select favourable conditions for larvae (Underwood, 1974; Foster et al., 1999; Freije & Al-Sayed, 2009).

Spatially asynchronous reproduction poses challenges for designing seasonal fishing closures and community-imposed harvesting rules in traditional fisheries. The finding that *T. militaris* has continuous reproductive development with the ability to spawn multiple times per year and in various environmental conditions is likely beneficial for sustainable resource harvest. However, should the need for further management intervention arise (currently, there are bag and size limits and marine park spatial closures in NSW (NSW DPI, 2018a)), a seasonal closure for this species is unlikely to achieve an improved population abundance or recovery if the fishery is overharvested. Furthermore, *T. militaris* is simultaneously regulated in NSW with other species, *L. torquata* and *L. undulata* (NSW DPI, 2023) and sea urchin species, under the NSW sea urchin and turban shell (SUTS) restricted fishery (NSW DPI, 2018b). Whilst the reproductive timing of *T. militaris* was reasonably consistent with *L. torquata*, it was different to that of *L. undulata* (Ward & Davis, 2002; Ab Lah et al., 2019). As spawning occurs over extended periods without the formation of large breeding aggregations and reproductive timing is inconsistent across the fishery, seasonal closures designed to protect spawning adults may be ineffective overall. Full spatial closures in marine sanctuaries for particular species may be more suitable for achieving management objectives around maintaining or increasing recruitment and abundance.

CHAPTER 4.

LONG-TERM MOBILITY OF A HARVESTED, ROCKY-REEF GASTROPOD (TURBINIDAE)



Chapter 4 has been modified as per university guidelines from the published paper:

Seinor, K., Purcell, S. W., Malcolm, H., Creese, R. G., & Smith, S. D. A. (2025). Long-term mobility of a harvested, rocky-reef gastropod. *Fisheries Management and Ecology*, e12794. doi:10.1111/fme.12794

Abstract

Stocks of *Turbo militaris* (Turbinidae) are under increasing harvesting pressure, but management is currently hampered by data deficiency. Management decisions for rocky-reef gastropod fisheries should consider long-term species mobility, yet this is often poorly understood. Therefore, mark-recapture was used to evaluate annual displacement and upshore-to-downshore movement of *T. militaris* in Eastern Australia. Tags were glued onto 676 snails, their positions georeferenced and recapture surveys were conducted after 6 and 12 months. Overall, 25% of tagged snails were recaptured. Snails moved an average of 20–21 m year^{-1} at subtropical sites and 34–44 m year^{-1} at temperate sites. Movement was non-directional, limited in upshore-to-downshore mixing and unrelated to animal size. *Turbo militaris* is neither sedentary nor site-attached, and small and large snails move similarly. Our findings suggest a limited capacity for adults to repopulate other tidal zones, thus recreational harvesting could impact intertidal snails.

4.1 Introduction

Information on species ecology and population dynamics, including movement, is essential for effective conservation and management (Leiva & Castilla, 2002; Martone & Micheli, 2012; Stieglitz & Dujon, 2017). Empirical data on species movement are particularly relevant for informing connectivity, population models and management (Pittman & McAlpine, 2001; Allen & Singh, 2016; Sheehan, 2019). Understanding the extent and limits of harvesting across habitats and the status of populations is necessary for informed fisheries management (Cooke, 1999; Fischer et al., 2022). Assessment of densities of benthic biota is easy to quantify in the short-term, but movement causes population density and structure to fluctuate over time (Cooling & Smith, 2015).

Movement is a primary ecological function that facilitates intraspecies connectivity (Nathan et al., 2008) and is central to many processes in marine animals, such as foraging, reproduction, predator–prey relationships and habitat use (Underwood, 1977; Chapman, 2000; Pittman & McAlpine, 2001; Allen et al., 2018). Animal movement influences species survival, reproductive success and resilience to disturbance, with highly connected populations more buffered against depletion from harvesting (Proudfoot et al., 2006; Cooling & Smith, 2015; Allen & Singh, 2016). For example, greater mobility could lower a species' extinction risk and vulnerability to exploitation pressure by enhancing aggregation behaviour for reproduction or facilitating seeking shelter from environmental perturbations or escape from predation (Joll, 1980; Coates et al., 2013; Hayakawa et al., 2021). Movement research can inform spatial management strategies, such as marine park zoning and reserve size (Shepherd, 1986; Glazer et al., 2003). Additionally, movement research is valuable for informing the extent and design of other studies that aim to collect empirical fisheries data, such as growth or mortality (Shepherd, 1986).

Movement can be driven by biological processes, such as for reproduction, with animals moving to find mates or to cluster for broadcast spawning, or movements in response to physiological tolerances, where reduced movement may occur in stressful conditions, such as suboptimal thermal ranges (Allen & Singh, 2016). Ecological drivers for movement include seeking food, which may be affected by resource availability, intraspecific competition or ontogenetic requirements (Hayakawa et al., 2018). Furthermore, animals may move in response to escaping predation or have reduced movement in predator-rich ecosystems (Allen & Singh, 2016). For marine gastropods, olfactory navigation drives movement behaviours for finding food, avoiding predators, forming breeding aggregations and selecting optimal habitats (Wyeth, 2019). Movements may also be modulated by environmental factors such as oceanographic conditions, where benthic animals may decrease mobility in turbulent waters to avoid accidental dislodgement.

Rocky shores are dynamic ecotones, where tides and waves generate a gradient of microhabitats across the shore, from the (supralittoral) splash zone to the intertidal (eulittoral) zone and shallow subtidal (infralittoral) zone (Underwood & Denley, 1984; Hawkins et al., 2016). Rocky shores are often heterogeneous, but the tidal gradient provides different biophysical conditions on different parts of the shore that influence associated biotic assemblages (Underwood & Denley, 1984). Movement research is specifically interesting for intertidal rocky shore species, because some species occur in specific shore zones while others are found across multiple zones (pers. obs.; Underwood, 2000). Population mixing and migration across the shore profile for these animals may facilitate access to refuges and foraging sites and influence predator–prey relationships (Chapman, 2000; Ettinger-Epstein & Kingsford, 2008; Allen et al., 2018). Documenting animal movement between intertidal and subtidal zones can increase an understanding of population dynamics, harvesting impacts and potential capabilities for animals to repopulate areas of low density that may have been depleted by harvesting (Proudfoot et al., 2006; Cooling & Smith, 2015; Hayakawa et al., 2018).

Marine gastropods are among the most abundant and diverse benthic taxa on rocky shores and shallow reefs, and many species are harvested worldwide (Leiva & Castilla, 2002). Ecological studies on marine gastropods are often limited (Creese, 1988), and small-scale, artisanal fisheries are generally under-represented in fisheries research (Rousseau et al., 2019). Few studies have examined long-term movement in marine gastropods; most studies usually cover short temporal scales (days or weeks). Furthermore, studies on intertidal gastropods have rarely compared movements among locations of differing latitudes. However, this information could be important for predicting changes in population dynamics in future climate conditions.

On intertidal rocky reefs in Australia, turban snails are among the most abundant herbivorous invertebrates (Hickman, 1998). *Turbo militaris* (Reeve, 1848) is a large (up to

130 mm shell height; pers. obs.) gastropod that colonises the eulittoral zone, the sublittoral fringe and the infralittoral zone on rocky reefs on the east coast of Australia (Cooling & Smith, 2015). The endemic distribution of *T. militaris* ranges from southern Queensland to southern New South Wales (NSW) (Beechey, 2005; Atlas of Living Australia, 2023) (Figure 4.1). In this region, oceanographic conditions are strongly influenced by the East Australian Current (EAC) (Ridgway & Hill, 2014). The EAC is a warm western boundary current that forms a large eddy field deviating from the coast between 31° S and 33° S before the southern extension (Phillips et al., 2022). The EAC drives a temperature difference and, thus, the benthic communities along the NSW coast. Subtropical waters occur throughout northern NSW, whereas the mid to south coast is typified by warm-temperate to temperate waters with a higher diversity and abundance of macroalgae (Lloyd et al., 2020). For *T. militaris,* reproductive periodicity has been found to differ between spatially separate regions of differing latitudes (Seinor et al., 2023), yet it is unknown if other ecological patterns (i.e., differences in movements) are present.

Harvesting of rocky shore invertebrates has dramatically increased over the last several decades (Anderson et al., 2011; FAO, 2024). In Australia, turban snails are collected culturally, commercially and recreationally. Turban snails are a traditional food resource for coastal First Nations Australians (Arrawarra Sharing Culture, 2009; Cooling & Smith, 2015). In NSW, turban snails are commercially harvested as part of the combined sea urchin and turban snail fishery (SUTS); the catch is highly variable, yielding approximately 4–22 t annually (Chick, 2023). Catch of *T. militaris*, a primary target in the SUTS fishery, has generally increased in the last decade, yielding 4.8 t in 2023 (7.6 t for all turban snail species combined) (NSW DPI, 2018b; Chick, 2023). Turban snails are commercially harvested year-round, where fishers hand-collect individuals by diving on shallow reefs (NSW DPI, 2018b). Recreational fishing for turban snails involves hand-collecting, primarily on intertidal zones of rocky shores. Recreational harvesting is especially prevalent at low tide when eulittoral habitats are easily accessible (pers. obs.). Observations of large groups of recreational harvesters on rocky shores highlight the potential risk of overharvesting snails in the accessible intertidal zone (Cooling & Smith, 2015). There are no data on the extent of the non-commercial catch of turban snails in Australia; however, the magnitude is likely similar to that of commercial harvest (DCCEEW, 2018a). Current regulations for harvesting turban snails in NSW include minimum legal-size limits (shell size >75 mm), daily bag limits (20 individuals) and spatial protection by marine sanctuary zones (NSW DPI, 2023, 2024). Commercial fishers must also comply with commercial exclusion zones, and there are limited entry rules (DCCEEW, 2018a).

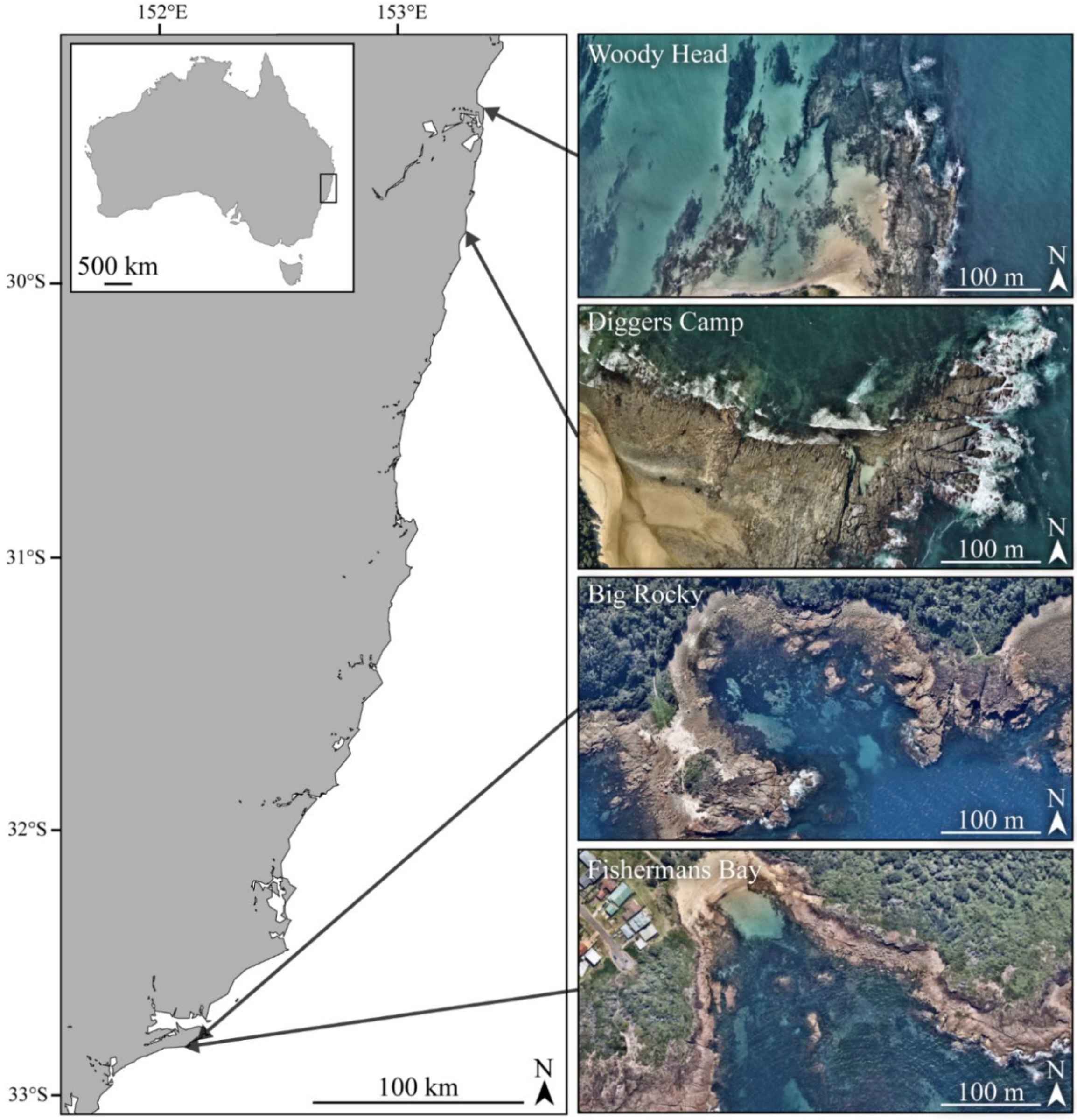


Figure 4.1. Location of the four rocky shore sites for mark-recapture surveys of *Turbo militaris* in New South Wales, Australia. Aerial images sourced from Nearmap (2024).

The large size and high-quality meat of *T. militaris* (Ab Lah et al., 2017b), coupled with high population densities on accessible intertidal rocky shores, make them a conspicuous and desirable target for human harvesting. Observations of increased harvesting of turban snails on Australia's coastline raise concerns about overharvesting and its long-term sustainability and suggest the need for stricter fisheries management (Cooling & Smith, 2015). However, scientific studies on turban snails are scarce, especially for the Australian subtropical endemic *T. militaris.*

Our research objectives were to determine if *T. militaris*: migrated between intertidal and subtidal zones; populations mixed on rocky shores; movement rate or direction differed among locations, and; movement rate or direction was associated with animal size or shell morphology. We aimed to document long-term movement of *T. militaris* and how movement varied across a fishery that extends from the subtropics to warm-temperate areas. Mark-recapture studies are common for assessing movements in aquatic gastropods (Underwood, 1977; Ault & Demartini, 1987; Michel et al., 2007; Hazlett, 2009; Coates et al., 2013; Stieglitz & Dujon, 2017; Capinpin Jr, 2018; Schlaff et al., 2020), commonly using low-invasive glue-on tags (Hamilton, 1978; Castell et al., 1996; Chapman, 2000; Ettinger-Epstein & Kingsford, 2008; Kienzle et al., 2022; Yeo et al., 2024). We used mark-recapture methods and Global Positioning System (GPS) waypoints of animals to quantify annual movement of *T. militaris* and both upshore movement (to a shallower depth or higher position on the shore) and downshore movement (to a lower position on the shore or deeper in the water) at four rocky shores along south-eastern Australia.

4.2 Methods

4.2.1 Study sites

Mark-recapture surveys included a single marking event and two recapture events. Sampling dates were planned around low swell conditions (<2 m) and spring low tides (<0.4 m above zero tidal datum) during daytime. The study was conducted at four rocky shore sites in NSW, Australia (Figure 4.1). Woody Head (29.4° S) and Diggers Camp (29.8° S) were subtropical sites where water temperatures ranged 26.8–18.3 °C and averaged 22.5 °C. Big Rocky and Fishermans Bay (both at 32.8° S) were temperate sites where water temperatures ranged 25.5–17.4 °C and averaged 21.1 °C. Water temperature data were obtained from October 2021 to November 2022 from the E.U. Copernicus Marine Service Information (https://doi.org/10.48670/mds-00321). Woody Head is open to fishing and frequented by recreational fishers. Diggers Camp is in the Solitary Islands Marine Park, where recreational collection of invertebrates is prohibited intertidally (NSW DPI, 2024). Commercial fishing is also prohibited at Diggers Camp, which is located within a SUTS commercial exclusion zone (DCCEEW, 2018a). Big Rocky and Fishermans Bay are in the Port Stephens – Great Lakes Marine Park within a habitat protection zone, where recreational and commercial harvesting is permitted (NSW DPI, 2024).

At Woody Head and Diggers Camp, intertidal rocky reefs extend from the shore to protect the leeward (western and northern) sides from onshore wind and prevailing southeasterly and southerly swells. Sandy beaches punctuate rocky shores throughout these regions. At both sites, intertidal zones have moderately complex topography and are strongly influenced by tides, mostly exposed at low tide, and submerged at high tide. Woody Head has small, protected bays and offshore patchy, shallow (to ~2 m depth) reefs that run parallel to the intertidal rocky shore, surrounded by gently sloping sandy substrate. At Diggers Camp, topography becomes highly complex farther from shore, with many rock crevices, large boulders and deep trenches. Offshore, rocky reefs gently slope from intertidal areas to ~6-m depth, where substrate becomes sandy. At both locations, habitat-forming biota such as *Idanthyrsus pennatus* and *Hormosira banksii* populate higher zones, red coralline algae occupy lower inundated areas and macroalgae dominate shallow subtidal and offshore reefs, mainly *Sargassum* spp. and *Ecklonia radiata*. At Diggers Camp, some scleractinian corals occur in the most protected subtidal reefs (Smith, 1988).

Big Rocky and Fishermans Bay are characterised by south-southeast facing bays along a rocky clifflike shoreline. Offshore small islands and scattered rocky outcrops offer protection from prevailing swell. Big Rocky is the most exposed site, where waves and turbulent water are frequent within the bay, whereas, at Fishermans Bay, the narrow shore topography offers more calm conditions. Rocky outcrops provide high habitat complexity adjacent to a moderately complex intertidal area that slopes gently into deeper (~2–3 m) water. Farther from the beaches, intertidal complexity increases to provide several small, protected coves and trenches along the sides of the bays. Edges of the bays are exposed at low tide and are dominated by turfing algae and coralline algae, whereas shallow subtidal regions are less complex and dominated by mixed macroalgal communities. At Big Rocky, urchin barrens and highly complex habitat associated with large boulders characterise deeper areas (~2–3 m). In contrast, at Fishermans Bay, *Caulerpa filiformis* is common within the bay, and the centre of the bay is primarily sandy, with some scattered rocky substrata. At the sites included in this study, *T. militaris* is primarily associated with habitat-forming species such as the tube-worm *I. pennatus*, the brown alga *Hormosira banksii* and the solitary ascidian *Pyura stolonifera* (Cooling & Smith, 2015).

4.2.2 Tagging

Mark-recapture surveys commenced by tagging at least 140 *T. militaris* at each site during October and November 2021. *Turbo militaris* were located by visual searches in the intertidal zone and by wading and snorkelling in the adjacent subtidal zone to a maximum depth of ~4 m. Searches were confined to preferred turban snail habitat. Individuals over a wide size range (Appendix B: Figure B1) were tagged with no preference for size class or shell morphology. Snails were collected and tagged from areas representing the full suite of intertidal and shallow subtidal habitats at each site (Appendix B: Figure B2). Upon collection, a numbered rubber band was placed around each snail before they were placed in a catch bag. Concurrently, a numbered buoy with a small lead weight was placed on the reef where the snail was collected. A handheld GPS (Garmin eTrex 10) was carried in the intertidal zone and towed on a diver's float to search the shallow subtidal. The GPS was set to log a track point every 30 seconds to record the search track. A dive watch was calibrated to the time on the GPS. Upon collection, the GPS was held over the location for >30 seconds, and the time was recorded. Later, time recordings from tracks were matched with each collection.

Snails were brought to shore, where maximum height (apex to anterior canal), maximum width (width of the final body whorl across the aperture) excluding spines and maximum width including spines were measured (mm) using Vernier callipers. On each shell, two small areas on the exterior of the final body whorl, perpendicular to the spiral crease, were prepared for tagging by removing the periostracum layer and algal or epifaunal growth. Tagging areas were sanded using a handheld, battery-operated rotary tool (Ozito 3.6V Rotary Tool) fitted with a conical diamond head piece. The area was then dried using a compressed air gun. Using cyanoacrylate gel glue (Selleys QuickFIX Supa Glue non-drip gel), two small, identically numbered plastic tags (Hallprint Glue-on Shellfish Tags) were glued to the shell (Figure 4.2). Tags were pressed onto the shell for a few seconds and allowed to cure for several minutes. Clear lacquer was painted over the tags, including a small area of surrounding shell, and allowed to dry for several minutes, as a protective layer against abrasion of tags and to increase tag retention.

Snails were returned to their point of collection by locating numbered buoys corresponding to the numbered band on each snail. The rubber band was removed, and snails were placed on rocky substratum with the aperture facing down. For each snail captured, the tagging process took up to 30 min. After release, snails were observed attaching their foot to the substrate, and some moved within minutes after their release.

Figure 4.2. Tagged *Turbo militaris* released at one Diggers Camp. Individual #0469, shell height: 81 mm, has smooth shell morphology and individual #0464, shell height: 71 mm, has spiny shell morphology.

4.2.3 Recapture

Recapture surveys were conducted approximately 6 months after tagging, during April and May 2022, and again approximately 12 months after tagging, during October and November 2022. Visual searches for tagged snails were conducted by expanding the search from tagging areas. The search extent (Appendix B: Figure B2) was limited to preferred *T. militaris* habitat, accessibility and safe working conditions. *Turbo militaris* can be cryptic, so searching included looking under ledges and in cracks, into holes and small caves, often by shallow diving in the subtidal zone to ~4 m depth. *Turbo militaris* frequently aggregate, so each snail in a cluster was removed and inspected for the presence of tags to ensure concealed tagged snails were found. Upon recapture, the tag number was recorded and a buoy was placed where the tagged snail was collected to ensure the snail was returned to the exact location following measurement. The collection location was recorded with the GPS, using the same method as during tagging. Shell height and width (with and without spines) were measured *in-situ* and the tag number was recorded. Tag loss was recorded for animals with only one of two tags.

4.2.4 Movement and elevation

GPS tracks from tagging and the recaptures were imported into ExpertGPS (https://www.expertgps.com/). A waypoint for the original locations of each tagged snail was created by locating a track point corresponding to the time a snail was tagged. Waypoints were also marked for all recaptures. Corresponding tagging and recapture waypoints were identified, movement was calculated by recording the distance between matched waypoints, and a movement track was fashioned. Movement direction was calculated by determining the bearing between starting and finishing geographic coordinates and converting the data into a circular object for analysis. Movement distance was corrected to an annual movement rate (m/year) to account for differences in time at liberty.

Aerial imagery for each location was sourced from Nearmap (2024), with specific imagery based on clarity (low cloud cover, minimal water reflection, low swells or waves and low tide). Matched tagging and recapture waypoints, movement tracks and aerial imagery were georeferenced in ArcGIS (ESRI, 2023) to create movement maps. Tagging waypoints and GPS search tracks were georeferenced in ArcGIS (ESRI, 2023) to create images of tag locations and search tracks (Appendix B: Figure B2). Maps were formatted in Adobe Illustrator (v28.3).

Remotely sensed topographic and bathymetric data were used to obtain an elevation point for each tagging and recapture waypoint. Lidar Aerial Survey data for each survey site from Geoscience Australia (2021) were imported into ArcGIS (ESRI, 2023). Lidar data were converted to a raster format and contour polygons were formed using a 0.1 m contour interval. The elevation (m) of each waypoint was extracted from contour polygons, and elevation change was calculated by subtracting the recapture elevation from the tagging elevation.

4.2.5 Statistical analysis

Permutational multivariate analysis of variance (PERMANOVA) was used to compare differences in movement distance, elevation change and movement direction among sites, with shell size (shell height at tagging) and shell morphology (ratio of shell width with spines to shell width without spines) as covariates. Annual movement and elevation change were transformed into natural logarithms (ln) to meet assumptions of variance homogeneity and normality. For snails recaptured twice, the first (6-month) recapture was omitted to avoid pseudo-replication, and the second (12-month) recapture was retained. This data simplification procedure was used to quantify and compare the displacement rate, but multiple recaptures were also qualitatively assessed for movement. Backwards-stepwise variable selection was used in separate PERMANOVA analyses for each response variable, followed by pairwise comparisons of significant effects. PERMANOVA analyses used Euclidean distance in the 'adonis2' function of the vegan package in R (R Core Team, 2021; Oksanen et al., 2024).

A paired *t*-test was used for snails recaptured twice to test for differences in movement rates between 6-month and 12-month recapture periods. Data from all four sites were pooled due to small numbers of snails recaptured twice at each site. For the paired *t*-test, movement was standardised to a 6-month rate (m/6 months) and $\text{Log}_{10}(x+1)$-transformed to satisfy assumptions of normality, variance homogeneity, and outlier influence. The paired *t*-test was performed using the stats package in R (R Core Team, 2021).

A logistic regression was used to assess the effect of shell height on recapture as a binary response. Logistic regression was performed using the 'glm' function in the stats package in R, specifying family as binomial (R Core Team, 2021). All statistical tests were assumed to be significant if $p \leq 0.05$.

4.3 Results

4.3.1 Tagging and recapturing

Of 676 turban snails tagged across four sites, 138 were recaptured (~20%) after 6 months and 53 were recaptured (~8%) after 12 months (Table 4.1). Tagging took three days at each site, except at Diggers Camp, which took two days with more personnel. On average, 62 snails were tagged per day. Recapture surveys took 2–4 days, with five hours per day at each site, by 2–4 personnel. The highest recapture rate after 6 months was at Diggers Camp (the site protected from intertidal harvesting), and the lowest was at Big Rocky. After 12 months, the highest recapture rate was at Fishermans Bay, and the lowest was at Woody Head (Table 4.1). Snails were mostly recaptured once (89% of all recaptures). Most snails recaptured twice were at Diggers Camp and Fishermans Bay (nine at each site). Only four snails were recaptured twice at Woody Head and one at Big Rocky. Three empty tagged shells were recovered, two during the 6-month recapture survey at Diggers Camp and one at a local Fisheries office by a member of the public that was tagged at Big Rocky.

Table 4.1. Descriptive results from mark-recapture surveys on *Turbo militaris* at two subtropical and two temperate rocky shore sites in New South Wales, Australia. Sample size (*n*), measurements of minimum (h_{min}) and maximum (h_{max}) shell height (mm), average shell height ($h_{average}$, mm ± SE) and average shell morphology ($\%_{spiny}$, i.e., animals with shell spine ratio >1) are given for tagged (time = 0), and recaptured snails (6-month recapture: time = 6, 12-month recapture: time = 12). The percentage of tagged animals recaptured (*r*), and the number of animals recaptured with only one tag (1tag) are given for the recaptures.

	Site	**time**	***n***	***r***	**1tag**	**h_{min}**	**h_{max}**	**$h_{average}$**	**$\%_{spiny}$**
Subtropical sites	Woody Head	0	188			51	87	70 (± 1)	84
		6	37	20	9	60	88	74 (± 1)	78
		12	8	4	3	68	87	75 (± 2)	100
	Diggers Camp	0	179			34	102	70 (± 1)	32
		6	58	32	27	50	97	72 (± 1)	45
		12	15	9	9	65	88	72 (± 2)	13
Temperate sites	Big Rocky	0	147			21	101	62 (± 1)	50
		6	12	8	3	57	85	74 (± 3)	75
		12	8	6	1	69	89	81 (± 3)	100
	Fishermans Bay	0	162			28	117	71 (± 1)	14
		6	31	19	7	67	103	79 (± 0)	19
		12	22	14	7	66	104	84 (± 2)	5

Tag loss (snails recaptured with only one tag) was 33% after 6 months at liberty and 37% after 12 months at liberty (Table 4.1). Partially attached tags were found on four snails. Recaptured snails often had one or both tags covered with algal or epifaunal growth, such as crustose coralline algae and small polychaete tube-worms (Appendix B: Figure B3).

4.3.2 Movement distance

Most snails (~78%) moved less than 30 m, and few moved <5 m (~12%) or over 100 m (~2.4%) (Figure 4.3). Snails moved shorter distances at subtropical sites (Woody Head = 21 m ± 3 m SE; Diggers Camp = 20 m ± 2 m SE) than at temperate sites (Big Rocky = 44 m ± 10 m SE; Fishermans Bay = 34 m ± 7 m SE) (Figure 4.4a). Annual movements were less variable at subtropical sites (Woody Head range = 3–81 m; Diggers Camp range = 1–106 m) than at temperate sites (Big Rocky range = 3–192 m; Fishermans Bay range = 1–257 m). Annual movement differed significantly among sites (PERMANOVA; $p = 0.044$, Appendix B: Tables B1 and B2), but not significantly between any pairs of sites (pairwise comparisons; $p > 0.05$).

For snails recaptured twice, movement averaged 10 m (± 2 m SE) in the first 6 months and 8 m (± 1 m SE) in the next 6 months (6 months to 12 months). The average movement of snails recaptured twice did not differ significantly over the first (6 month) and second (12 month) periods at liberty ($p = 0.49$, Appendix B: Table B3).

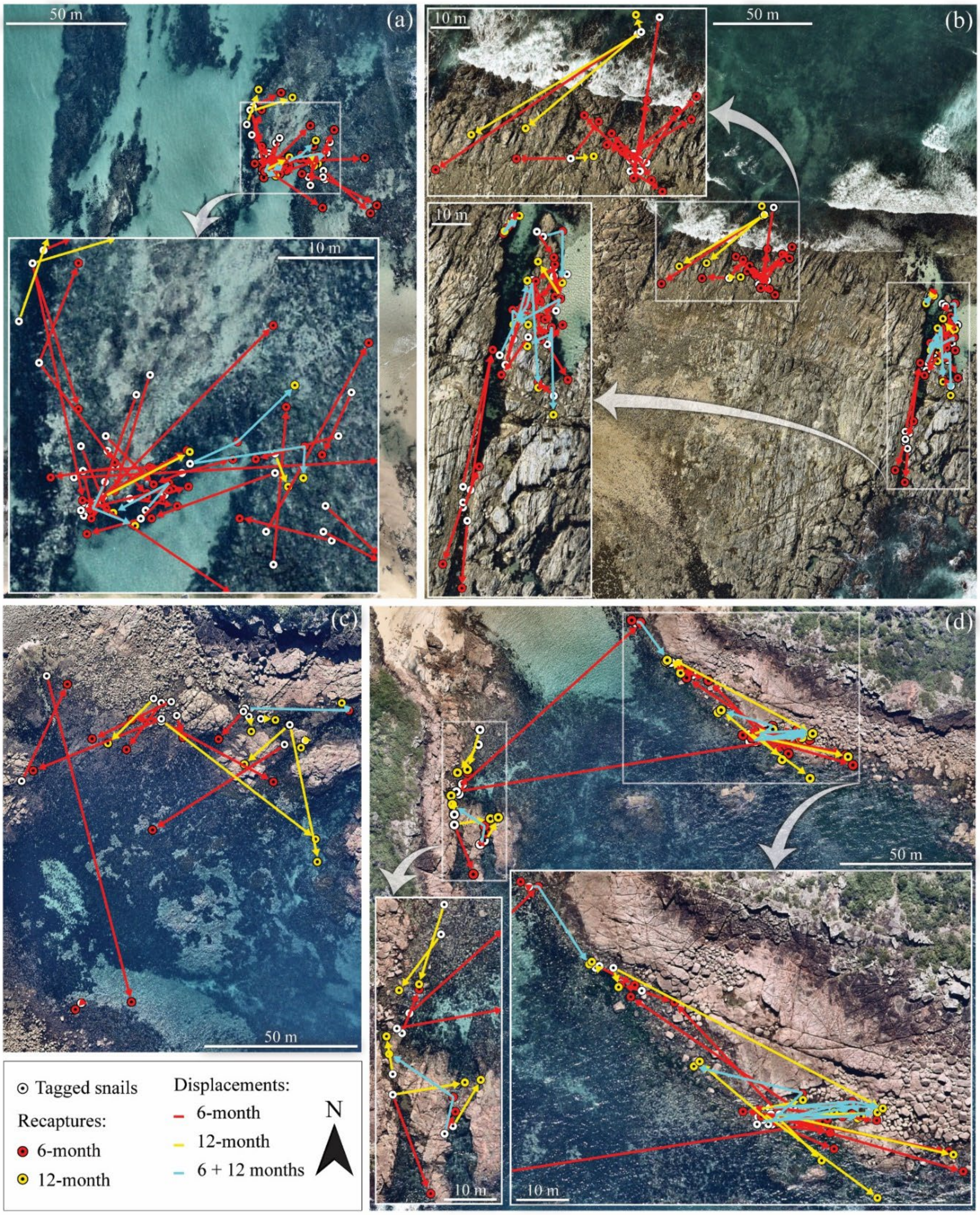


Figure 4.3. Displacements of *Turbo militaris* from mark-recapture surveys at Woody Head (a), Diggers Camp (b), Big Rocky (c) and Fishermans Bay (d), New South Wales, Australia. Aerial images sourced from Nearmap (2024).

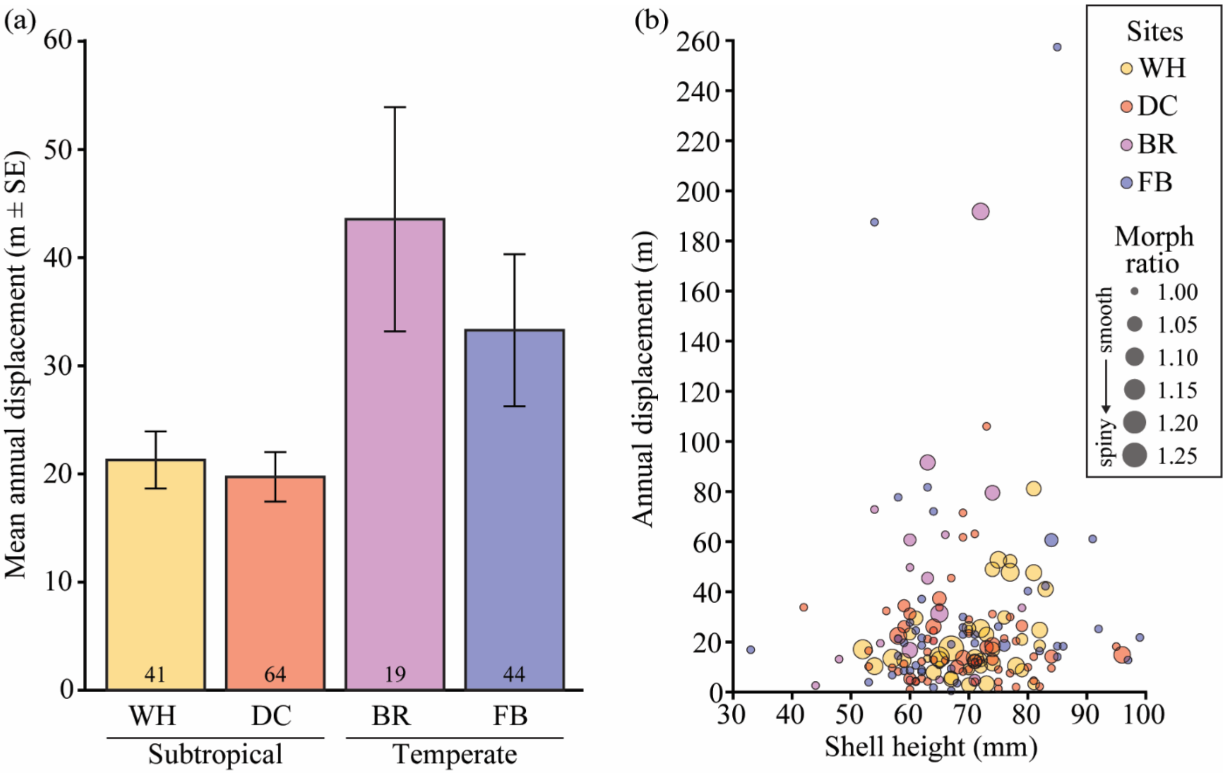


Figure 4.4. Mean annual displacements (m ± SE) of *Turbo militaris* from mark-recapture surveys at four rocky shore sites, Woody Head (WH), Diggers Camp (DC), Big Rocky (BR) and Fishermans Bay (FB) (a) in New South Wales, Australia. Numbers at the bottom of the bars represent the sample size at each site. Relationship between shell height (mm) at tagging and annual displacements (m) of individuals (b), showing the morphology ratio (ratio of shell width with spines to shell width without spines) as bubbles.

4.3.3 Shell size and morphology

Average shell height of snails at tagging was ~70 mm at all sites except Big Rocky, where average shell height was smaller (Table 4.1). A wide size range of snails were tagged at each site, except at Woody Head, where few small and few large snails were found (Table 4.1, Appendix B: Figure B1). The size range of recaptured snails was narrow, especially at Woody Head (Table 4.1). The recapture rate was not related to shell height (p = 0.923, Appendix B: Table B4). At tagging, snails were of predominantly spiny morphology at Woody Head, mostly smooth at Diggers Camp and Fishermans Bay, and had an approximately equal proportion of smooth and spiny animals at Big Rocky (Table 4.1). Recaptured snails at Woody Head and Big Rocky were of predominantly spiny morphology, and mostly smooth at Diggers Camp and Fishermans Bay (Table 4.1).

Snails of different sizes and shell morphologies occurred in similar habitats. Snails of different sizes often clustered together, with small snails generally found behind large snails. Movement distance, elevation change, and direction were not significantly related to shell height (*p* = 0.113, Figure 4.4b, Figure 4.5a and Figure 4.6) or shell morphology (*p* = 0.333, Figure 4.4b) (Appendix B: Tables B1 and B2).

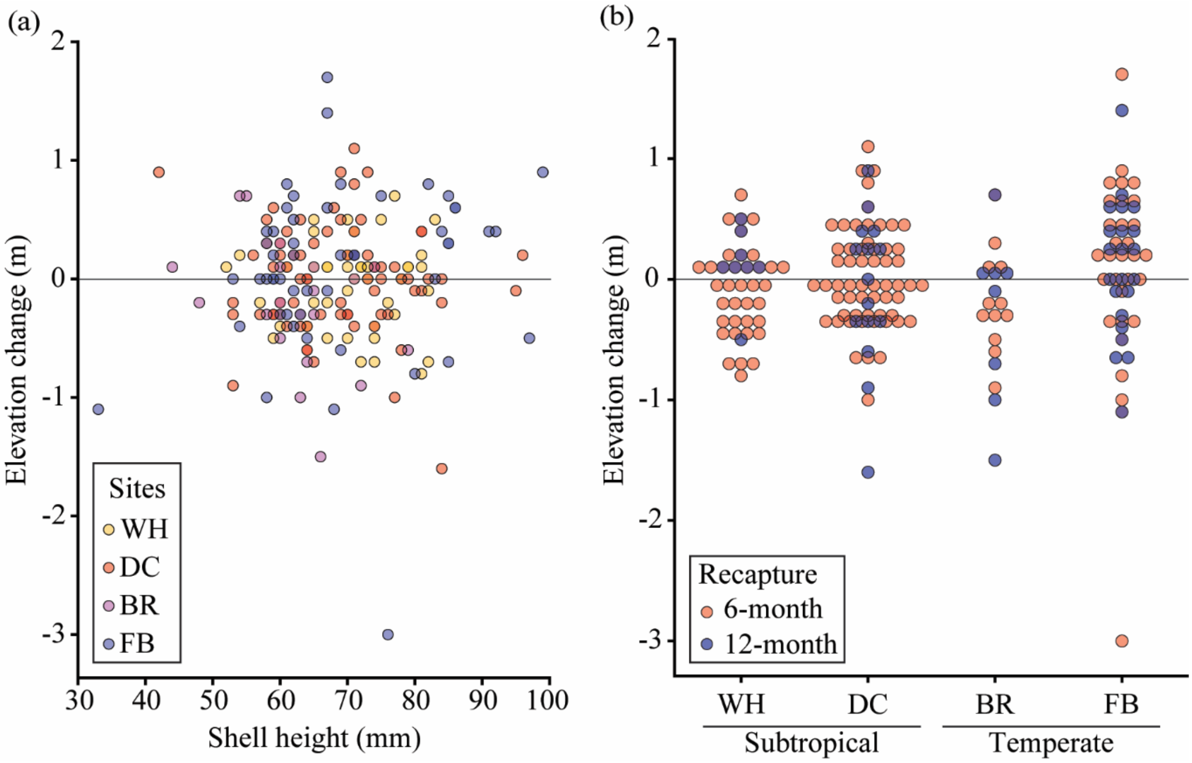


Figure 4.5. The relationship between shell height (mm) at tagging and change in elevation (m) of *Turbo militaris* (a), and the change in elevation (m) of *T. militaris* over two recapture periods (b), from mark-recapture surveys at four rocky shore sites, Woody Head (WH), Diggers Camp (DC), Big Rocky (BR) and Fishermans Bay (FB) in New South Wales, Australia.

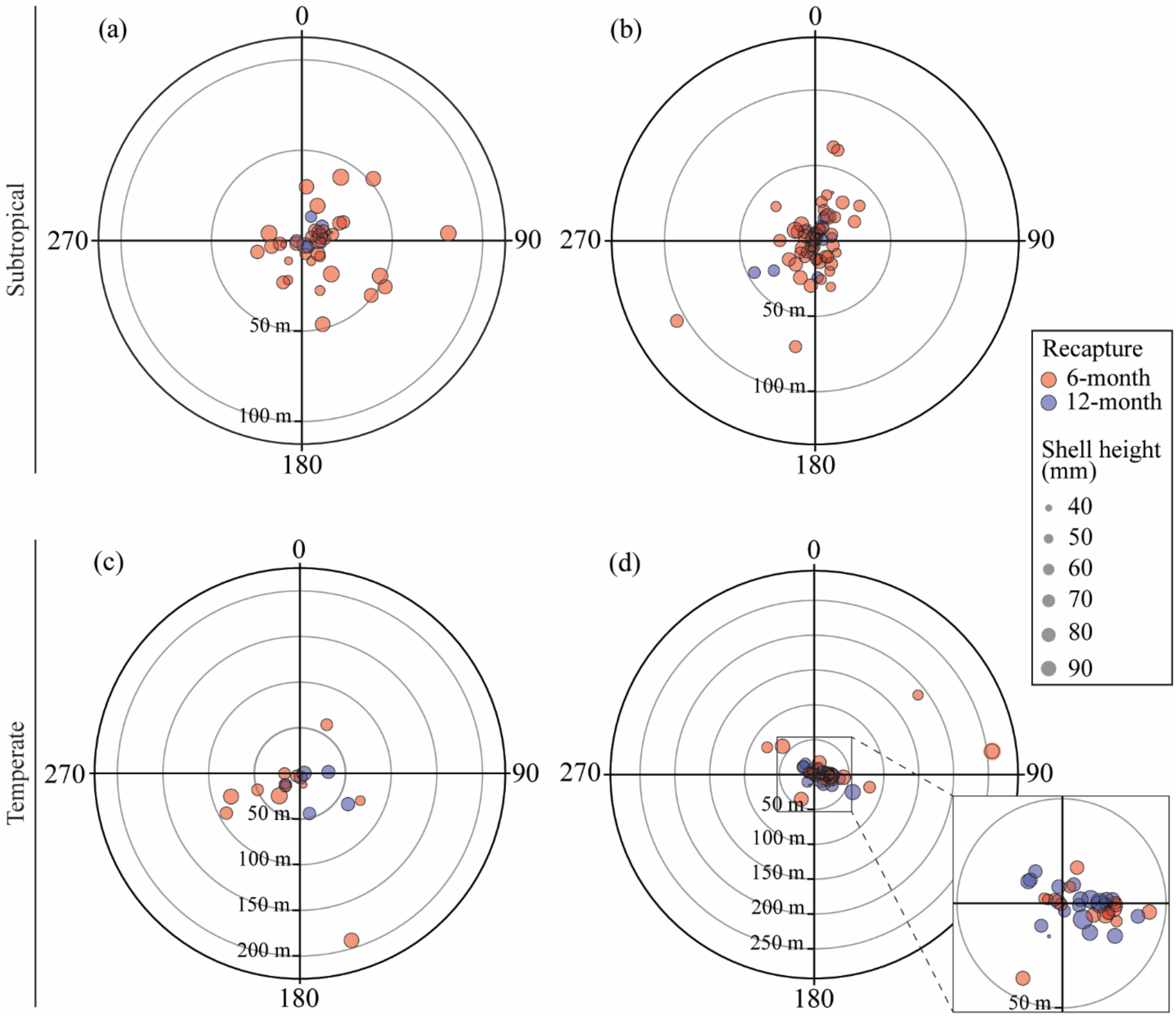


Figure 4.6. Direction and distance of annual displacements of *Turbo militaris* over two recapture periods at (a) Woody Head, (b) Diggers Camp, (c) Big Rocky and (d) Fishermans Bay, New South Wales, Australia. Shell height (mm) at tagging is shown as bubbles.

4.3.4 Movement

Movement of *T. militaris* was haphazard, with no apparent common direction, and snails tagged in the same area often travelled in opposing directions (Figure 4.3 andFigure 4.6). Mixing was extensive, with no evidence of home-ranging (Figure 4.3). Snails were generally found in known favourable habitat and rarely in unfavourable habitat, such as sand. Snails moved within areas where habitat provided suitable rocky structures and refuges, such as around small, protected coves, and fringe habitat at subtropical sites (Figure 4.3a,b) or around rocky outcrops at temperate sites (Figure 4.3c,d). Movement rates varied, but most snails were recaptured within the same topographic feature where they were tagged (movements were not extensive) and snails mixed within these localities (Figure 4.3). For example, at Diggers Camp, recaptured snails were found within two areas where they had been tagged but varied in movement within these clusters (Figure 4.3b). Snails recaptured during both 6-month and 12-month recapture surveys were generally not recaptured in the same location both times (Figure 4.3).

Turbo militaris mixed between intertidal and subtidal zones on each rocky shore (Figure 4.3), but in no specific direction (Figure 4.3 and Figure 4.6) or change in elevation (Figure 4.5b, Appendix B: Figure B4). At all sites, snails moved across, up, and down the shore. At all sites, nearly equal percentages of snails moved upshore (45%) and downshore (44%), and some (11%) did not change elevation. Animals often moved across the shore, commonly along edge habitat, such as on the northeastern shores at temperate sites (Figure 4.3e,d) or along edge habitats at subtropical sites (Figure 4.3b). Most snails were recaptured in intertidal or the adjacent shallow subtidal areas, but rarely in the deep (>2 m) offshore habitat (Figure 4.3). Most snails tagged on deep subtidal reefs (~3 m) were not recaptured (Figure 4.3, Appendix B: Figure B2).

4.4 Discussion

4.4.1 Movement

On rocky shores in south-eastern Australia, *T. militaris* were fairly localised and moved only ~20–44 m per year. Our findings are similar to another similar-sized Australian turbinid, *Lunella torquata,* that moved <3 m per day and up to 30 m (for large snails) per month (Ettinger-Epstein & Kingsford, 2008). Other smaller turbinids (and trochids) moved ~1 m per month (Yeo et al., 2024). In contrast, abalone species of similar size move greater distances, including 200–400 m in 10 months by *Haliotis discus* in South Korea (Hwang & Shin, 2010), 20–250 m in 6 months by *H. laevigata* in South Australia (Shepherd, 1986), 1–150 m per month by *H. rufescens* in California (Ault & Demartini, 1987) and 7.8–80 m in 14 months by *H. corrugata* in California (Coates et al., 2013). Last, a similarly sized gastropod, *Rochia nilotica*, moved 30–40 m in three weeks in Northern Philippines (Capinpin Jr, 2018) and 24 m in one month in the Solomon Islands (Clarke & Komatsu, 2001).

We quantified long-term movement, but short-term movement of *T. militaris* is up to 3 m per day (unpublished data), like the similar-sized crown conch, *Melongena corona,* that moved ~7 m per day (Hamilton, 1996). Larger queen conch, *Aliger gigas* (almost 3-times larger than *T. militaris*), move large distances on sand bottoms (Glazer et al., 2003; Doerr & Hill, 2013; Stieglitz & Dujon, 2017), with annual movement of 170–330 m (Hesse, 1979). Movement and habitat use may differ over diurnal cycles (Hayakawa et al., 2018), although gastropods are generally nocturnal (Hughes, 1986). Herbivorous gastropods are more mobile at night, to forage and avoid predators (Ault & Demartini, 1987; Chapman, 2000; Taniguchi & Rogers-Bennett, 2001). In our study, turban snails did not actively move during the day at low tides when we sampled, so low mobility and use of refugia during daytime may affect detectability of snails to harvesters (Lasiak, 1991). Further studies of short-term movements, and nocturnal activity of *T. militaris* would enhance understanding of the ecology of this species.

Movements of intertidal marine gastropods may be affected by oceanographic conditions and seascape topography, which may explain why we found *T. militaris* movement was more variable at south-facing temperate sites that predominantly received south-easterly swells and winds that often caused waves and turbulent water onshore. Movement may result from turbulent water (Walsby, 1977), which could explain the few large displacements and high displacement variability at these temperate, more exposed sites. However, rough water conditions could limit movement of gastropods that clamp down on substrate or seek shelter during rough seas (Walsby, 1977; Stoner & Lally, 1994). Shell morphology may positively influence protection in turbulent conditions, because protuberances like spines may allow snails to wedge into substrate for security (Kurihara et al., 2006). Understanding how oceanographic conditions affect dispersal of benthic animals is complex, yet important, especially if storm events increase in size and occurrence (Sheehan, 2019).

Turbo militaris mixed haphazardly in intertidal and shallow subtidal zones in areas of suitable turban snail habitat. Turban snails are generally restricted by the presence of suitable habitats which include highly complex topography (Ettinger-Epstein & Kingsford, 2008; Smoothey, 2013; Cooling & Smith, 2015) and as generalist herbivores, includes reefs with high abundances of macroalgae (including turfing algae, coralline algae and erect macroalgae) (Walsby, 1977; Worthington & Fairweather, 1989; Ettinger-Epstein &

Kingsford, 2008; Hayakawa et al., 2018; Lloyd et al., 2020). Some rocky shore gastropods are home ranging, such as some limpets (Mackay & Underwood, 1977; Creese, 1980) and the abalone, *H. corrugata* (Coates et al., 2013), while others are nomadic, moving haphazardly such as the periwinkle, *Littorina littorea* (Petraitis, 1982). High variability in movement distance and direction of *T. militaris*, without large movement, suggest that this species might occupy large ranges within which they move randomly. Haphazard movement was especially apparent for snails recaptured after both 6 months and 12 months, with none remaining in the same location, thereby suggesting snails have no home site. Movement of marine gastropods differs between habitat types (Yeo et al., 2024). In our study, patches of optimal substrate were sometimes isolated by unfavourable substrate, such as sand, which may have constrained movement at some sites (i.e., the offshore reefs at Woody Head). Long-term movement patterns of herbivorous snails over seasonal or interannual timescales could fluctuate in response to changes in macroalgal communities (Hayakawa et al., 2021). Whether mobility in our study remains the same or changes from year to year could be a key consideration for managing this species. Future studies should address interannual movement and microhabitat use to forecast population changes in response to habitat changes.

Individuals of differing sizes and shell morphologies (ranging from smooth, through incipient bumps, to prominent spines (Beechey, 2005; Smith et al., 2007)) often coexist in the same habitats (Beechey, 2005). When the snails are aggregated in tight clusters, smaller individuals are generally found sheltering behind larger individuals (pers. obs.), suggesting that larger animals could have greater displacement as they can move out of the refuges more readily. However, in our study, the size of *T. militaris* was similar among areas and unrelated to movement distance, direction, and the extent of upshore-to-downshore movement. Our findings contrast to other studies of gastropod movement (Hesse, 1979; Shepherd, 1986; Ault & Demartini, 1987; Ettinger-Epstein & Kingsford, 2008; Doerr & Hill, 2013; Stieglitz & Dujon, 2017; Capinpin Jr, 2018), perhaps because small snails that might not move far were under-represented in our study. Mobility and spatial segregation is size-related in other species of turbinid and trochid gastropods, wherein large individuals occupy deeper waters (Takada, 1996; Taniguchi & Rogers-Bennett, 2001; Ettinger-Epstein & Kingsford, 2008; Seinor et al., 2020), where ontogenetic habitat shifts are facilitated by downward movement (Walsby, 1977; Capinpin Jr, 2018; Hayakawa et al., 2018). Large snails may move greater distances and mix more across habitats (Ettinger-Epstein & Kingsford, 2008). In contrast, smaller snails are cryptic, less mobile and often remain sheltered in shallow, complex habitats that offer protection (Castell et al., 1996; Taniguchi & Rogers-Bennett, 2001; Smoothey, 2013), such as shallow areas of (articulated coralline) algal turf (Walsby, 1977; Worthington & Fairweather, 1989; Hayakawa et al., 2018). Other marine gastropods, such as abalone and queen conch, are similar in movement and habitat use (Hesse, 1979; Shepherd, 1986; Ault & Demartini, 1987; Doerr & Hill, 2007; Stieglitz & Dujon, 2017). In contrast, our study and others that found no size-related movement (Hamilton, 1996; Marshak et al., 2006; Hazlett, 2009) illustrate that movement is not universal across the class Gastropoda.

4.4.2 Mark-recapture

Recapture rates of tagged *T. militaris* in our study (25% overall) were similar to other studies using similar methods, including a 24% recapture rate of *A. gigas* over three years in St. John, U.S. Virgin Islands (Doerr & Hill, 2013) and a ~9% recapture rate of *L. torquata* over ~ three years in NSW (Kienzle et al., 2022). More frequent recapture surveys generally increase the recapture rate of marine gastropods, such as a 90% recapture rate from daily sampling for three months (Hazlett, 2009) and a 58% recapture rate from periodic sampling over 11 years (Ault & Demartini, 1987).

Tagged snails may not have been recaptured in our study due to reduced detectability of tagged animals or tag loss, similar to 18% tag loss in another mark-recapture study of *L. torquata* using similar glue-on tags (Ettinger-Epstein & Kingsford, 2008). Many gastropods, such as abalone and turban snails (including *T. militaris*), occupy narrow rock crevices (Shepherd, 1986; Ault & Demartini, 1987), so glue-on tags may shed from abrasion against rock or other shells. Biofouling of tags is also a problem that can reduce detectability (Heslinga & Orak, 1984), as in our study. A higher recapture rate could result from using more conspicuous tags (Castell et al., 1996) or permanent tags (Heslinga & Orak, 1984; Kikutani, 1991; Prince, 1991; Doerr & Hill, 2013; Stieglitz & Dujon, 2017).

Whilst our recapture searches were extensive (Appendix B: Figure B2), our study may be biased towards shorter movement distances, or shallow areas, due to sampling limitations. However, during our recapture surveys, we found many non-tagged snails up to ~500 m away from tagging locations. Furthermore, no tagged *T. militaris* were found at two nearby rocky shores that were frequently visited during the field campaign. One of these sites was ~1 km away from Woody Head, separated by sand and patches of algae-covered substrate, and the other was adjacent (~200 m away) to Big Rocky, separated by exposed rocky coastline with suitable turban snail habitat. These observations indicate that long-distance movement did not likely explain a large proportion of non-recaptured snails. Additionally, some snails, may have moved to inaccessible areas within sites (i.e., more turbulent areas) (Ault & Demartini, 1987). For example, the coastline surrounding the Big Rocky site has suitable snail habitat that is generally inaccessible for sampling due to high wave action, which could have reduced recapture rates at this site. *Turbo militaris* prefer highly complex habitats and can be found in depths of up to 20 m (Mohring, 2007; Cooling & Smith, 2015), so snails may have moved to areas that were inaccessible to snorkelling. The use of snorkelling limited the ability to safely sample deeper waters and thoroughly search complex subtidal habitats, likely resulting in an underrepresentation of snails in these areas.

Tagged snails in our study might have been removed by natural predation or human harvesting, as we observed fishers collecting invertebrates from shore at Big Rocky and Woody Head and the recapture rate was higher at Diggers Camp that was closed to harvest (NSW DPI, 2024). Removal by natural predators was also possible, as we observed notable numbers of natural predators, *Dicathais orbita* and *Octopus tetricus* (Taylor & Glover, 1999; Steer & Semmens, 2003) at some sites and *O. tetricus* preying on a tagged snail at Big Rocky.

Handling snails for tagging may cause stress during removal from the water and preparing shells for tagging by scrubbing off epibiota (Prince, 1991). For example, short-term movements by *T. militaris* were similar for snails tagged with glue-on tags and a quicker, temporary numbered band placed on the shell (unpublished data). Over two time periods, handling stress increased movement up to a couple of metres per day for a few days (unpublished data). Increased movement several days post-tagging has been demonstrated in other marine invertebrates, including gastropods (Shepherd & Godoy, 1989; Werner et al., 1995), crustaceans (Atkinson et al., 2005; MacArthur et al., 2008) and echinoderms (Shiell, 2006). Nevertheless, our study examined movements over a longer timescale, diluting short-term effects.

Our mark-recapture sampling design was robust, because the study was over an extended timeframe, at spatially separated sites and for a wide size range of snails. Furthermore, we measured movement from the starting position of each snail, unlike other studies that tracked movement from a common starting origin where animals were released after tagging (Walsby, 1977; Shepherd, 1986; Clarke & Komatsu, 2001; Capinpin Jr, 2018; Yeo et al., 2024).

4.4.3 Fishery management implications

For *T. militaris*, connectivity between intertidal and subtidal zones was limited in our study, with snails mostly mixing between the eulittoral zone and infralittoral fringe, and movement to and from deeper subtidal regions was not apparent. *Turbo militaris* can be highly abundant and densely aggregate in the eulittoral zone, where they are readily harvested at low tide, so our findings suggest that harvesting could deplete snails in shallow areas. Strong upshore movement of adult snails as a response to lower intraspecific competition into intertidal areas, where recreational harvesting pressure is highest, would have suggested a stock recovery mechanism by which subtidal animals replenish the harvested intertidal stock to buffer the whole population (Lasiak, 1991; Proudfoot et al., 2006; Cooling & Smith, 2015). However, movement was haphazard in our study, with limited upshore movement, which suggests that the potential for adults to migrate upward and repopulate depleted sites is limited. However, at sites where harvesting is prohibited (Diggers Camp) or limited in accessibility (Big Rocky), release from competition for resources to facilitate upward migration was likely limited. In addition, harvesting at other sites may have been insufficient to reduce intraspecific competition.

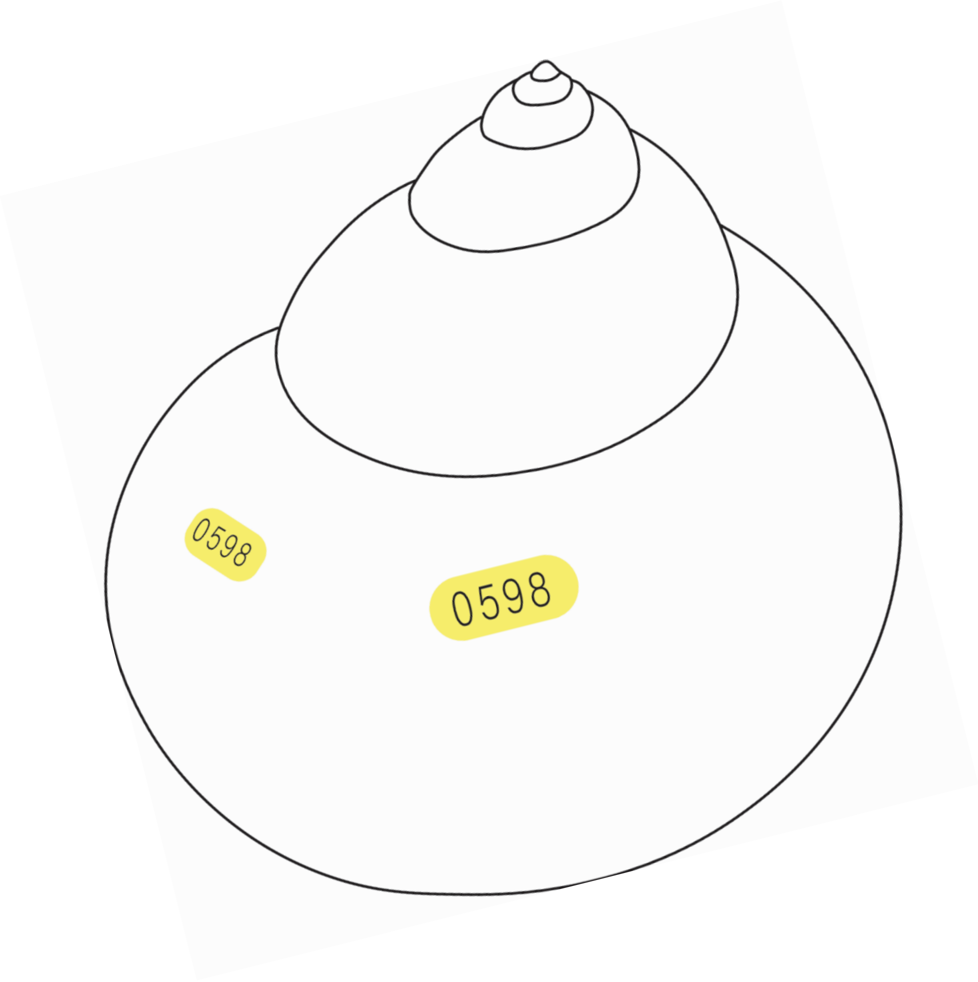
Non-directional movement we found suggests that movement of snails upshore to the intertidal zone, where they were available for collection, was countered by our finding that snails also moved equally downshore. Such movement patterns may provide conservation benefits to subtidal snails, wherein snails remaining in or moving to deeper habitats may be more safeguarded from recreational harvesting by occupying habitats that are less accessible (Cooling & Smith, 2015). However, conservation benefits of natural refuges are likely to be disproportionate across sites due to commercial fishing. Our study was constrained to the intertidal shore and adjacent shallow subtidal reefs, so future studies of movement and connectivity on deeper reefs would be valuable for informing commercial fishery harvest strategies.

Population dispersal for most aquatic gastropods is primarily driven by pelagic larvae movement, facilitating broader scale connectivity (Cowen & Sponaugle, 2009; Allen et al., 2018; Sheehan, 2019). Adults, in contrast, have slower locomotion and are often considered to have a more modest effect on population dispersal (Nathan et al., 2008; Sheehan, 2019; Wyeth, 2019). In NSW, many rocky shores are often punctuated by patches of sand or long stretches of sandy coastline (unsuitable habitat). The findings from our study suggests that unsuitable habitats may inhibit snail movement to nearby areas, so adult snails might be constrained to each rocky shore. Thus, adult movement would likely facilitate connectivity to only localised areas of suitable habitat, but haphazardly. *Turbo militaris* are not genetically differentiated across NSW (Nimbs et al., 2023), so populations at isolated rocky shores would need to be linked by larval supply.

Our study of *T. militaris* expands previously limited knowledge of turbinid gastropods and provides empirical data to support management of this important, spatially restricted species. Due to the limited movement of snails to other areas, spatial protection would be suitable for safeguarding existing adult populations in high-harvest areas. To protect against local depletion by harvesting, management should consider enhancing the existing network of spatial protection for *T. militaris* in NSW. Spatial management of rocky shores with suitable habitat as 'no-take' areas would complement other measures, such as size and bag limits, to ensure long-term sustainability of large vulnerable intertidal gastropods such as *T. militaris*.

CHAPTER 5.

LATITUDINAL VARIATION IN AGE AND GROWTH OF A HARVESTED, MARINE GASTROPOD (TURBINIDAE)



Chapter 5 is in preparation for submission to a peer-reviewed academic journal.

Abstract

Harvested marine resources require ecological knowledge to inform effective fisheries management. Marine gastropods, including turban snails (Turbinidae), are highly sought for human harvest. In Australia, *Turbo militaris* is culturally, commercially and recreationally fished in New South Wales (NSW), yet there is limited biological knowledge to inform its management. This study uses mark-recapture to assess growth and develop age-and-growth models for *T. militaris* at four rocky shores in NSW. Growth varied across subtropical to temperate regions spatially separated by ~350–400 km. Temperate snails attained a larger asymptotic size than subtropical snails (108 mm, 94 mm, for temperate and subtropical snails, respectively), a greater growth coefficient (*K*) (0.57 year^{-1}, 0.29 year^{-1}), higher natural mortality (*M*) (0.57 year^{-1}, 0.37 year^{-1}) and lower longevity ($T_{\max}$) (5 years, 10 years). Sexual maturity (36.5 mm shell height, 95% CI: 34.5–38.3 mm) was attained by temperate snails at 0.7 years (estimated age range: 0.7–0.8 years), allowing approximately 1.5 years of reproduction before entering the fishery at 78 mm shell height, whereas subtropical snails reach maturity at 1.7 years (estimated age range: 1.6–1.8 years) and have approximately 4.4 years before reaching the harvestable size. Our findings indicate that current minimum size-limits are appropriate across the fishery in terms of ensuring population replenishment. This study highlights the disparities in life-history parameters across latitudes within a species of Gastropoda. The fast-growing temperate snails' shorter lifespan and higher mortality suggest greater resilience to stress due to higher turnover. In contrast, the subtropical snails are likely to have greater vulnerability to environmental stress or depletion if overfishing occurs due to slower recovery.

5.1 Introduction

Demands on marine resources as seafood have led to an increased pattern of stocks fished above sustainable limits (FAO, 2024), negatively impacting global food security and future human health (Golden et al., 2021; Tacon, 2022). Thus, underutilised or small-scale fisheries, including marine gastropods, are increasingly used as alternatives to supplement overfished stocks (Leiva & Castilla, 2002; Anderson et al., 2011). Harvested species must be managed effectively to ensure future sustainability (Teixeira & Silva, 2023), which relies on relevant biological information on target species. For example, commercial harvest quotas and recreational bag limits are informed by the growth rates and longevity of target species (Perry et al., 1999). However, there is often a lack of research to inform management decisions for regional or small-scale fisheries (Anderson et al., 2011).

Biological and ecological data provide essential information for predicting population responses to stress, such as from heavy harvesting or future climate conditions. Life-history studies on target species are pivotal for identifying overfishing, guiding effective decision-making for conservation measures, and informing fisheries management and harvest strategies (Cochrane, 2002; Anderson et al., 2011; Quist et al., 2013). Age and growth studies provide essential life-history parameters in fisheries science, such as growth rate, maximum size, longevity, age/size at maturity, age at recruitment into the fishery and natural mortality rate (Das, 1994; Ramesh et al., 2009; Quist et al., 2013; Kienzle et al., 2022). For management, age and growth research helps to determine time between sexual maturity and recruitment to the fishery, informing biologically appropriate fishery regulations such as allowable catch, bag limits and size limits (Das, 1994; Cochrane, 2002; Quist et al., 2013; Keane et al., 2014; Ashfaq et al., 2019). Age and growth studies, combined with information on reproduction can guide biologically appropriate size-limits. Specifically, information on reproductive periodicity, fecundity, growth rate, size, and age at maturity can be used to model a harvesting size that allows for a period of reproductive activity before entering the fishery (McShane & Naylor, 1995; Stoner et al., 2012; Prince & Hordyk, 2018).

Direct observations, including mark-recapture field studies, are the most accurate way to determine age (Quist et al., 2013). Mark-recapture experiments use measurements of individual growth increments in the field, providing data suitable for age-and-growth modelling (Henry & Jarne, 2007; Quist et al., 2013; Hollyman et al., 2018b). Mark-recapture has been widely used to study growth in a range of marine gastropods (Frank, 1969), including abalone (Day & Fleming, 1992; Mgaya & Mercer, 1994; Catchpole et al., 2001; Dixon & Day, 2004), conch (Appledoorn, 1988; Peel & Aranda, 2012), murex (Vasconcelos et al., 2006), trochus (Smith, 1987) and turban snails (McLachlan & Lombard, 1981; Bourgeois et al., 1997; Martone & Micheli, 2012; Keane et al., 2014; McCann & Johnson, 2021; Kienzle et al., 2022).

The von Bertalanffy growth function is the most widely used method for mathematical modelling of age and growth in fisheries science, (von Bertalanffy, 1938; Quist et al., 2013) and has been applied to model growth in a range of marine gastropods (Frank, 1975; McLachlan & Lombard, 1981; Smith, 1987; Bruton et al., 1991; Day & Fleming, 1992; Mgaya & Mercer, 1994; Vasconcelos et al., 2006; Cárdenas & Aranda, 2014). The form of the von Bertalanffy growth function includes a growth rate declining with size and the asymptotic size reached later in life (von Bertalanffy, 1938). Key life-history parameters are derived from growth modelling. These include asymptotic size, the average maximum size (L_∞), and the Brody growth co-efficient (K), the rate (year^{-1}) at which an animal approaches asymptotic length (Froese & Pauly, 2000).

Growth models are fundamental to estimating key fisheries parameters, including longevity (T_{max}) and natural mortality (losses from non-fishing causes) (M) (Pauly, 1980; Froese & Pauly, 2000). Size at first sexual maturity (LM_{50}) is a common fishery metric to inform size limits, defined as the size at which half the population of a given size class are reproductively mature; age can then be modelled using an inverse von Bertalanffy equation (von Bertalanffy, 1938). Age and growth parameters provide insights into fishing resilience, overfishing vulnerability, recovery potential and population dynamics (Then et al., 2015). These parameters are essential for fisheries assessments and informing management strategies such as sustainable fishing limits (Frank, 1975; Das, 1994).

Marine gastropods have a logarithmic growth pattern, where growth slows as the individual ages or achieves a larger size (Smith, 1987; Vasconcelos et al., 2006; Peel & Aranda, 2012). Slower growth may coincide with maturity as energy is diverted from somatic growth to reproduction (Prince et al., 1988); at this time, some species have determinate growth (Frank, 1969). Moderate rates of growth have been estimated for trochus species, *Tectus pyramis* (Frank, 1969) and *Rochia nilotica* ($K = 0.25$ year^{-1}, $L_\infty = 146.5$ mm) (Smith, 1987).

Several studies on the large abalone *Haliotis tuberculata* (L_∞ = >100 mm) indicate that growth rate ranged from fast (K = 0.45 year^{-1}) to moderate (K = 0.25 year^{-1}) (Mgaya & Mercer, 1994). Fast growth occurred in the medium-sized murex, *Hexaplex trunculus* (K = 0.41 year^{-1}, L_∞ = 82.76 mm) (Vasconcelos et al., 2006) and the large conch, *Aliger gigas* (K = 0.36 year^{-1}, L_∞ = 251 mm) (Peel & Aranda, 2012). Large species are generally longer lived, such as *Turbo sarmaticus,* which can live up to 11 years (Bruton et al., 1991), *Haliotis tuberculata* and *R. nilotica* up to 15 years (Smith, 1987; Mgaya & Mercer, 1994), and *A. gigas* up to 19 years (Cárdenas & Aranda, 2014).

Growth in marine gastropods can exhibit interspecific (Smith, 1987; Vasconcelos et al., 2006), seasonal (Frank, 1969), habitat-associated (McShane et al., 1988; Boman et al., 2019) or geographical variability (McShane & Naylor, 1995; Stoner et al., 2012). Furthermore, size at maturity can vary within a single species over different spatial scales (Stoner et al., 2012; Boman et al., 2018; Borsetti et al., 2018). Geographical trends in growth are not uniform. Some species (i.e., *Buccinum undatum*) exhibit larger sizes and faster growth in cooler regions of higher latitudes (Dehnel, 1955; Emmerson et al., 2020), while some others (i.e., *Tegula funebralis*) may grow faster in tropical regions (Frank, 1969, 1975). Faster growth at warmer temperatures has been found in laboratory studies of the whelk *Rapana venosa* and juvenile abalone, *Haliotis iris*; however, this depends on animal size and thermal limits (Searle et al., 2006; Hu et al., 2021). Therefore, latitudinal differences in growth would be hard to predict.

In Australia, turban snails, *T. militaris*, *Lunella torquata* and *L. undulata* are targeted by commercial, cultural and recreational fishers. Turban snails are commercially harvested through the combined sea urchin and turban snail (SUTS) fishery in New South Wales (NSW) (NSW DPI, 2018b; Chick, 2023). *Turbo militaris* is a primary target in the SUTS fishery, and harvesting of this species has generally increased over the last decade (*T. militaris* yielding 4.8 t in 2023) (NSW DPI, 2018b; Chick, 2023). The stock status of turban snails in the SUTS fishery is ‘undefined’ due to limited data (Rowling et al., 2010; Stewart et al., 2015). The extent of non-commercial harvesting of turban snails in NSW is undefined, but is likely to be of a similar magnitude to commercial harvesting (DCCEEW, 2018a). Turban snails are a traditional resource for First Nations Australians, and cultural harvesting is still practised in many Indigenous communities (Smith et al., 2006; Arrawarra Sharing Culture, 2009). In NSW, *T. militaris* and *L. torquata,* are also popular targets for recreational fishers collecting invertebrates on intertidal rocky shores (NSW DPI, 2023). Turban snail fisheries in NSW are governed by minimum legal-size limits (shell size >75 mm), bag limits (20 individuals per person, per day) and spatial regulations through marine park zoning and commercial fishing exclusion zones (NSW DPI, 2018b, 2023, 2024).

Turbinids are a nutrient-dense species that are increasingly important to fisheries, and potentially vulnerable to the threats of both overharvesting and climate change (Leung et al., 2017; Ab Lah et al., 2018; Son et al., 2020), yet there are few studies on their life-history. Globally, age and growth research is limited to seven turbinid species across eight studies (McLachlan & Lombard, 1981; Sire & Bonnet, 1984; Bourgeois et al., 1997; Gluyas-Millán et al., 2000; Pulfrich & Branch, 2002; Martone & Micheli, 2012; Keane et al., 2014; Kienzle et al., 2022). Studies of growth in Australian turban snails are limited to two species, *L. undulata* and *L. torquata* (Keane et al., 2014; Kienzle et al., 2022) and data on size at maturity is restricted to the smaller species, *L. undulata* (Keane et al., 2014). In Australia, biologically appropriate management of turban snail fisheries is constrained by limited life-history data, especially in NSW where *T. militaris* comprises most commercial catch and is a primary recreational target. There are no studies on age, growth, longevity, natural mortality or size at maturity for *T. militaris*, despite the ecological and fisheries significance of this species and the clear need for relevant biological data to support informed management.

This study aimed to use mark-recapture to assess the growth rate across a range of size classes and develop age-and-growth models for *T. militaris* from subtropical and temperate regions of NSW. Specific objectives were to: assess the average maximum size; infer longevity and natural mortality from size-at-age curves; determine the age at legal harvesting size; and establish size and age at first maturity. This work will directly support the management of turban snails in NSW. More broadly, it also provides insights into the general trends in age and growth for marine gastropods over latitudinally separate regions and potential outcomes for fished populations in future climate conditions.

5.2 Methods

5.2.1 Mark-recapture surveys

Mark-recapture surveys were conducted at two subtropical rocky shore sites (Woody Head, 29.4° S and Diggers Camp, 29.8° S) and two temperate sites (Big Rocky and Fishermans Bay, both at 32.8° S) in NSW, Australia (Figure 5.1a). The warm poleward flowing East Australian Current (EAC) deviates from the coast between 31° S and 33° S forming an eastern extension before the southern extension, a poleward system of eddy fields (Suthers et al., 2011; Phillips et al., 2022), facilitating a substantial temperature difference between the subtropical and southern temperate regions in our study. Water temperatures are warmer at subtropical sites; during the study the water temperature averaged 22.5 °C and ranged from 26.8 °C to 18.3 °C (Figure 5.1b). At the temperate sites, the water temperature was cooler, averaging 21.1 °C and ranged from 25.5 °C to 17.4 °C (Figure 5.1b).

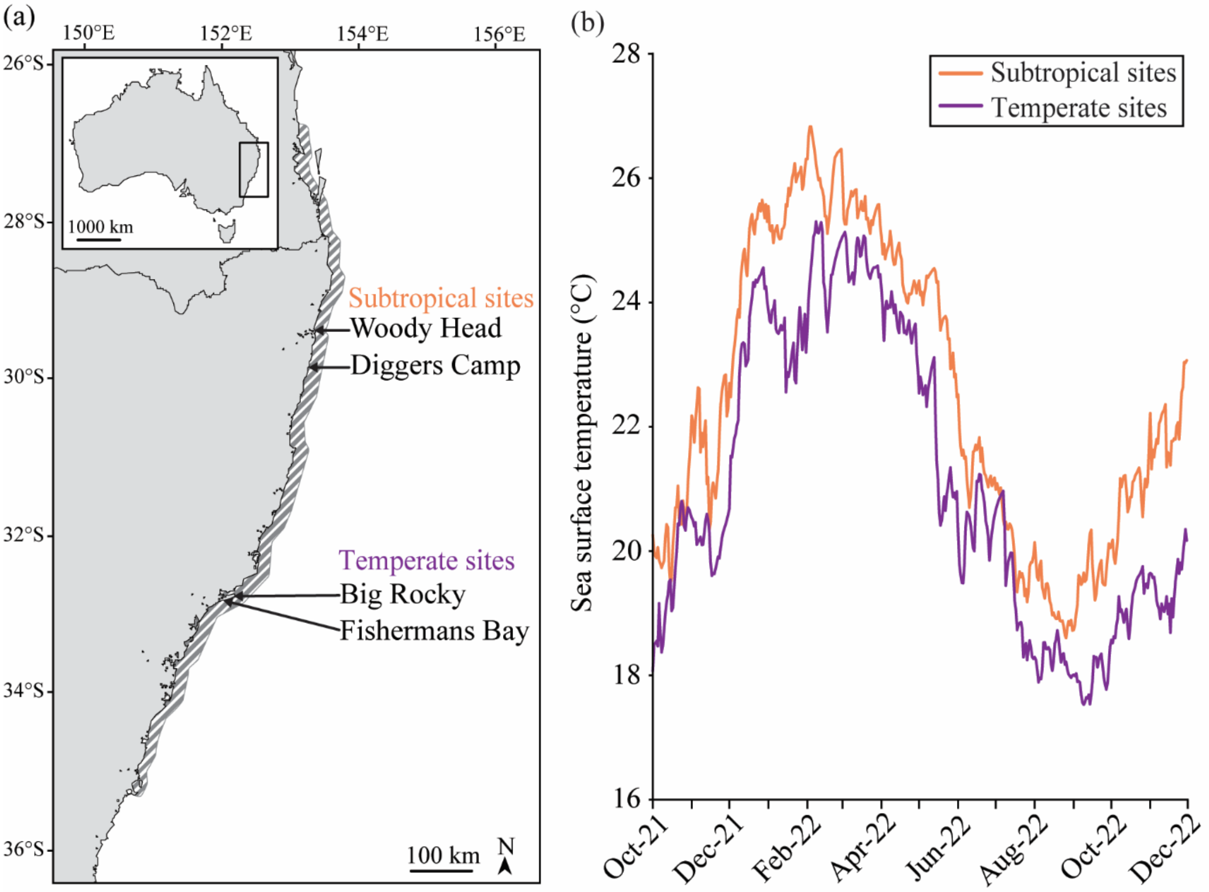


Figure 5.1. The approximate distribution of *Turbo militaris* (striped shading) and the location of the two subtropical study sites (Woody Head and Diggers Camp) and the two

temperate study sites (Big Rocky and Fishermans Bay) in New South Wales, Australia (a). Sea surface temperature at the subtropical and temperate sites throughout the study (data: E.U. Copernicus Marine Service Information; https://doi.org/10.48670/mds-00321) (b).

At each site, >140 *T. militaris* from intertidal and shallow subtidal reefs were tagged using twin, numbered glue-on tags (Seinor et al., 2025) (Figure 5.2a). There was no sampling preference for size class during tagging surveys and all animals encountered were measured and tagged. Recapture surveys occurred at approximately 6 months and 12 months after tagging. At tagging and each recapture event, the maximum shell height (apex to anterior canal) and maximum shell width (width of the final body whorl across the aperture) were measured to ± 1 mm using Vernier callipers (Figure 5.2b). Growth increment data were later extracted for age-and-growth modelling. Details of the mark-recapture experiments are provided in a parallel study on the movement of *T. militaris* (Seinor et al., 2025).

Figure 5.2. *Turbo militaris* tagged with twin glue-on numbered tags at Woody Head, New South Wales, Australia (a) and the maximum shell height measurement (b).

5.2.2 Growth modelling

For age-and-growth modelling, data from Diggers Camp and Woody Head were pooled to represent the subtropical sites and data from Big Rocky and Fishermans Bay were pooled to represent the temperate sites. Low recapture numbers and exploratory analysis deemed pooling data by region necessary to gain sufficient replication for analysis. For animals recaptured at both 6 and 12 months ($n = 23$), the final recapture data were used, and the first recapture data were omitted to avoid pseudo-replication.

Shell height was chosen as the metric for growth modelling due to the presence of spines on some animals, which potentially inflated the width measurements. Correlation analysis revealed that shell height and width (without spines) were highly correlated ($R = 0.97$; Appendix C: Figure C1).

Measurements of shell height at recapture minus the shell height at tagging provided data on growth increment. A standardised growth increment was calculated to correct for varying time at liberty (Equation 1).

$$(L_2 - L_1)(r/T) \qquad \text{(Equation 1)}$$

Where: L_1 = shell height at tagging (mm), L_2 = shell height at recapture (mm), r = recapture timeframe (years) and T = time at liberty (years).

For age-and-growth modelling, the Brody growth coefficient (K) and the theoretical average maximum shell height (asymptotic height) (L_∞) for the subtropical and temperate sites were parameterised using Fabens' model (Fabens, 1965) (Equation 2).

$$L_2 - L_1 = (L_\infty - L_1)(1 - e^{-KT}) \qquad \text{(Equation 2)}$$

Age-at-size curves were generated for the subtropical and temperate sites using the K and L_∞ parameters in the von Bertalanffy growth function (von Bertalanffy, 1938; Quist et al., 2013) (Equation 3).

$$L_t = L_\infty(1 - e^{-K(t - t0)}) \qquad \text{(Equation 3)}$$

Where: L_t = height at age t, t = age and $t0$ = expected height at age 0, assumed as zero (Appledoorn, 1988; Martone & Micheli, 2012; Quist et al., 2013). Longevity ($T_{\max}$) was approximated according to the Pauly (1980) equation (Pauly, 1980; Froese & Pauly, 2000) (Equation 4).

$$T_{\max} = 3K^{-1} \qquad \text{(Equation 4)}$$

To estimate overall natural mortality (M), the updated model derived from Pauly (1980) was used (Then et al., 2015) (Equation 5).

$M_{est} = 4.118K^{0.73}L_{\infty}^{-0.333}$ (Equation 5)

The age at the legal size-limit of shell height was calculated using an inverse von Bertalanffy growth function (von Bertalanffy, 1938; Mackay & Moreau, 1990; Froese & Pauly, 2000) (Equation 6).

$t = t0\text{-}\ln(1\text{-}Lt/L_{\infty})/K$ (Equation 6)

The legal size limit of shell width for turban snails in NSW is 75 mm (NSW DPI, 2018b, 2023), which corresponds to a shell height of 78 mm for *T. militaris* (Appendix C: Figure C1); therefore, in Equation 6, L_t was substituted with 78 mm.

5.2.3 Size at first maturity

Up to 50 turban snails (not tagged) were collected from the subtropical and temperate regions within a target size range of <50 mm shell height. The maximum shell height was measured, the shell cracked open, and the soft-bodied animal was removed. The gonad and digestive gland were visually assessed for first maturity; the female gonad has a dark green colour, and the male gonad has a cream colour (Seinor et al., 2023). Where no gonad development could be seen, and only the dark brown of the digestive gland was visible, the animal was classed as immature (as in, Keane et al., 2014). For representation of the larger size classes (>50 mm shell height), snails collected from a previous study on reproductive periodicity were included in the analysis (Seinor et al., 2023).

The height at which 50% of the population had reached first maturity (LM_{50}) was modelled using Bayesian regression. Preliminary analysis revealed that the separate models for each region yielded similar results (Appendix C: Figure C2). Therefore, data from both regions were combined in a single model. Age at first maturity was calculated using an inverse of the von Bertalanffy growth function (Equation 6) (von Bertalanffy, 1938; Mackay & Moreau, 1990; Froese & Pauly, 2000), where L_t was substituted with LM_{50}.

Age-and-growth modelling were performed in DataFit 9.0 (Datafit, 2009) and SigmaPlot Version 15.0. Bayesian regression analysis was performed using the sizeMat package in

RStudio (RStudio Team, 2020; Torrejon-Magallanes, 2020; R Core Team, 2021). Graphing was performed in SigmaPlot Version 15.0 and RStudio (RStudio Team, 2020; R Core Team, 2021).

5.3 Results

A total of 676 *T. militaris* were tagged across the four sites. Tagged turban snails were within a wide size range (21–104 mm) with similar size distributions among the subtropical and temperate sites (Appendix C: Figure C3). The recapture attempts recovered 90 tagged turban snails after six months at the subtropical sites and 43 at the temperate sites. After 12 months at liberty, 23 snails were recaptured at the subtropical sites, and 30 were recaptured from the temperate sites. At the subtropical sites, 13 snails were recaptured at both 6-month and 12-month recapture attempts (double recaptured), and 10 snails were double recaptured at the temperate sites. Recaptured snails were medium to large size (50–104 mm) and retained similar size distributions among pooled sites (Appendix C: Figure C4). Recaptured snails are the same as those mentioned in a parallel study on movement (Seinor et al., 2025).

5.3.1 Growth increment

For a given size of turban snail, the growth increment of shell height was generally greater at the temperate sites than at the subtropical sites after 6 and 12 months (Figure 5.3). The growth increment generally decreased with increasing animal size for both the subtropical and temperate snails (Figure 5.3). On average, turban snails at the temperate sites grew 10.4 mm (± 1 mm SE) after 6 months and 18.8 mm (± 1.4 mm SE) after 12 months whereas, at the subtropical sites, snails grew 3.3 mm (± 0.3 mm SE) after 6 months and 7.0 mm (± 0.7 mm SE) after 12 months. There was greater variability in the growth increment at the temperate sites (Figure 5.3).

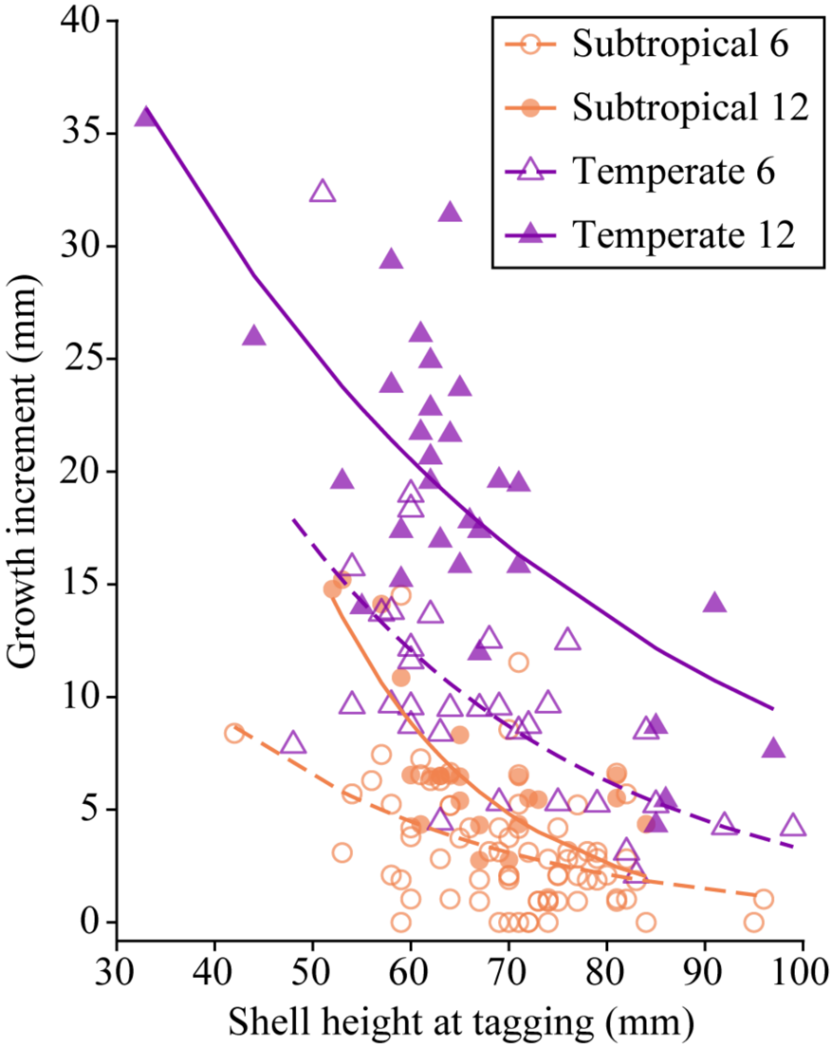


Figure 5.3. Relationship between shell height at tagging (mm) and standardised growth increment (mm) of *Turbo militaris* after 6 and 12 months at liberty at two subtropical sites (Subtropical 6 and Subtropical 12) and two temperate sites (Temperate 6 and Temperate 12) from mark-recapture experiments in New South Wales, Australia. Lines were fitted by an exponential decay function ($y = ae^{-bx}$).

5.3.2 Age-and-growth modelling

Age-and-growth modelling was done for 100 individuals from the subtropical sites and 63 individuals from the temperate sites. Age-at-size curves demonstrated that younger *T. militaris* grew rapidly, and growth slowed as the snails approached the average maximum shell height (L_∞) (Figure 5.4). The growth models indicated that the snails at the temperate sites grew faster and attained larger sizes than those at the subtropical sites (Figure 5.4). The Fabens' models were statistically significant (p <0.01), deriving an R^2 value of 0.41 for the model for subtropical sites and 0.63 for the temperate sites. Fabens' equations parameterised Brody growth coefficients (K) were 0.29 yr^{-1} (± 0.05 SE) for the subtropical sites and 0.57 yr^{-1} (± 0.1 SE) for the temperate sites (Table 5.1).

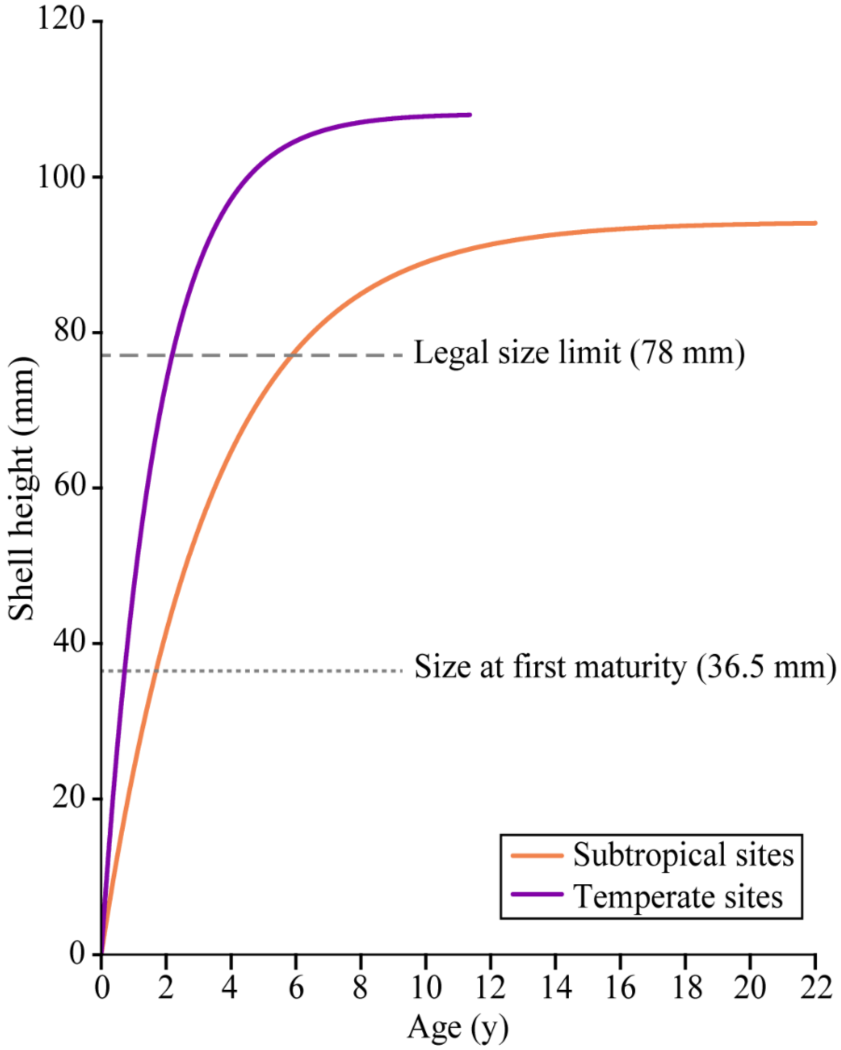


Figure 5.4. Estimated age-at-size curves derived from the von Bertalanffy growth function for *Turbo militaris* from two subtropical sites and two temperate sites in New South Wales, Australia. The dashed line represents the shell height at the legal-size limit and the dotted line represents the shell height at first sexual maturity.

The model produced a greater average maximum shell height of temperate *T. militaris* and an average maximum shell height that was 14 mm smaller at the subtropical sites (Table 5.1). The estimation of longevity was nearly double at the subtropical sites compared to the temperate sites (Table 5.1). The overall natural mortality rate for *T. militaris* at the subtropical sites was estimated at 0.37 yr^{-1} across all size classes and 0.57 yr^{-1} at the temperate sites (Table 5.1).

Table 5.1. Results from age-and-growth modelling for *Turbo militaris* at subtropical (n = 100) and temperate sites (n = 63) in New South Wales, Australia. Growth parameters of (L_∞) asymptotic shell height (mm ± SE) and (K) the Brody growth coefficient (yr^{-1} ± SE) were derived from Fabens' model. Estimates of ($T_{\max}$) longevity (years), (M) natural mortality (yr^{-1}) and age (years; 95% CI) at sexual maturity (LM_{50} = 36.5 mm; 95% CI: 34.5–38.3 mm) and legal harvesting size (78 mm shell height) were derived from the von Bertalanffy growth function. Years of maturity before reaching the age of legal size (Years mature/unfished) was calculated as the age at legal-size minus the age at LM_{50}.

Sites	L_∞	K	$T_{\max}$	M	**Age at LM_{50}**	**Age at legal-size**	**Mature/ unfished**
Subtropical	94 (5)	0.29 (0.05)	10.3	0.37	1.7 (1.6–1.8)	6.1	4.4 (4.3–4.5)
Temperate	108 (6)	0.57 (0.10)	5.3	0.57	0.7 (0.7–0.8)	2.2	1.5 (1.5–1.6)

5.3.3 Size and age at maturity

The size at first maturity (LM_{50}) was calculated as 36.5 mm shell height (95% CI: 34.5–38.3 mm) (Figure 5.5). According to the age modelling, it took snails at the subtropical sites almost twice as long as the temperate snails to reach first maturity (Table 5.1). *Turbo militaris* snails at subtropical sites were estimated to reach the minimum legal-size limit (shell height of 78 mm) almost three times slower than snails at the temperate sites (Figure 5.4). Thus, the subtropical sites had a greater number of years in which turban snails were mature before reaching the legal size (Table 5.1).

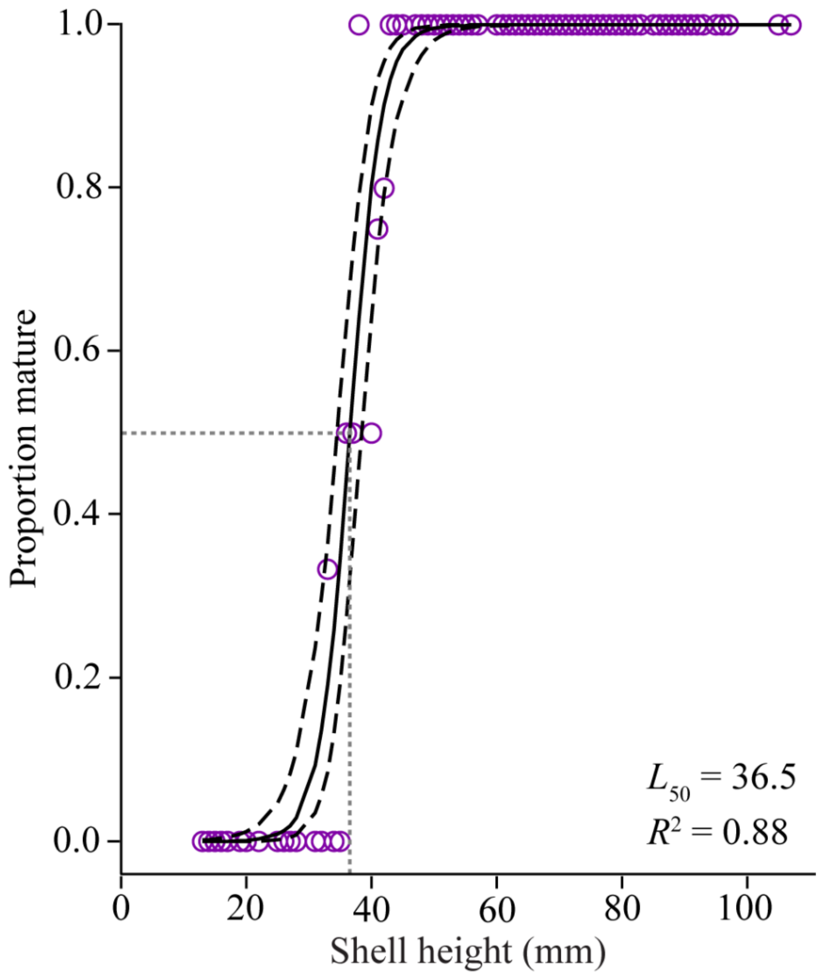


Figure 5.5. Shell height (mm) and proportion of *Turbo militaris* at first maturity (LM_{50}), from individuals from subtropical and temperate regions in New South Wales, Australia. Solid line indicates model fit from Bayesian regression analysis and dashed lines indicate 95% confidence intervals. Grey dotted line indicates the shell height at 0.5 proportion mature.

5.4 Discussion

This study presents the first estimates of the age and growth of the harvested Australian turban snail, *T. militaris*. While latitudinal differences in growth were apparent between subtropical and temperate populations, overall, *T. militaris* are moderately long-lived, mature at less than a third of maximum size and are moderate-to-fast growing (K = 0.57 year^{-1} vs. 0.29 year^{-1} and L_∞ = 108 mm vs. 94 mm, for temperate and subtropical snails, respectively). For *T. militaris,* most of the growth is estimated to be attained within the first

2 (temperate snails) to 3 years (subtropical snails), which is consistent with other turbinid gastropods (Bruton et al., 1991; Ramesh et al., 2009; Keane et al., 2014). Temperate snails reached legal height (~78 mm shell width) in ~2 years, whereas growth in the subtropical snails slowed at ~50 mm shell height (~3 years), and legal size was not reached for ~6 years. Temperate snails are estimated to reach maximum size in around 5 years and subtropical snails in around 10 years.

The instantaneous growth rate of *T. militaris* is comparable to other marine gastropods in other families, including *Hexaplex trunculus* and *A. gigas* (Vasconcelos et al., 2006; Peel & Aranda, 2012). In contrast, tropical, comparable-sized gastropods, *Haliotis tuberculata* and *R. nilotica* (in Guam) exhibited slower instantaneous growth rates (Smith, 1987; Mgaya & Mercer, 1994). Regarding productivity, K values >0.3 year^{-1} are considered to be high, moderate values range from 0.10 to 0.30 year^{-1}, low values range from 0.15 to 0.05 year$^{-1,}$ and very low values are <0.05 year^{-1} (Froese & Pauly, 2000). Fast growth is estimated in other turban snails, such as the largest turbinid species, *T. marmoratus* ($K = 0.32$ year^{-1}, L_∞ = 303 mm shell diameter) (Bourgeois et al., 1997), and the smaller subtropical species, *T. cidaris* ($K = 0.35$ year^{-1}, L_∞ = 62 mm shell width) (Pulfrich & Branch, 2002). Fast growth is also consistent with other turbinid species in the Australian fishery, including the warm-temperate *L. torquata* (female: $K = 0.41$ year^{-1}, L_∞ = 88 mm shell width and male: $K = 0.43$ year^{-1}, L_∞ = 94 mm shell width) (Kienzle et al., 2022) and the smaller, more temperate species *L. undulata* ($K = 0.45$–0.53 year^{-1}, L_∞ = 47–62 mm shell width) (Keane et al., 2014).

Latitudinal disparities in life-history parameters were apparent between subtropical and temperate populations of *T. militaris* separated by ~350–400 km or ~3° of latitude in NSW. *Turbo militaris* from lower (subtropical) latitudes had slower growth, attained smaller average maximum sizes and had longer lifespans than snails from higher (temperate) latitudes. This trend was also apparent for *L. undulata* in Tasmania, although over a shorter latitudinal range (Keane et al., 2014). In contrast, the growth and maximum size of *T. sarmaticus* differed between regions in South Africa, with faster growth and smaller sizes occurring in warmer regions (McLachlan & Lombard, 1981; Pulfrich & Branch, 2002). Studies on *M. undosa* in Baja, California also revealed latitudinal disparities, albeit with conflicting results: Martone and Micheli (2012) found faster growth and larger snails at lower (warmer) latitudes compared to those at 3° of latitude higher (cooler); Gluyas-Millán et al. (2000) found faster growing snails at higher (cooler) latitudes. These studies suggest that spatial variation in life-history parameters is inconsistent within the family Turbinidae, likely reflecting species-specific responses to environmental factors.

Biophysical variables such as water temperature and food availability can influence metabolic rate and, thus, energy allocation (Atkinson, 1994; Martone & Micheli, 2012). Environmental conditions are likely a major driver of the latitudinal disparities in this study rather than genotypic differences, as a recent study has demonstrated no genetic differentiation across the *T. militaris* population in NSW (Nimbs et al., 2023). In this study, the water temperatures in the temperate (southern) region were generally cooler year-round than in the subtropical (northern) region (Figure 5.1b). The preferred water temperature (daytime) of *T. militaris* is 22 °C (Ab Lah et al., 2017a), which is more frequently and extensively exceeded in the subtropical region (Figure 5.1b). In warmer subtropical waters, snails are closer to their thermal limits, requiring higher metabolic activity, resulting in less energy for growth, leading to smaller-sized animals (per age) (Atkinson, 1994). In cooler climates, animals may grow faster and larger due to lower metabolic energy requirements and optimal thermal conditions may promote activity (i.e., consumption and digestion) and thus more energy generated for processes including growth (Atkinson, 1994).

Turban snails (including *T. militaris*) are generalist herbivores that graze on various macroalgae, including turfing, coralline and erect forms (i.e., *Ecklonia radiata*) (Walsby, 1977; Worthington & Fairweather, 1989; Ettinger-Epstein & Kingsford, 2008; Hayakawa et al., 2018; Lloyd et al., 2020). On reefs where food availability is reduced or nutritional quality is low, metabolic demands might not be met, affecting energy resources directed to growth (Martone & Micheli, 2012). Studies have demonstrated higher growth rates in marine herbivores that consumed high-quality algae or mixed algal diets offering a range of nutritional benefits (Foster et al., 1999; Aquilino et al., 2012). Similarly, a higher food availability (abundance of algae) has been linked with faster growth rates in marine gastropods (including turban snails) (Joll, 1975 as cited in Keane et al., 2014; Day & Fleming, 1992; Dixon & Day, 2004; Martone & Micheli, 2012). Algae assemblages vary along the east Australian coast, where temperate waters on the mid to south coast support a high diversity and abundance of macroalgae (Lloyd et al., 2020). Faster growth of *T. militaris* in temperate regions, could result from higher nutritional quality of temperate macroalgae species (i.e., *E. radiata*) (Shalders et al., 2023). Whereas, slower growth of *T. militaris* in the subtropical regions might have resulted from reduced diversity and abundance of macroalgae or increased competition for food resources (Zarco-Perello et al., 2020).

The parameter estimates derived from the von Bertalanffy growth model should be interpreted with caution, as the model may fail to accurately estimate growth in small snails. In this study, juvenile and small snails were underrepresented (few recaptured snails < 50 mm shell height), limiting the reliability of the model in describing early growth. A strong representation of larger individuals and minimal representation of small individuals can result in an underestimation of the Brody growth coefficient (k) and overestimate the asymptotic size (L_∞) (Bourgeois et al., 1997). Additionally, growth can vary between individuals (Figure 5.3) and some snails have periods of zero growth (Frank, 1969). Therefore, some caution is warranted when applying model outputs for fishery management planning.

In this study, temperate snails reached maturity in <1 year at around a third of their asymptotic size. For subtropical snails, due to slower growth and smaller average maximum size, maturity was reached at a size slightly greater than a third of asymptotic size after just over 2 years, which is comparable to the large snail, *M. undosa* (McCann & Johnson, 2021). Our findings are consistent with studies of other medium-to-small turban snails, *T. cidaris, L. undulata* and *L. smaragda*, all reaching sexual maturity at a size below half their maximum size (Walsby, 1977; Pulfrich & Branch, 2002; Keane et al., 2014). In contrast, for large-sized turban snails, *T. marmoratus*, *T. sarmaticus* and *M. undosa*, sexual maturity is reached at a size close to, or greater than half their maximum size (Devambes, 1961 as cited in Yamaguchi, 1988; Lasiak, 1991; Igari et al., 2001; Pulfrich & Branch, 2002; Martone & Micheli, 2012).

The subtropical population of *T. militaris* were relatively long-lived (>10 years), which is similar to the longevity of the large subtropical turban snails, *M. undosa* (McCann & Johnson, 2021) and *T. sarmaticus* (Bruton et al., 1991). The temperate snails, in comparison, were short-lived, with approximately half the life span of subtropical snails. Our study reflects a general trend for marine gastropods where longevity is related to size, where larger, faster-growing species have shorter life spans (Frank, 1969). Estimates of natural mortality of *T. militaris* in the subtropical populations were similar to those for other exploited marine gastropods, *A. gigas* ($M = 0.29$ year^{-1}) (Cárdenas & Aranda, 2014) and *M.*

undosa ($M = 0.29$ year^{-1}) (Gluyas-Millán et al., 2000). In comparison, the natural mortality rate for temperate *T. militaris* was much higher ($M = 0.57$ year^{-1}), which could be due to a harsher wave climate or increased rates of predation. The fast-growing temperate snails' shorter lifespan and higher mortality suggests a high turnover, which may provide a greater resilience to harvesting pressure (Froese & Pauly, 2000). In contrast, the higher longevity and lower natural mortality of the subtropical snails indicates a slower turnover. Therefore, the subtropical snails could have higher vulnerability to overfishing due to a slower recovery from depletion if overfishing occurs (Pauly, 1980) or be more susceptible to other environmental impacts that effect both large and small individuals (i.e., climate change, disease or habitat loss).

Our findings suggest that the current minimum legal-size limit allows *T. militaris* in both the subtropical and temperate regions multiple opportunities to spawn prior to entering the fishery. The young age and small size at sexual maturity in *T. militaris* allow for more than one year of reproductive activity at the temperate sites and more than four years at the subtropical sites before entry into the fishery. As *T. militaris* spawn periodically throughout the year (Seinor et al., 2023), this potentially allows for multiple reproductive events. Similar findings have been observed for other turbinid fisheries where size limits allow for at least one year or more of reproductive activity before harvesting (Igari et al., 2001; Pulfrich & Branch, 2002; Keane et al., 2014).

Marine invertebrates, including turban snails, show a positive relationship between individual size and fecundity (Cupul Magaña & Torres-Moye, 1996; Llordra, 2002; Martone & Micheli, 2012). As a result, small (newly mature) individuals may be less fecund, producing fewer gametes than larger individuals. The faster-growing temperate snails likely have a higher reproductive output per age than subtropical snails because faster growth increases size-at-age. However, the 1–2 year reproductive window between maturity and fisheries size in the temperate snails could lead to serious reductions in spawning potential in highly exploited populations. The slow-growing subtropical snails though smaller, live longer therefore offering more opportunities for reproduction which may even out the reproductive output over the lifetime of the snail. Additionally, the smaller subtropical snails had over four years of reproductive activity prior to entering the fishery compared to less than two years for the temperate snails. The lower potential reproductive output per age in subtropical snails could be offset by having more reproductive events before being harvested. Future studies on size-based fecundity across both regions are essential for determining the relative number of eggs that could be spawned in each year after maturity, within each population. This information is essential for determining the biological appropriateness of minimum legal-size limits and for understanding the relationship between growth and productivity in *T. militaris*.

Turbo militaris is a valuable fisheries resource in NSW, and these findings have implications for its management. Coastal waters are rapidly warming on the east Australian coast (Suthers et al., 2011; Ridgway & Hill, 2014), and growth of *T. militaris* is likely driven by environmental conditions along a latitudinal gradient. Therefore, in future climate conditions, turban snails in currently temperate regions, may become more slower-growing and attain smaller maximum sizes due to poleward warming waters. Due to the functional role of turban snails (as large herbivorous grazers) (Anderson et al., 2011) and their high desirability as a fisheries resource (Ab Lah et al., 2017b; Santhanam, 2018; Romolo et al., 2021), future impacts on turban snail populations will have ecological, cultural and socio-economic consequences. These consequences may include altered ecosystems, inequity of access to resources, economic losses from small-scale fisheries, and adverse implications for traditional harvesting and cultural values (Smith et al., 2006; Arrawarra Sharing Culture, 2009). Population monitoring and research on life-histories (i.e., growth, maturity and fecundity) across a harvested species' range, is crucial to inform management regimes and ensure sustainable use of fisheries in a changing climate. These studies are especially relevant for species spanning large geographical ranges and in climate change hotspots, such as *T. militaris*.

CHAPTER 6.

GENERAL DISCUSSION

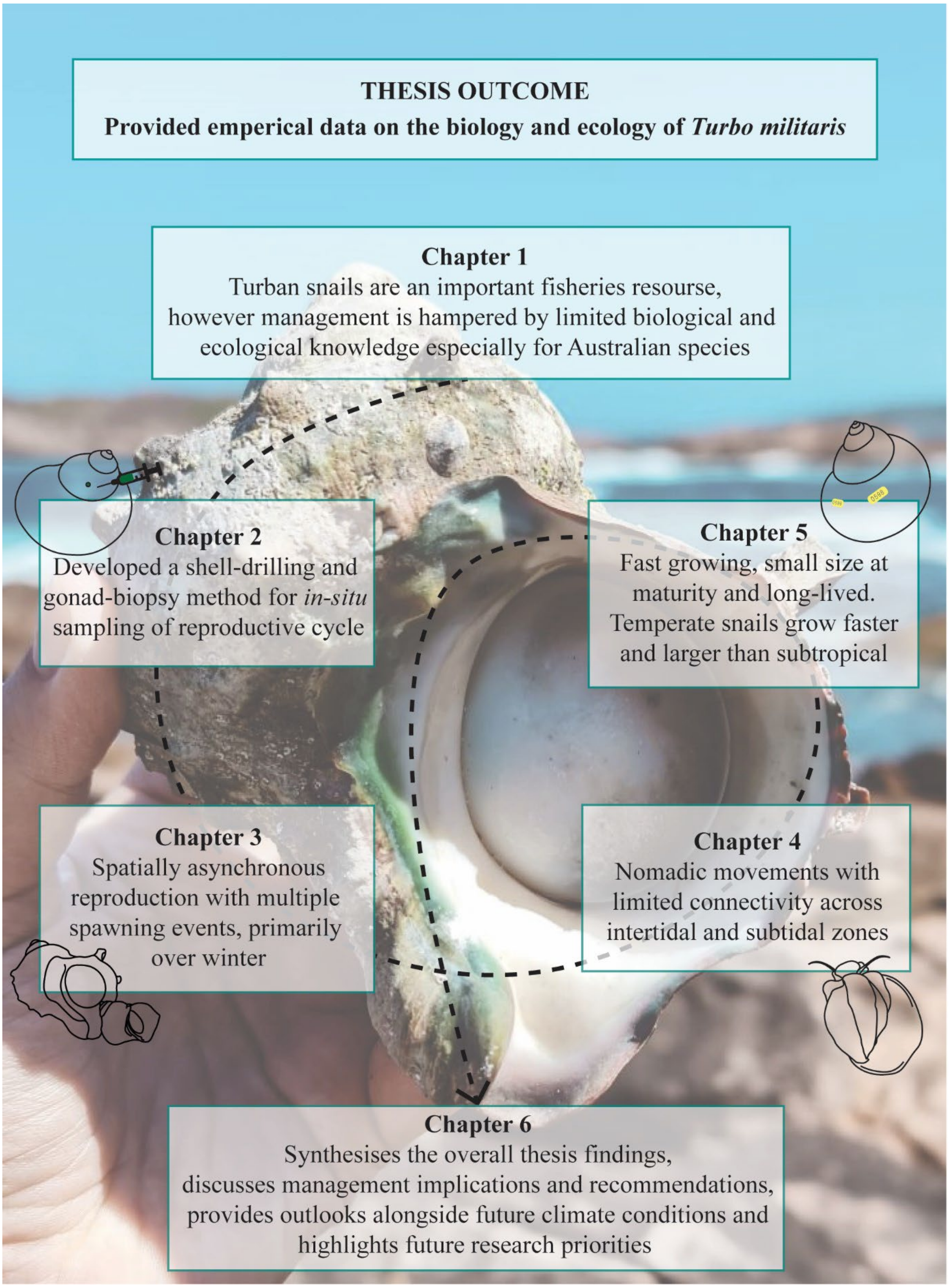
6.1 Synthesis: elevating knowledge on *Turbo militaris*

Turbo militaris is one of the dominant gastropods on intertidal rocky shores and shallow subtidal reefs in subtropical and warm-temperate eastern Australia and is a valuable fisheries resource in New South Wales (NSW). Concerns regarding increased harvesting of turban snails in NSW (Cooling & Smith, 2015) emphasised the need for evaluating fisheries management strategies to sustain stocks. However, until now, data to support the management of turban snails in NSW was limited. Without knowledge of reproduction, movement, age and growth, there are strong constraints on developing informed management strategies. This thesis consequently aimed to enhance the knowledge base on the biology and ecology of *T. militaris*.

To address this aim, a non-lethal method was developed for sampling reproductive condition (Chapter 2) and, using this method, documented the reproductive cycle of *T. militaris* (Chapter 3). Non-lethal methods have particular application in highly protected marine areas where destructively sampling of flora and fauna is undesirable or not permitted. Knowledge on reproduction can inform management strategies, by determining at what size individuals become reproductive, and if there are seasonal reproductive patterns. This information can be used to ensure reproduction can occur before animals reach harvestable size and if there are discrete periods when harvesting should be avoided. Details about the movement of *T. militaris* on intertidal rocky shores also helps determine if adult populations are able to replenish harvested areas (i.e., intertidal habitats) from adjacent areas where harvesting pressure may be lower (i.e., subtidal areas) (Chapter 4). Through mark-recapture and reproductive studies, age and growth was assessed and size at maturity was established (Chapter 5), which are essential parameters for the development of effective management. By sampling at geographically separate locations with a latitudinal range of ~3° in NSW, it was possible to provide insights into the spatial variability of life-history parameters of *T. militaris* within its endemic range. The thesis findings expand the current knowledge base on biological and ecological traits of turbinid gastropods and highlight species-specific variation within the family. Overall, this thesis has substantially advanced our understanding of the biology of *T. militaris*. This work provides empirical data that, when considered in combination, can improve efforts to sustainably manage this important, spatially restricted species (Figure 6.1).

6.2 Implications for fisheries management

In NSW, *T. militaris* are managed in combination with *Lunella torquata* and *L. undulata*, under both the recreational fishery and the sea urchin and turban snail (SUTS) commercial fishery (Table 1.1). Given that the three similar species can be difficult to identify and tell apart by some recreational harvesters (pers. obs.), there is a management (compliance) advantage in having a shared size and bag limit. Shared management regulations make it much easier for fishers to comply with regulations and not unintentionally break the law through error or carelessness; therefore, compliance and enforcement are also simpler. However, setting appropriate uniform management regulations across an entire fishery can be difficult where species have regional differences in life-history traits (Chapter 3 and 5) or there are differences between simultaneously managed species (Table 6.1). Ideally, management regulations should be applied at appropriate spatial scales and to the specific species from which the informing data were derived (Day & Fleming, 1992). Uninformed management (such as inappropriate size or bag limits) could result in a greater risk of overharvesting in some populations, or suboptimal utilisation of stocks.



THESIS OUTCOME
Provided emperical data on the biology and ecology of *Turbo militaris*

Chapter 1
Turban snails are an important fisheries resourse, however management is hampered by limited biological and ecological knowledge especially for Australian species

Chapter 2
Developed a shell-drilling and gonad-biopsy method for *in-situ* sampling of reproductive cycle

Chapter 5
Fast growing, small size at maturity and long-lived. Temperate snails grow faster and larger than subtropical

Chapter 3
Spatially asynchronous reproduction with multiple spawning events, primarily over winter

Chapter 4
Nomadic movements with limited connectivity across intertidal and subtidal zones

Chapter 6
Synthesises the overall thesis findings, discusses management implications and recommendations, provides outlooks alongside future climate conditions and highlights future research priorities

Figure 6.1. Conceptual diagram outlining the outcomes of the thesis: Fishery biology and ecology of the marine snail, *Turbo militaris*.

Table 6.1. Life-history traits of three harvested Australian turban snails. Study regions in parentheses. Bold text represents the data derived from this thesis. *NA* = data not available.

	Turbo militaris	***Lunella torquata***	***Lunella undulata***
Distribution	Southern QLD to southern NSW	QLD, along southern coastline to mid-north WA	Southern QLD, along southern coastline to mid-north WA and Tas
Population density (ind. m^2)	0.25 – 7.5 (intertidal NSW) 0.23 – 0.63 (subtidal NSW)	0.2 – 7 (NSW) 0.04 – 0.95 (WA) < 2.2 (WA)	8 – 92 (intertidal NSW) 15 – 21 (subtidal Tas) 0.05 – 0.6 m (subtidal Tas)
L_∞ (mm)	**94 (subtropical NSW)** **108 (temperate NSW)**	Female: 88.2 Male: 93.7	46.87 – 61.93 (Tas)
K ($year^{-1}$)	**0.29 (subtropical NSW)** **0.57 (temperate NSW)**	0.41 (female NSW) 0.43 (male NSW)	0.40 – 0.53 (Tas)
LM_{50} (mm)	**36.5 mm (NSW)**	*NA*	23.2 – 26.2 (Tas)
Age at sexual maturity (years)	**1.7 (subtropical NSW)** **0.7 (temperate NSW)**	*NA*	1.1 – 1.6 (Tas)
Age at legal size (years)	**6.1 (subtropical NSW)** **2.2 (temperate NSW)**	*NA*	2.8 – 6.7 (Tas)
Time between maturity and legal size (years)	**4.4 (subtropical NSW)** **1.5 (temperate NSW)**	*NA*	1.7 – 5.1 (Tas)
M ($year^{-1}$)	**0.37 (subtropical NSW)** **0.57 (temperate NSW)**	*NA*	*NA*
T_{max} (years)	**10.3 (subtropical NSW)** **5.3 (temperate NSW)**	*NA*	~10 (Tas)

Spawning season	**Long spawning season, primarily in winter, but with other events throughout the year. Ripest in warmer months. Asynchronous spawning between locations (northern and mid NSW)**	Long spawning season, biannual spawning in autumn – winter and spring – summer. Asynchronous spawning between locations (Sydney and southern NSW) Long spawning season with peak spawning in summer (Perth, WA)	Long spawning season, spring – autumn. Continuous gametogenesis (Sydney, NSW) Two spawning events during autumn and summer. Ripest in early autumn and early summer (northern NSW) Long spawning season spring – autumn. Asynchronous spawning between locations (Tas)
Fecundity	*NA*	*NA*	*NA*
Early life-history	*NA*	*NA*	*NA*
Habitat	Lower intertidal and shallow subtidal to ~ 20 m. Biogenic structure (ascidian and tubeworm) and high complexity	Shallow rocky shores 2 – 20 m depth. Algae dominated reefs and kelp forests. High complexity from biogenic structure (canopy forming algae and red turfing macroalga)	Lower littoral, low-mid rockpools and sublittoral. High complexity from biogenic structure (canopy forming algae, ascidian and red turfing macroalga)
Movement	**Limited, non-directional long-term movement, generally remain within preferred habitat.** **20–21 m year^{-1} (subtropical NSW)** **34–44 m year^{-1} (temperate NSW)**	Most move 1-5 m month^{-1}. Some extensive short-term movements up to 30 m month^{-1}. Remain in localised kelp forests (NSW)	Limited short-term movement, Higher mobility in spring/summer. Maximum mobility up to 150 m year^{-1} (Tas)
References	(Mohring, 2007) (Cooling & Smith, 2015) **(Chapter 3)** **(Chapter 4)** **(Chapter 5)**	(Joll, 1980) (Ward & Davis, 2002) (Vanderklift & Kendrick, 2004) (Ettinger-Epstein & Kingsford, 2008) (Wernberg et al., 2008) (Smoothey, 2013) (Kienzle et al., 2022)	(Underwood, 1974) (Worthington & Fairweather, 1989) (Edgar et al., 2004) (Smoothey, 2013) (Keane et al., 2014) (Ab Lah et al., 2019)

The findings on reproduction (Chapter 3), size at maturity and growth of *T. militaris* (Chapter 5) indicate that the current minimum size limit may be biologically appropriate for this species. The current size limit allows for multiple reproductive events, as *T. militaris* can spawn periodically (at least three times) throughout the year (Chapter 3). The small size at sexual maturity allows temperate snails more than one year of reproduction before reaching legal harvesting size and over four years for subtropical snails (Chapter 5). Therefore, the subtropical snails have the potential to reproduce up to 13 times and the temperate snails up to 5 times before being legally harvested (Chapter 3 and 5).

At the field sites included in this thesis, many large *T. militaris* (up to 130 mm shell height) were found. From the mark-recapture experiments (Chapter 4 and 5) over 20% of tagged snails across both subtropical and temperate regions were above the minimum size limit (75 mm shell width). A presence of large individuals could indicate populations are not being overfished. However, due to their high intertidal abundance, *T. militaris* are easily accessible to recreational fishers at low tide. The lack of upshore movement to intertidal zones limits population recovery, making intertidal snails particularly susceptible to local depletion (Chapter 4), while subtidal snails may gain some protection due to reduced accessibility (Cooling & Smith, 2015). The clear habitat preferences and limited adult movement of *T. militaris* (Chapter 4) and other simultaneously managed species (Table 6.1), likely constrains snails to particular shores or regions of habitat. Therefore, turban snails may be highly susceptible to local depletion by harvesting as there is a limited capacity for exploited stocks to be replenished by adult movement from neighbouring populations.

Further management intervention may be required if *T. militaris* populations are depleted through heavy harvesting, or the loss of suitable habitat. Information on total population sizes and the impacts of harvesting will inform the suitability of recreational catch limits. Additionally, stock assessments would help to inform whether total allowable catch limits should be established in the SUTS fishery. Further management intervention could involve differentiated total allowable catches (commercial fishery) or stricter input controls, such as enhanced spatial protections in vulnerable regions. These may help balance resource use, allowing higher harvesting in less vulnerable regions whilst safeguarding more vulnerable populations (i.e., subtropical). Harvesting may need to be restricted at the northern distributional limit until robust population assessments clarify whether climate change is driving a southward range contraction.

Given the limited mobility (Chapter 4) and extended, asynchronous reproduction (Chapter 3) of *T. militaris* and other Australian turban snails (Table 6.1), spatial protection offers a suitable management approach to protect existing adult snails at locations with high harvesting pressure. Spatial management may provide optimal outcomes in terms of enhancing local population abundance, protecting adult snails, sustaining them as breeding populations and promoting population connectivity via larval dispersal (Nimbs et al., 2023). Spatial protection measures can effectively safeguard populations of benthic invertebrates such as turban snails from harvesting where greater abundances of *T. militaris* can be found in sanctuary zones or areas of low accessibility (pers. comm. Dr. Hamish Malcolm). Spatial protection should encompass areas with preferred turban snail habitat (i.e., intertidal regions with high complexity and abundance of macroalgae) (Worthington & Fairweather, 1989; Ettinger-Epstein & Kingsford, 2008; Smoothey, 2013; Cooling & Smith, 2015). Locally tailored no-take zones may offer protection in specific habitats yet allow harvesting in adjacent areas (such as the intertidal protection at Diggers Camp (NSW DPI, 2024)). Intertidal protection of invertebrates and diving-only harvest restrictions are used in other states (Table 1.1) and could be one solution to expanding spatial protection networks in NSW.

Placing spatial protection in areas where stocks are depleted or harvesting pressure is high will help manage impacted populations locally by mitigating overexploitation risks. However, management planning should also allow stakeholder access to resources by allowing fishing in some areas or permitting certain activities (i.e., cultural harvesting). Protecting shores that are less accessible or currently under low harvesting pressure will also be important to safeguard naturally abundant populations (Cooling & Smith, 2015), as anthropogenic threats can change spatially over time. Spatial management of rocky shores with suitable habitats as 'no-take' areas would complement other measures, such as size and bag limits, to ensure the long-term sustainability of large vulnerable intertidal gastropods such as *T. militaris*. Enhancing spatial management regimes through marine park zoning will benefit turban snail populations whilst aligning with global biodiversity goals of increasing the area of marine habitat under protection (DCCEEW, 2023).

Indigenous communities hold a deep connection to Country (including Sea Country), and cultural fishing fosters connection to Country, an expression of spiritual values and a means to feed family and community (Trân et al., 2016; State of New South Wales, 2023).

Recreational fishing regulations that limit cultural fishing can adversely impact cultural identity and connection, livelihoods and the generational sharing of traditional fishing knowledge (Faulkner, 2000; Trân et al., 2016). In NSW, cultural provisions for Aboriginal fishers include different harvesting limits for some species, waived fishing fees and special access for culturally significant species, sites or ceremonies (State of New South Wales, 2023). Management of culturally significant species or locations should be informed by Indigenous knowledge holders and communities to develop effective harvest strategies that respect traditional practices, allow cultural access rights and integrate traditional management in decision-making (Schnierer & Egan, 2016). Conducting research, monitoring, and management planning in conjunction with traditional owners allows scientists to meaningfully engage with Indigenous communities and learn about culture and traditional knowledge (i.e., traditional fishing methods). Co-designed research and management also facilitates participation and training opportunities for traditional owners (Arrawarra Sharing Culture, 2009; State of New South Wales, 2023; Fredericks et al., 2025). For this research, I engaged with the Yaegl community for permissions to work on Yaegl Country and a cultural officer, Uncle Ferlin Laurie, was involved in the mark-recapture surveys at Diggers Camp (Chapter 4 and 5). Turban snail (Gugumbal) are a traditionally significant resource for coastal First Nations Australians (Smith et al., 2006; Arrawarra Sharing Culture, 2009), therefore future population monitoring, management and harvest strategies should be determined in collaboration with traditional owners.

6.3 Outlook for future climate conditions

Warming poleward waters are impacting marine species through range shifts, topicalization habitat loss, and altered life-history traits (Ridgway & Hill, 2014; Phillips et al., 2022). The southeast Australian seaboard is a region of accelerated ocean warming and a global climate change hotspot (Hobday & Pecl, 2013). The East Australian Current (EAC) is rapidly warming and facilitating the poleward movement of marine species (Suthers et al., 2011) with predictions indicating further intensification, especially in temperate regions south of ~32° S (Ridgway & Hill, 2014; Champion et al., 2021; Gervais et al., 2021; Phillips et al., 2022). For benthic species with limited movement, like *T. militaris* (Chapter 4), range expansions are generally driven by planktonic larval movement which are strongly influenced by ocean currents, including the cold-core eddies of the southern EAC (Suthers et al., 2011; Pinsky et al., 2020). With an endemic distribution in the path of the EAC, *T. militaris*, has experienced a poleward range extension in recent decades. Under future climate scenarios, including a stronger EAC, it is likely that the population will continue to shift poleward, potentially resulting in its establishment in more temperate waters, while populations become diminished in subtropical regions. Additionally the EAC has facilitated the poleward range expansion and increased occurrence of harmful algal blooms (Hallegraeff et al., 2020). These algal blooms which can be harmful to marine molluscs (Neves et al., 2021) occur during Spring and late Summer on the southern NSW coastal shelf from the Port Stephens region (Harrison et al 2011; Hallegraeff et al., 2020). Therefore these events may indirectly threaten the southern populations of *T. militaris*.

Turbo militaris was first documented in the Sydney region in the 1960s (pers. comm. Dr. Phil Coleman) and was first observed on the Illawarra coast in 2000 (Benkendorff, 1999). Currently, dense populations can be found in the Sydney region (pers. comm. Dr. Gary Hamer) and as far south as Wollongong (pers. comm. Dr. Jeremy Day). During fieldwork for a parallel study, in April 2021, Dr. Hamish Malcolm and I searched around the Wollongong/Shellharbour region over several days at multiple rocky shores with suitable habitat for *T. militaris*. We found one live snail at Barrack Point (34.6° S) and a few empty shells on the shore. Yet, snails were collected from Plantation Point, Jervis Bay (35.1° S) in August 2021 for a study on genomics (Nimbs et al., 2023). One individual has been sighted at Guerilla Bay in 2011 (35.8° S) (iNaturalist, 2025), otherwise *T. militaris* are not currently documented south of Jervis Bay (GBIF.org, 2025; pers. comm. Dr. Nathan Knott). The current southern distributional boundary is unknown but is likely to occur on the south coast of NSW around the Jervis Bay area.

As waters are predicted to warm and the preferred thermal temperature of *T. militaris* (22 °C (Ab Lah et al., 2017a)) is increasingly exceeded in the subtropical distribution, the species faces the risk of range contraction in the subtropics. In a parallel study in 2021, we failed to find any individuals at the previous northern distributional limit at Mooloolaba, Queensland (26.7° S). The most recent northernmost sightings of *T. militaris* were at Caloundra, Queensland (26.8° S) in 2017, and at Burleigh Heads, Queensland (28.1° S) in 2024 (iNaturalist, 2025). There have been no other recorded observations of live *T. militaris* in Queensland since the early 2000s (GBIF.org, 2025). This suggests a progressive contraction at lower latitudes, which could intensify harvesting pressure on subtropical populations that may already be vulnerable due to slower growth (Chapter 5).

Given the lack of genetic separation within the species' restricted distribution (Nimbs et al., 2023), the large differences in growth (Chapter 5) and spatial asynchronicity in the reproductive cycle of *T. militaris* (Chapter 3) are likely driven by environmental conditions. Environmental factors such as water temperature and macroalgal assemblages vary latitudinally along the east Australian coast (Shalders et al., 2023) and are likely driving variability in growth of *T. militaris*. Thus, future changes in ocean climate may impact the life-history traits of *T. militaris*, altering reproductive timing, movement patterns and habitat suitability and growth.

Warming waters may disrupt spawning capacity, as reproductive cycles are linked to water temperature (Chapter 3), leading to shifts in reproductive periodicity under future climate conditions. Future predictions of increased occurrence and severity of storm events (Sheehan, 2019) could impact spawning periodicity. Temperate populations of *T. militaris* appeared to spawn in rougher seas (Chapter 3) which, according to other studies on turban snails, likely triggers synchronised spawning (Grange, 1976b; Yamaguchi, 1988; Dwiono et al., 2001) and facilitates population connectivity through larval dispersal (Grange, 1976b). In contrast, *T. militaris* in subtropical regions spawned in calmer conditions (Chapter 3), which offers potential advantages for fertilisation success (Denny & Shibata, 1989; Simon & Levitan, 2011). Furthermore, storm events could increase snail dispersal through accidental displacements of adult snails in rough water conditions (Walsby, 1977). Although, as adult turban snails are restricted to coastal rocky reefs and rarely found crossing sand, there is potential for increased mortality, especially if displaced offshore >20 m (Chapter 4). *Turbo militaris* associates with the vulnerable habitat formed by *Idanthyrsus pennatus* (Chapter 4; Cooling & Smith, 2015), which has undergone notable collapses during recent intense low-pressure systems off southeastern Australia which bring heavy rainfall, strong winds and rough seas (pers. obs.). Increased storm events could further endanger these important, fragile habitats and associated *T. militaris* populations.

Climate change is likely to have regionally variable effects on *T. militaris* populations and their fisheries. Ocean warming associated with future climate scenarios may result in slower-growing and smaller-sized snails particularly for warm-water populations.

Furthermore, warming waters and a strengthening EAC may cause a poleward trend of slower-growing, smaller snails with lower natural mortality and hence a slower population turnover in the more temperate regions in NSW. Similar trends may be observed in other species with latitudinally variable life-history traits, such as *L. undulata* in Australia (Keane et al., 2014), *T. cornutus* in South Korea (Lee et al., 2014) or *Megastraea undosa* in California (Gluyas-Millán et al., 2000). Impacts to these fisheries could include lower biomass available for harvest due to slower-growing and smaller-sized snails, increased vulnerability to overfishing and reduced stock resilience due to slower population turnover. These factors will likely present management challenges in the future, including the need to adjust regulations, and economic consequences, such as reduced resource availability.

As large herbivorous grazers, turban snails have a key functional role in rocky reef ecosystems (Wernberg et al., 2008; Anderson et al., 2011) and they have high value as a fisheries resource. Therefore, potential changes to their distribution or life-history traits may bring ecological, cultural and socio-economic consequences. Ecological impacts include altered ecosystems through changes in herbivory or competition for resources. For example, *T. militaris*, which was once absent along the NSW mid-south coast, is now outnumbering *L. torquata* (pers. comm. Dr. Jeremy Day), potentially intensifying competition for macroalgae. Furthermore, altered species distributions may result in inequitable resource access, economic losses in small-scale fisheries, and adverse effects on traditional harvesting and cultural values for First Nations Australians. Cultural and economic displacement may lead to fishers seeking other, potentially less sustainable resources, or travelling to harvest, increasing costs and impacting traditional practices.

6.4 Future research priorities

6.4.1 Distribution and latitudinal disparities

Given the uncertainty regarding the distribution of *T. militaris* and the latitudinal disparities in reproduction and growth (Chapter 3 and 5), a key priority for future research includes determining the species current distribution and predicting changes to distribution under future climate change. Assessment of populations throughout southern Queensland could determine to what extent subtropical populations are being lost at the equatorward end of the distribution, whilst sampling throughout southern NSW would determine the extent of the poleward extension and confirm the observations of *T. militaris* at higher latitudes. Documenting the current distribution could include targeted surveys in suitable turban snail habitats by scientists and traditional owners, collating data from broader-scale studies (such as marine park monitoring) and by verifying sightings from citizen scientists (i.e., iNaturalist.com). To determine the extent of a range shift or extension, data could be collated with museum records or traditional knowledge to construct historical distributional ranges over time and used to map historic, current and future habitat suitability. After determining the current distribution of *T. militaris,* stock assessments could be conducted along the full geographic range to inform appropriate catch limits (commercial fishing). To assess population size, mark-recapture surveys (as in Chapter 4 and 5) and monitoring surveys, such as the current monitoring by DPIRD to evaluate the impacts of harvesting in the SIMP should be conducted.

In this thesis, reproduction (Chapter 3), mobility (Chapter 4) and growth (Chapter 5) of *T. militaris* has been documented at two spatially separate regions in NSW, separated by about 3° of latitude. However, the current distribution spans approximately 8° of latitude (Figure 1.7) and the geographic scope of the surveys was constrained due to the selection of appropriate study sites. The latitudinal disparities found in this study (Chapter 3 and 5) could be further explored by extending the geographical spread of sites, particularly closer to the distributional ends (i.e., in northern NSW or southern Queensland). Of the <20 sites originally visited in preparation for this study, the chosen sites represented locations that had suitable habitat, abundant populations of *T. militaris*, were easily accessible, safe (for the field team) in a range of environmental conditions and where travel expenses were within budget constraints. The choice of sites on the NSW mid-north coast also avoided locations where turban snail monitoring was occurring in the SIMP by DPIRD. Future studies could determine if life-history traits change gradually across a latitudinal gradient, suddenly diverge or if there is a disjunct distribution of life-history traits. Locations to explore for future research could be around southern Queensland (if *T. militaris* is still found to occur there), mid-range locations around the mid-north coast or Sydney, and southern sites around Wollongong and Jervis Bay. Furthermore, including offshore reefs such as at the Solitary Islands (mid-north coast region NSW) or Broughton Island (Port Stephens region, NSW) could provide further information more applicable to informing commercial harvest strategies in the SUTS fishery.

6.4.2 Population connectivity

The limited mobility of adult turban snails (Chapter 4) and the genetic similarity across the population (Nimbs et al., 2023) supports the hypothesis that connectivity is primarily driven by larval transport. Early life-history information, including larval dispersal capabilities, is currently lacking for Australian turbinids (Table 6.1) and is clearly an important focus for future research. By modelling larval dispersal, we can gain an understanding of biological connectivity which is important in identifying and, if needed, protecting key breeding populations. Oceanographic modelling and larval sampling can be used for examining larval movement using physical and biological data (Schilling et al., 2020; Hinchliffe et al., 2021). Of particular interest is whether the strengthening EAC might enhance southward larval flow and population connectivity. Integrating larval dispersal and duration, settlement cues and thermal tolerance could provide more accurate projections of current and future distributions of *T. militaris.*

From a parallel study, a high proportion (88%) of snails collected on the NSW south coast (Plantation Point, Jervis Bay) were large-sized (>80 mm shell height) (Nimbs et al., 2023). Further observations of turban snails in the Jervis Bay region indicate that *T. militaris* found on the NSW south coast are primarily large-sized, with smaller individuals rarely found (pers. comm. Dr. Nathan Knott). These observations could indicate that the population of large snails in Jervis Bay represent a larval recruitment pulse. The mean size of the large snails collected at Plantation Point was 100 mm shell height, which are estimated 4.5 years old, according to the temperate snail growth model (Chapter 5), implying that the snails were recruited in early 2017. Oceanographic modelling could help to determine whether past environmental conditions could have driven a strong larval recruitment pulse and predict if recruitment is likely to increase with changing ocean conditions. As ocean currents and temperature play a major role in facilitating larval movement (Pattiaratchi & Siji, 2020), potential drivers of larval recruitment could include unusually high sea surface temperatures (Commonwealth of Australia, 2018) or the presence of El Niño events, which strengthen the EAC (Pattiaratchi & Siji, 2020). Alternatively, smaller snails may have gone undetected if the juvenile habitat was not searched, which is possible given that observers were not actively looking for small turban snails. This raises the possibility that the apparent absence of small *T. militaris* in southern NSW reflects observational limitations rather than a true absence.

Turban snails likely settle in shallow areas of turf algae and kelp holdfasts, as these habitats are where the small juveniles have mostly been found (Chapter 5; Smith & Rule, 2002). Macroalgae is highly abundant on the NSW south coast (Lloyd et al., 2020; Shalders et al., 2023) and potentially offer suitable settlement habitats for juvenile snails. However ocean warming, and the introduction of invasive species (e.g., urchin species), could result in the loss of macroalgae habitats with lasting consequences for *T. militaris*.

6.4.3 Fecundity and fisheries productivity

Information on reproductive output is required for assessing population resilience, stock sustainability and building biological appropriate management strategies (Officer, 1999; Llordra, 2002; Hoggarth et al., 2006). Given the latitudinal disparity in growth across different regions in the *T. militaris* fishery (Chapter 5), further studies on recruitment potential (i.e., fecundity and larval connectivity) are required for a comprehensive assessment on resilience across the fishery (Table 6.1). Estimates of reproductive output across subtropical and temperate regions will help understand how disparities in growth (Chapter 5) may impact productivity. Conceptually, by considering the timing and frequency of spawning, estimated at three times per year (Chapter 3), combined with growth models to predict age-at-size (Chapter 5) and size-based fecundity data we could provide an estimate of reproductive output. However there are no data on fecundity of *T. militaris* (or any harvested Australian species; Table 6.1), therefore research on size-based fecundity is a priority for future work.

Many invertebrates, including turban snails have a higher fecundity with larger adult size (Mgaya & Mercer, 1994; Komatsu et al., 1995; Llordra, 2002; Linse et al., 2006; Martone & Micheli, 2012). The temperate snails are larger at a given age than subtropical snails (Chapter 5), consequently, the temperate snails may have a higher reproductive output per age. Over the lifetime, lower reproductive output in the subtropical snails could be offset in terms of reproductive potential as the subtropical snails are longer-lived. Furthermore, the longer period between maturity and legal fisheries size in subtropical snails (Chapter 5) allows for extra years of reproduction. Thus, in subtropical populations, the longer time between maturity and legal fishing size offers more reproductive time and may offset the potentially higher fecundity associated with larger snails in the temperate population.

Actual fecundity measurements would involve rearing animals in controlled conditions and inducing spawning (Murakoshi et al., 1993; Lee, 1997). Once spawned, oocytes can be collected by filtering the water and resuspended in a known volume of water where oocytes can be counted from a subsample and the total spawned fecundity can be calculated (Llordra, 2002). For *T. militaris* spawning cues are not known, but for other turban snails these can include rough water or temperature fluctuations (Grange, 1976b; Yamaguchi, 1988; Dwiono et al., 2001; Matoto et al., 2002; Freije & Al-Sayed, 2009; Lee et al., 2014). The association of reproductive cycle with environmental variables for *T. militaris* (Chapter 3) could help in the conditioning and timing to trigger spawning if enhancement of the fishery is required in the future.

To obtain potential fecundity (total oocytes in the gonad) from field collected snails, the ovary can be dissected and oocytes counted (Llordra, 2002). An understanding of the reproductive cycle (Chapter 3) will help to determine the best timing, when the gonads are ripest, for assessing potential fecundity. As turban snails have a very high number of oocytes (Murakoshi et al., 1993; Komatsu et al., 1995; Ramesh et al., 2010), including *T. militaris* (pers. obs.), this can be achieved by counting or measuring oocytes in a subsample, then back calculating this to represent the whole gonad (Komatsu et al., 1995; Ramesh et al., 2010; Martone & Micheli, 2012). However, as the actual eggs available for fertilization in broadcast spawners may differ from the number of eggs in the ovary, histological techniques to determine the number of mature oocytes in the ovary may provide a means to estimate actual fecundity, if researchers are unable to induce spawning (Llordra, 2002). Drill-biopsy (Chapter 2) could also be used to help assess fecundity by facilitating selection of females and potentially sampling a known gonad biopsy volume counting eggs and projecting to volume of reproductive material for different sized snails.

6.4.3 Future studies on growth

The findings on growth disparities across latitudes (Chapter 5), underscore the need for further work to assess growth across the latitudinal gradient. Field-based studies, such as mark-recapture are a common method for aging marine animals. However, mark-recapture methods are time-intensive, require repeated sampling over long periods, and can be particularly challenging in marine environments. Additionally, the effectiveness of mark-recapture experiments can be compromised by factors such as tag loss, emigration, predation or harvesting of tagged animals. Analysing growth rings on calcified structures offers an alternative approach that may be more useful, especially in regions where mark-recapture studies are impractical. Given the logistical challenges of mark-recapture studies, growth band analysis could provide a more feasible method for expanding age and growth studies for *T. militaris* across a broader geographical range.

Unique to turban snails is a markedly calcified operculum, which potentially presents an opportunity for age determination using growth striae if growth bands could be validated. Growth band studies have been successful in *M. undosa* (Gluyas-Millán et al., 2000), although the formation of the opercula is less complex than the paucispiral operculum in genus *Turbo*. Growth band studies have been attempted for *T. sarmaticus*; however, the study presented equivocal results for attributing banding to growth (Foster, 1997). A study on *T. setosus* found three types of banding in the opercula: translucent stress bands, daily bands and sub-daily bands (Sire & Bonnet, 1984). In order to assess the potential to accurately count growth bands in *T. militaris*, I undertook studies using fluorochrome marking techniques to determine growth ring periodicity in the operculum. Whilst the fluorochrome marking was successful, the consistency of bands could not be reliably determined. Details of the fluorochrome marking methods and results are outlined in Appendix D.

To build on the current work, Laser Ablation Inductively-Coupled – Mass-Spectrometry (LA ICP-MS) techniques could be used to investigate the consistency of growth cycles by analysing strontium or magnesium ratios to calcium (Appendix E). Oxygen isotope analysis presents an alternative method to estimate age in marine gastropods (Bökenhans et al., 2016; Hollyman et al., 2018a). Oxygen isotope profiles and element ratios in shells can relate to sea temperature and therefore be used to determine growth periodicity (i.e., ratios fluctuate seasonally) (Sosdian et al., 2006; Spence et al., 2010; Bökenhans et al., 2016; Hollyman et al., 2018a). LA ICP-MS or oxygen isotope analysis on the opercula could be used to estimate age in *T. militaris.* Elemental ratios have been used for age studies in other shelled molluscs including magnesium:calcium in the whelk *Neptunea antiqua* (Richardson et al., 2005) and in oysters using LA ICP-MS (Spence et al., 2010; Durham et al., 2017). Additionally, the mussel *Pinna nobilis* was aged using strontium:calcium and magnesium:calcium (Richardson et al., 2004) and the cone snail *Conus ermineus* using strontium:calcium (Sosdian et al., 2006). Furthermore, LA ICP-MS techniques can be used to detect elements such as manganese, copper, iron, nickel or barium, as found in bivalves (Barrat et al., 2023; Benthotage et al., 2023). Elements such as manganese be useful for validation of LA ICP-MS results, and this could be achieved through manganese marking (Hawkes et al., 1997). Additionally, trace elements may be used to detect perturbations from environmental events (e.g., flooding and heatwaves) and, alongside a timeline of these events, trace elements could be useful for validation.

6.5 Conclusion: towards an informed fishery for *Turbo militaris*

This thesis has substantially improved our knowledge of the harvested marine gastropod, *T. militaris*. This research provides empirical data that enhances our understanding of population dynamics and can be used to inform regulations to support the management of turban snails in NSW. By revealing disparities in life-history parameters across latitudinally separate populations, this work offers essential insights into climate change impacts on this species and serves as a foundation for future research. This research on *T. militaris* exemplifies how spatial-scale studies are especially relevant for informing fisheries management and conservation for species spanning across geographical ranges and climate change hotspots. By addressing data deficiencies, this work advances our understanding of this species' biology and ecology and identifies future research priorities. These findings will substantially contribute to the objective management of *T. militaris*, an ecologically important species and a valuable resource for cultural, recreational and commercial fisheries.

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APPENDICES

APPENDIX A. Chapter 2 supplementary material

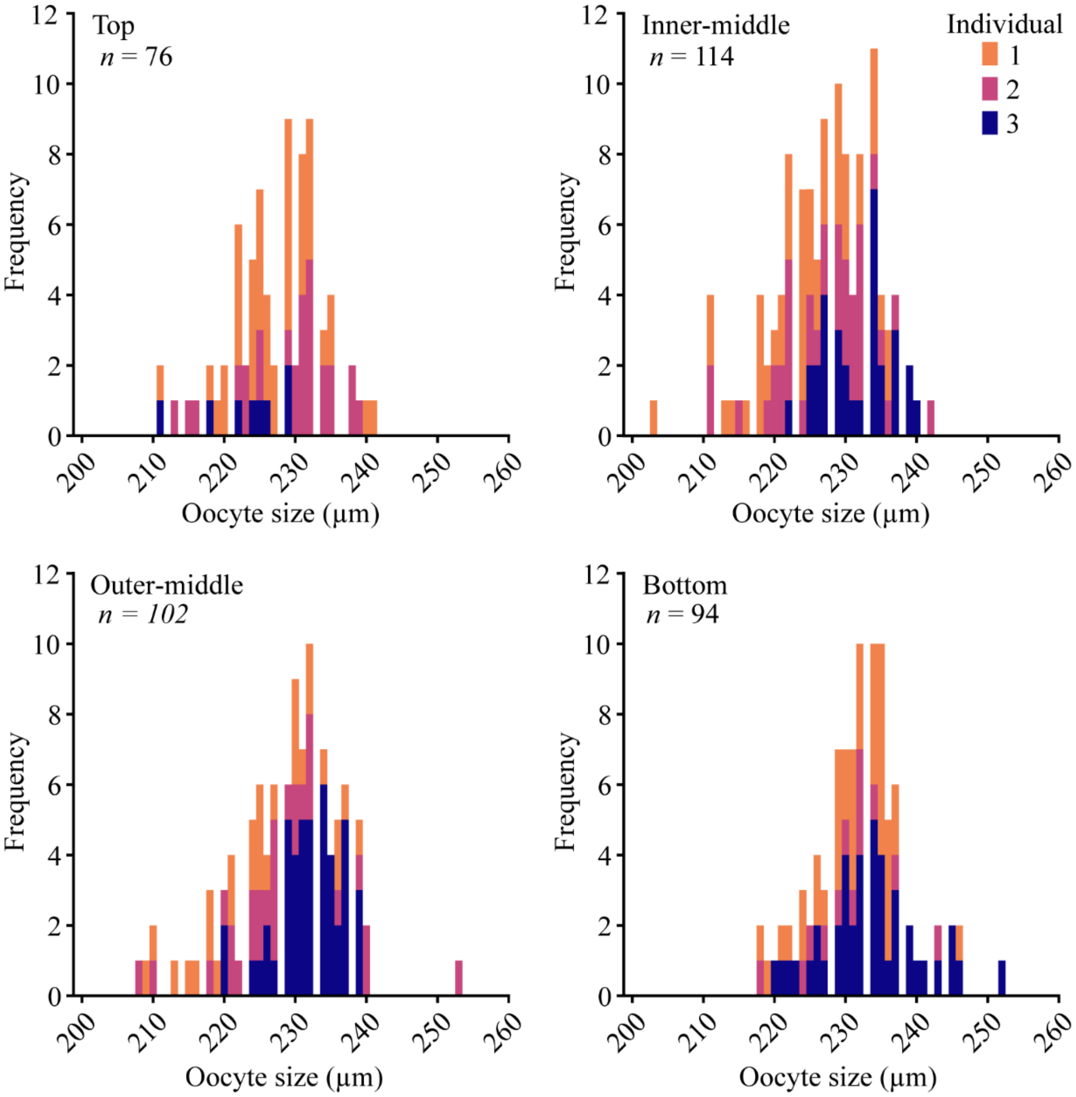

Figure A1. Oocyte size frequencies of *Turbo militaris* (*n* = 3) from the top, inner-middle, outer-middle and bottom regions of the female gonad.

APPENDIX B. Chapter 4 supplementary material

Table B1. Multivariate PERMANOVA results for annual displacement distance, elevation change and displacement direction of *Turbo militaris* at four locations in New South Wales, Australia, with shell height (mm) and shell morphology (ratio of shell width with spines to shell width without spines) as covariates.

Source	*df*	*SS*	R^2	*F*	*p*
Location	3	54.77	0.048	2.772	0.005
Shell height	1	13.54	0.012	2.055	0.113
Shell morphology	1	7.70	0.007	1.169	0.333
Residual	162	1066.99	0.934		
Total	167	1143.00	1		

Table B2. Results of back step-selection PERMANOVA analysis for annual displacement distance, elevation change and displacement direction of *Turbo militaris* at four locations in New South Wales, Australia.

Source	*df*	*SS*	R^2	*F*	*p*
Annual displacement distance					
Model	3	7.92	0.047	2.723	0.044
Residual	164	159.08	0.953		
Total	167	167.00	1		
Elevation change					
Model	3	3.08	0.018	1.028	0.375
Residual	164	163.92	0.982		
Total	167	167.00	1		
Displacement direction					
Model	3	8.10	0.049	2.787	0.044
Residual	164	158.90	0.952		
Total	167	167.00	1		

Table B3. Results from a paired *t*-test comparing the difference in displacement distance of *Turbo militaris* between the six- and twelve-month recapture timeframes for animals captured on both occasions from mark-recapture experiments in New South Wales, Australia.

	Mean difference	SD	SE	95% CI		*df*	*t*	*p*
				Upper	Lower			
Six - Twelve	0.085	0.253	0.121	-0.167	0.337	22	0.699	0.492

Table B4. Results of logistic regression on the effect of shell height (mm) or *Turbo militaris* on recapture from mark-recapture studies over 12 months at four locations in New South Wales, Australia.

	Estimate	SE	*z*	*p*
Intercept	-1.169	0.049	-2.365	0.018
Shell height	0.001	0.007	0.096	0.923

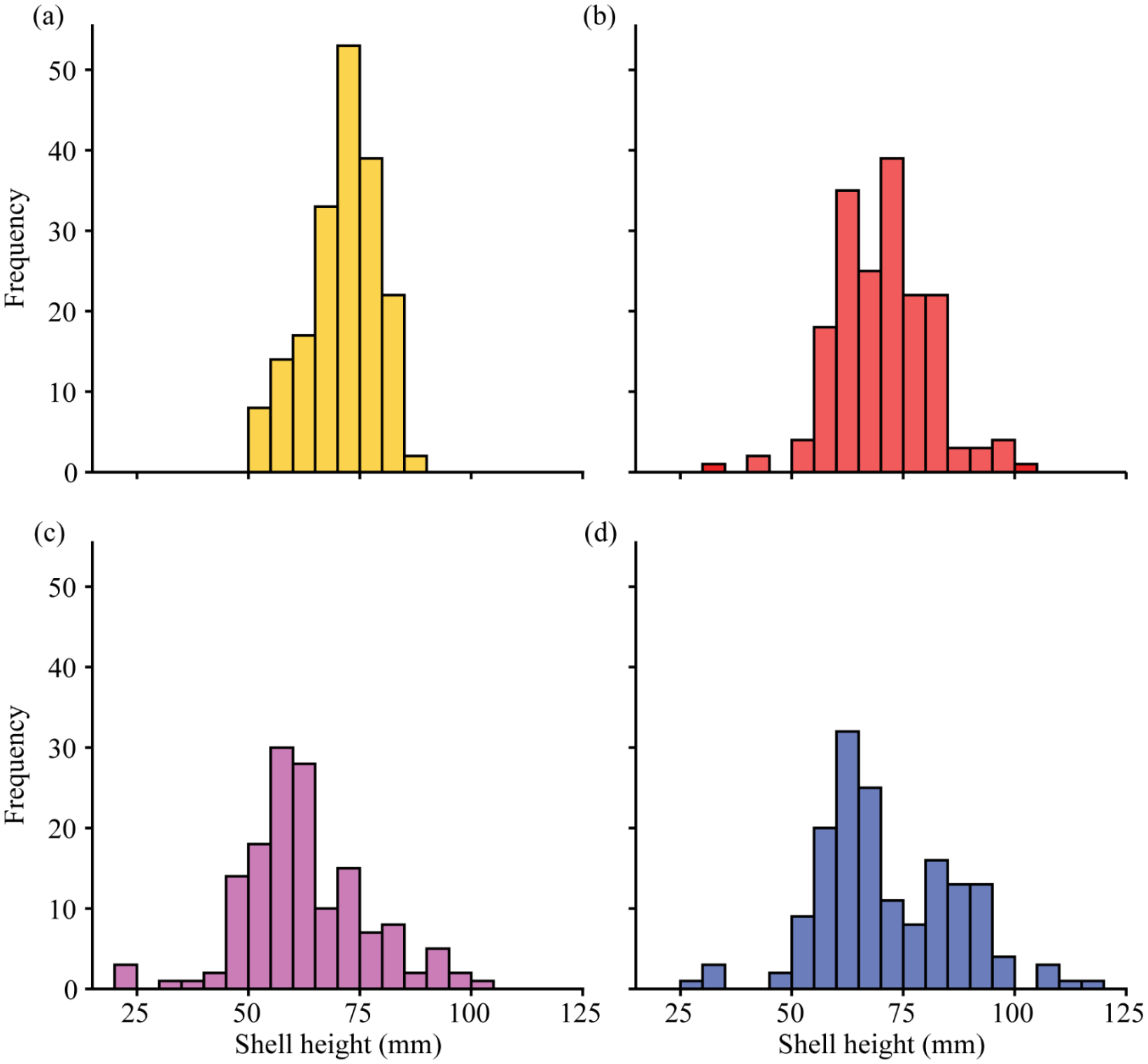

Figure B1. Size-frequency histograms of the shell height (mm) at tagging of *Turbo militaris* during mark-recapture studies at Woody Head (a), Diggers Camp (b), Big Rocky (c) and Fishermans Bay (d), New South Wales, Australia.

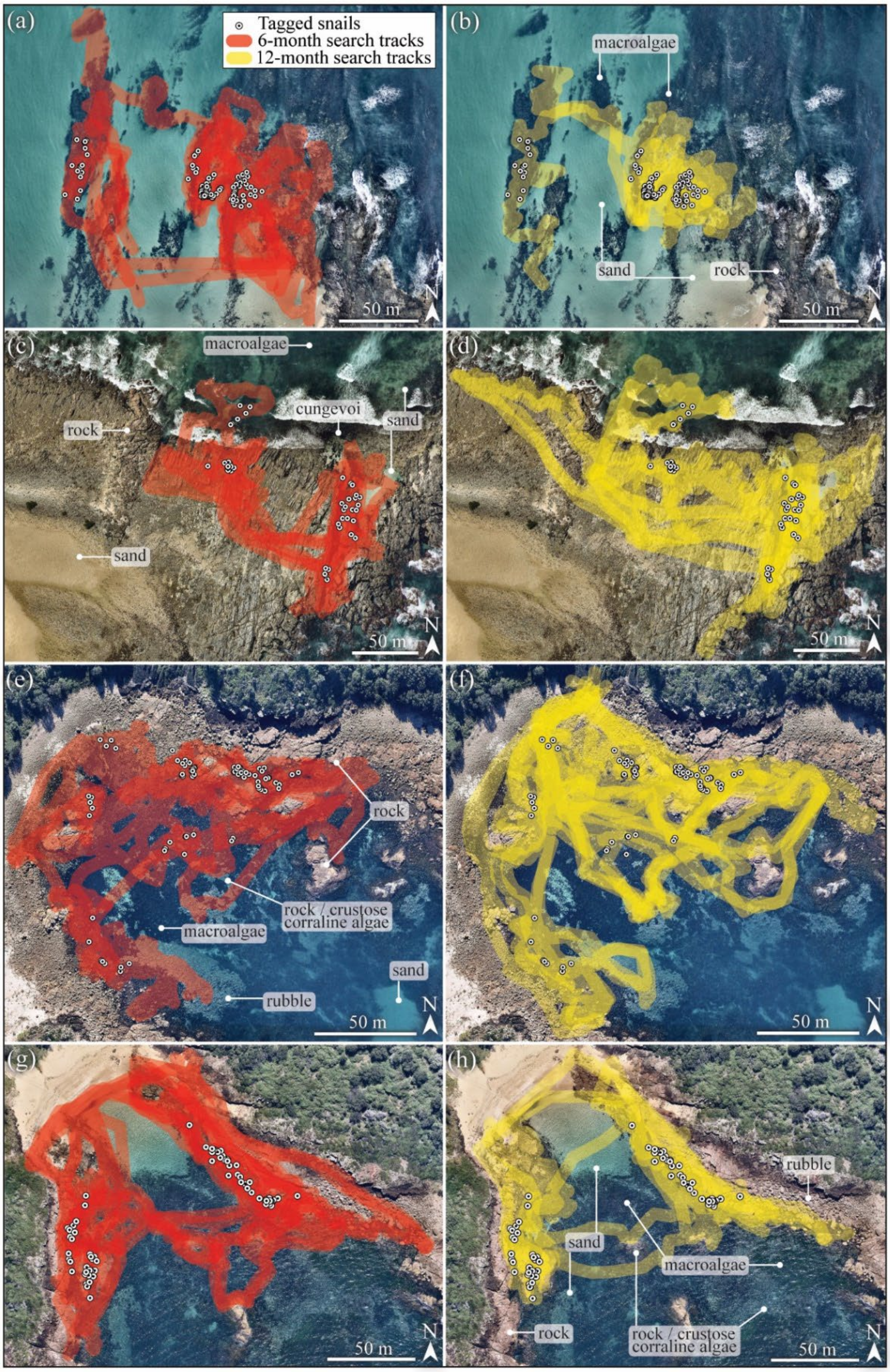

Figure B2. Location of tagged *Turbo militaris* and recapture search tracks at Woody Head (a, b), Diggers Camp (c, d), Big Rocky (e, f) and Fishermans Bay (g, h), New South Wales, Australia. Habitat features labelled. Aerial images sourced from Nearmap (2024).

Figure B3. A tagged *Turbo militaris* recaptured at one of the field sites, showing growth from non-geniculate crustose coralline algae over the tags. Location of the tags indicated by the black ovals. Animal height: 70 mm.

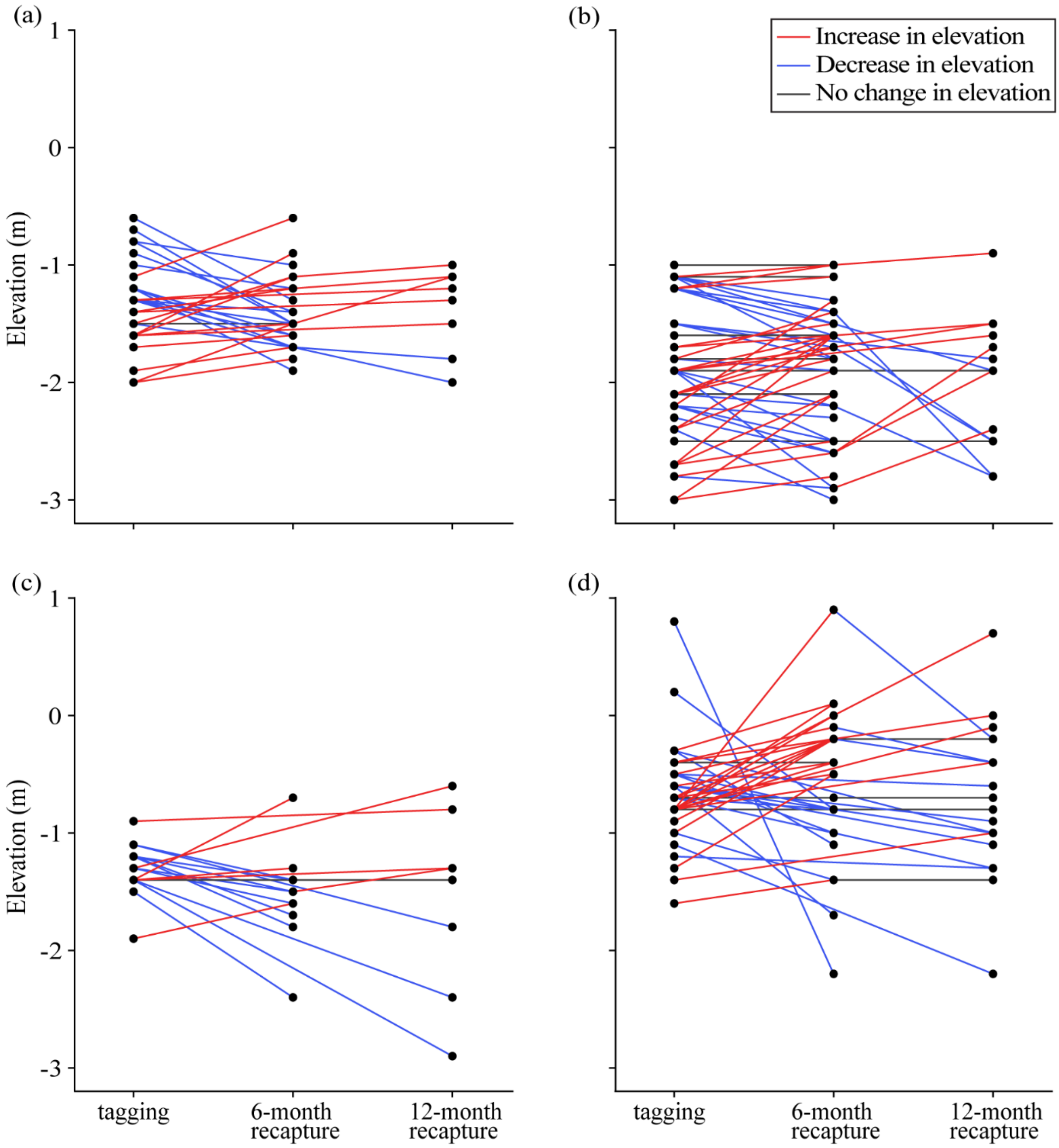

Figure B4. Elevation at tagging and recapture after 6 months and 12 months or *Turbo militaris* at Woody Head (a), Diggers Camp (b), Big Rocky (c) and Fishermans Bay (d), New South Wales, Australia.

APPENDIX C. Chapter 5 supplementary material

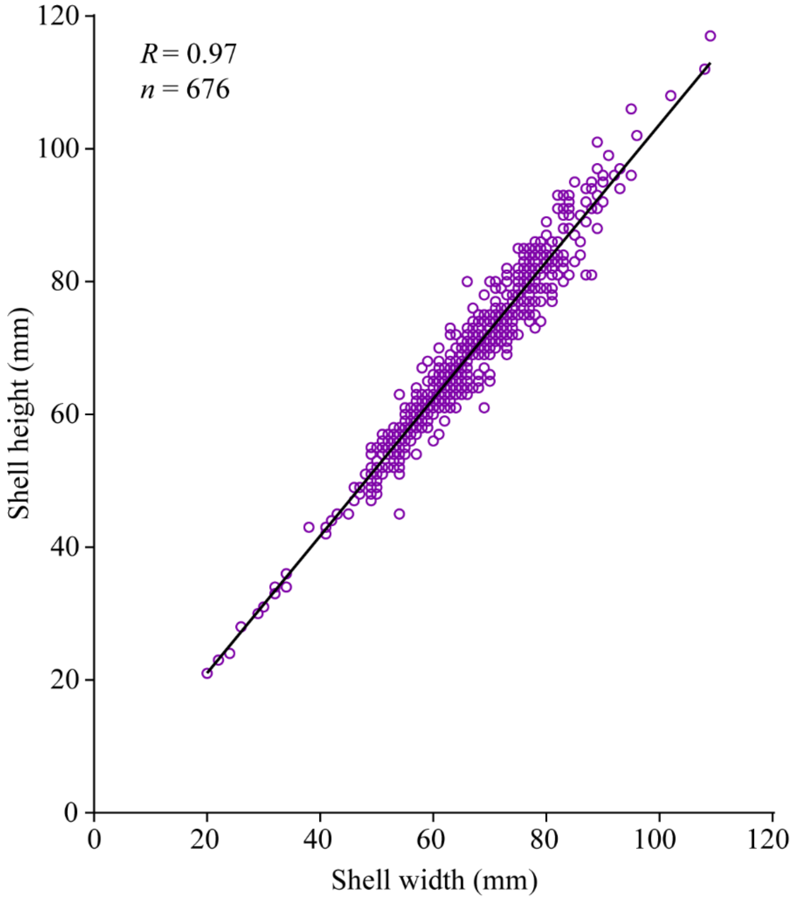

Figure C1. Correlation between shell height (mm) and shell width (mm) of *Turbo militaris* at the time of tagging from the mark-recapture study in New South Wales, Australia.

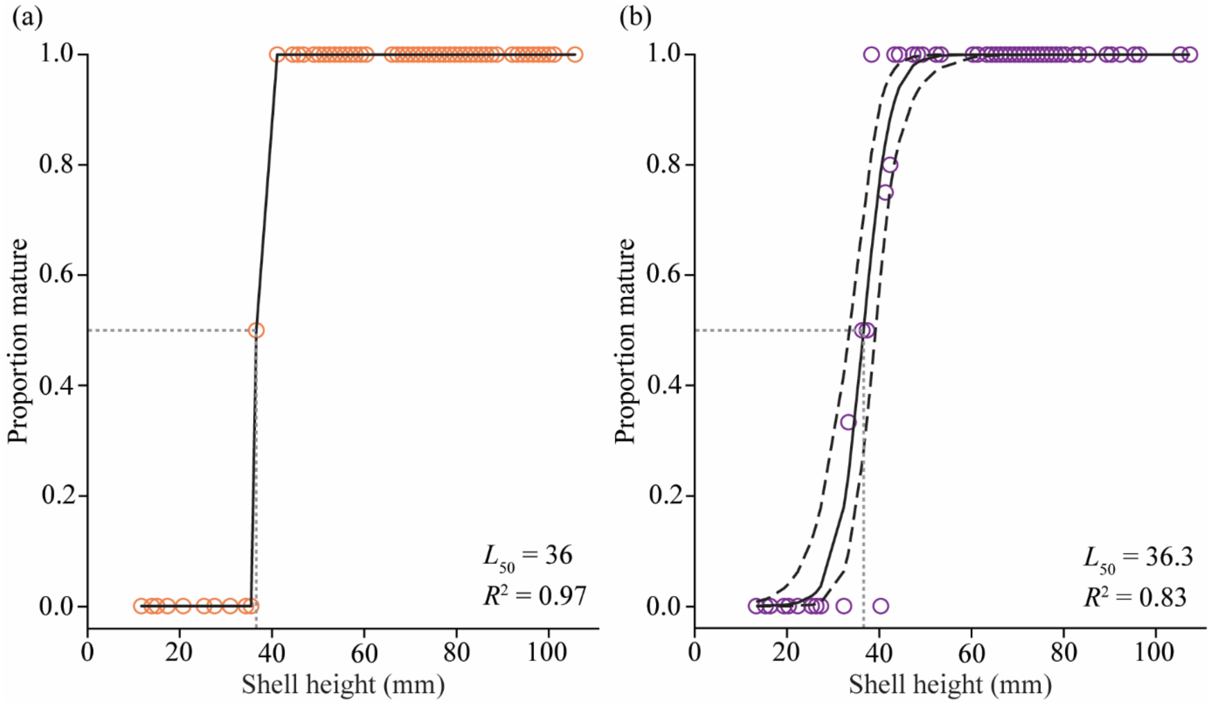

Figure C2. Shell height (mm) and proportion of *Turbo militaris* at first maturity from subtropical (a) and temperate (b) regions in New South Wales, Australia. The solid line indicates model fit from Bayesian regression analysis, and dashed lines indicate 95% confidence intervals. The grey dotted line indicates LM_{50}, the shell height at 0.5 proportion mature.

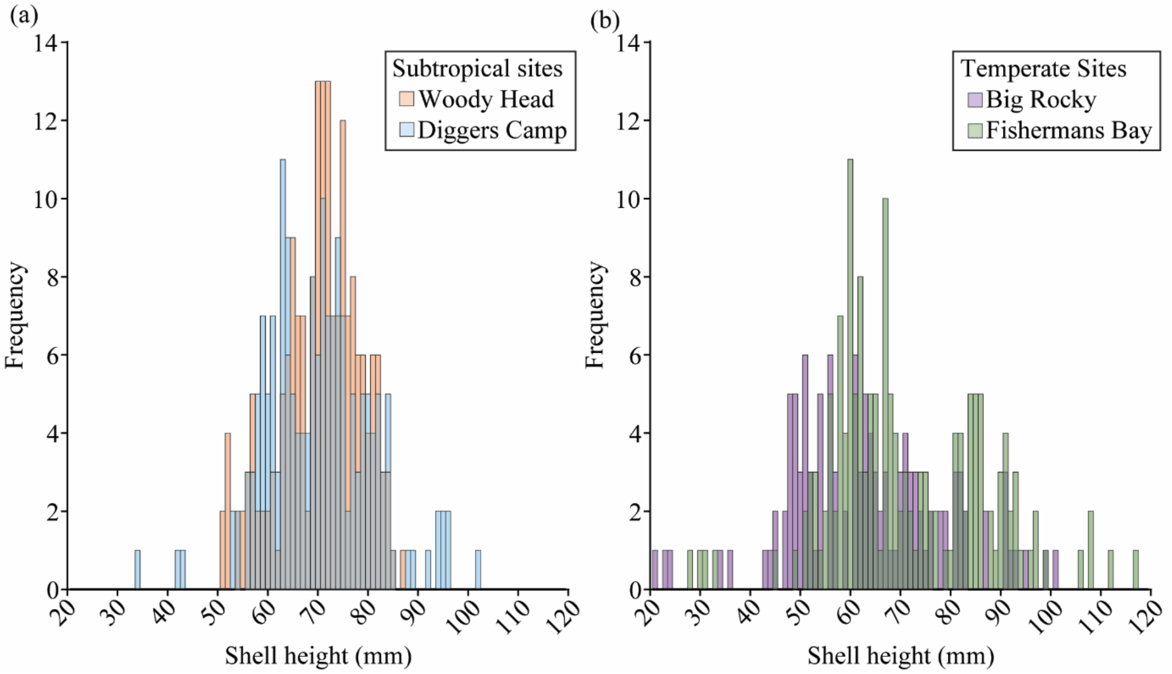

Figure C3. Size frequency histograms of height at the time of tagging for *Turbo militaris* at two subtropical sites (a) and two temperate sites (b) in New South Wales, Australia.

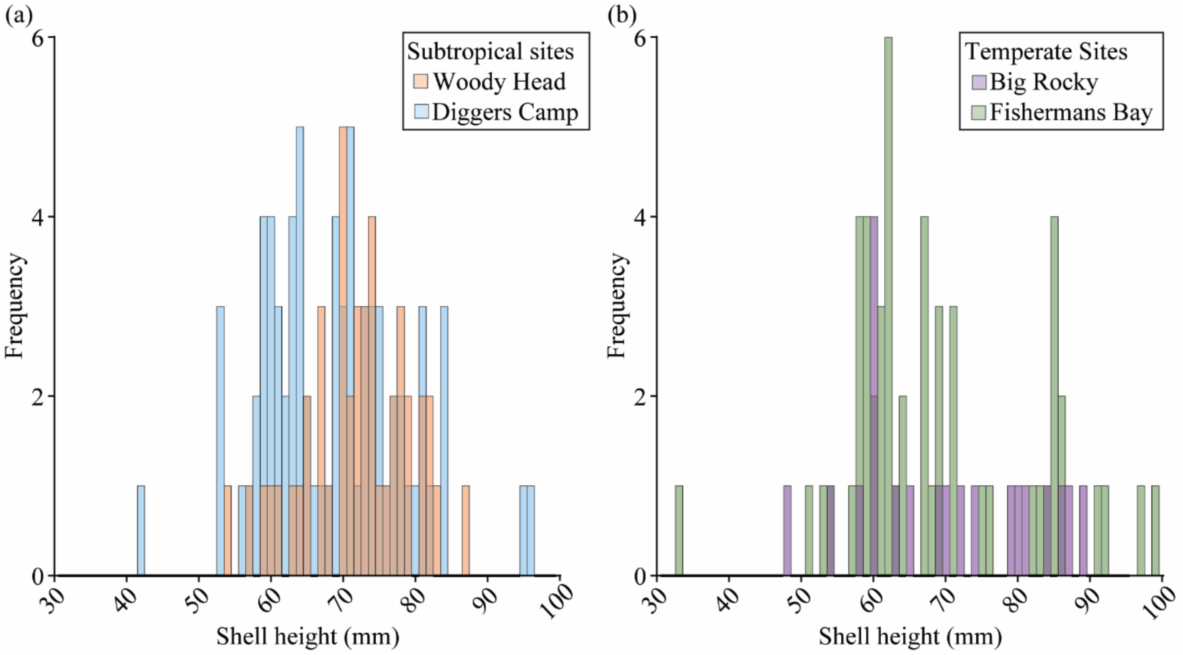

Figure C4. Size frequency histograms of height at time of recapture (6 and 12 months combined) of *Turbo militaris* at two subtropical sites (a) and two temperate sites (b) in New South Wales, Australia.

APPENDIX D. Fluorescent marking in the opercula of *Turbo militaris*

Aim

This work aimed to establish the periodicity of growth striae in the operculum of *Turbo militaris*. The specific objectives were to successfully obtain a fluorescent mark from calcein and tetracycline in the operculum and to determine if the number of growth bands between the marks (if two marks were present) or to the growing edge correlates to the number of days (or another cyclic measure) at liberty. Fluorochrome marking techniques have been used to determine a daily ring deposition in *T. setosus* (Sire, 1984; Sire & Bonnet, 1984).

Methods

Twenty *Turbo militaris* within a wide range of sizes were collected from two rocky shores in New South Wales, Diggers Beach (30.3° S, 153.2° E) and Woody Head (29.4° S, 153.4° E). Upon collection, the turban snails were placed in a bucket with a small amount of seawater and transported to the National Marine Science Centre (NMSC) immediately. The maximum height, maximum width without spines and maximum width with spines were measured to the nearest mm using Vernier callipers. At the NMSC, turban snails were placed into a raceway tank with continual water flow and aeration and allowed to acclimatise for five days.

Following acclimatisation, turban snails were removed from the tanks and placed in a large bucket with aeration and continual water flow of filtered seawater. A calcein fluorochrome solution was prepared by dissolving 2 g of calcein powder in filtered seawater adjusted to a pH of approximately 6. Water flow to the bucket was stopped, and the water was filled to 20 L. The calcein solution was added to the water (Figure D1) to produce a final solution of 200 mg / L. The bucket was covered, insulated with shade cloths, and left for 12 hours. After 12 hours, the turban snails were removed, rinsed in seawater, and placed back in the raceway. Approximately three months later, the turban snails were subject to a tetracycline fluorochrome solution using the same method.

Figure D1. Fluorochrome bathing of *Turbo militaris*; individuals in 20 L of filtered seawater and calcein at 200 mg / L concentration.

The turban snails were housed in the raceway tank for 12 months. In the tank, bricks and blocks were added to enhance biofouling and provide refuges for turban snails. Mixed algae collected from nearby rocky shores were added to the tanks periodically. Added algae, combined with heavy natural biofouling, meant the turbos could graze *ad libitum.* Throughout the housing period, four individuals perished, and eight were removed earlier than the 12-month period for investigation of the success of fluorochrome marking. The remaining snails were removed and dissected at the cease of the 12-month housing period.

The opercula were prepared in dark conditions to avoid deteriorating the fluorochrome marks. The maximum height, maximum width without spines and maximum width with spines were measured to the nearest mm using Vernier callipers. The shell was cracked open using a hammer, and the soft body and operculum were removed. The maximum diameter of each operculum was measured to the nearest 0.1 mm using digital Vernier callipers. Sex was visually determined by viewing the colour of the gonad: dark green for females and cream for males.

Each operculum was immersed in water and cleaned by brushing with a coarse brush to remove organic matter. Opercula were set in polyester clear casting resin (Figure D2a). Thin sections, ~0.5 mm were cut using a low-speed cutting saw with a wafered diamond edge blade (Figure D2b). Sections were cut perpendicular to the foot attachment on the opercula across the widest point, ensuring the section aligned through the centre of the growth spiral. Each section was mounted onto glass slides using super glue. The top side of each section was polished on a series of fine grain (240, 600 and 1200 grit) wet and dry sandpaper on a low-speed wet orbital sander. The polished samples were rinsed in ultrapure water.

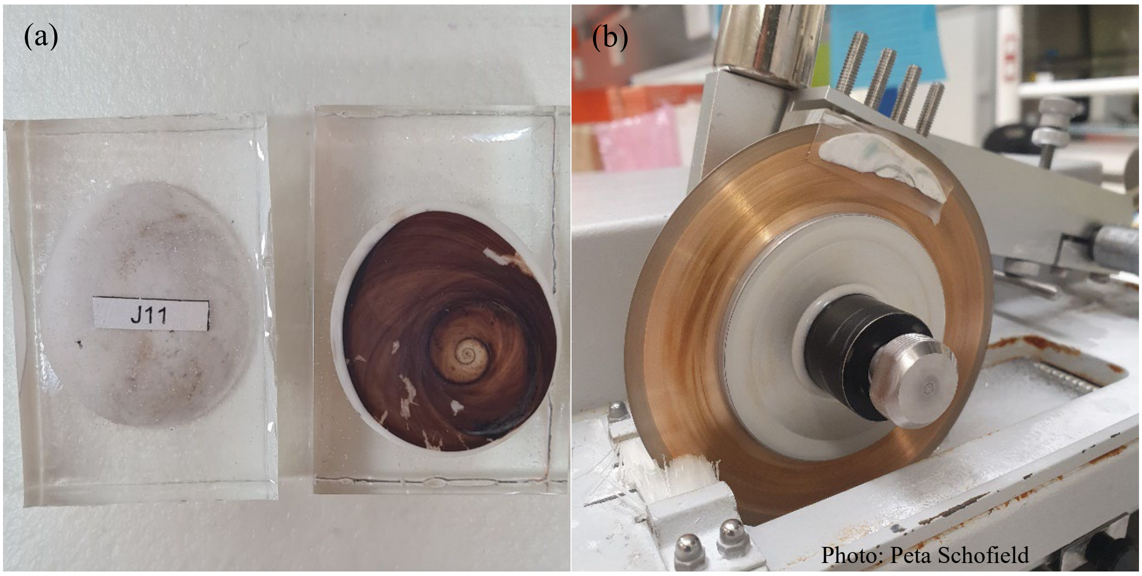

Figure D2. *Turbo militaris* operculum set in clear casting polyester resin blocks (a). A thin section cut perpendicular to the foot attachment surface using a low-speed saw with a diamond edge blade (b).

Each opercula section was viewed using 40 x magnification on a biological microscope (Olympus BX53) fitted with a fluorescent lamp illuminator (Lumen Dynamics X-Cite 120Q). Each sample was viewed under ultraviolet light for detection of fluorescent marks. Where a fluorescent mark was present, photomicrographs of the region including the mark to the growing edge were taken under ultraviolet light, using a microscope-fitted camera (MIcrome 20 Pro). The same region was then photographed under transmitted LED light. Photos were imported into Adobe Lightroom (v28.3), where the photo merge tool was used to stitch the images together for each sample. On the images taken under LED light, the location of the fluorescent mark was noted and the number of bands between the fluorescent mark and the growing edge was counted using the count tool in Adobe Photoshop (v28.3).

Results

The average shell height of snails at the start of the experiment was 75 mm (± 3 mm SE). The maximum growth increment for snails that remained in the tanks for ~12 months was 4 mm; however, some snails had a zero-growth increase over the study.

Fluorescent marking had a 44% success rate with marks visible in 10 opercula. The calcein mark appeared a yellow-green colour under ultraviolet light and the tetracycline was orange (Figure D3a). Of the successfully marked individuals, six opercula had a calcein mark and four opercula had both calcein and tetracycline marks.

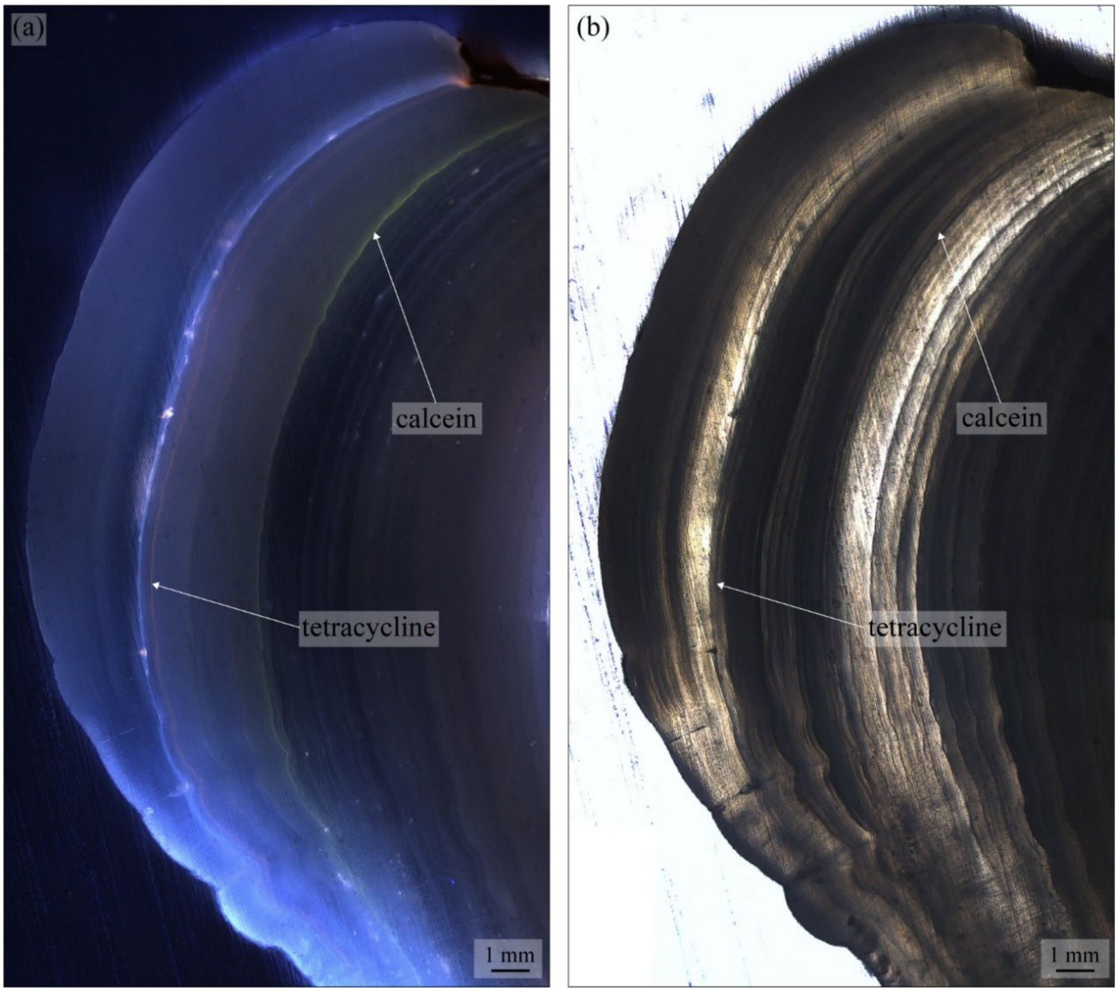

Figure D3. *Turbo militaris* opercula viewed under ultraviolet light showing a calcein and a tetracycline mark (a). The same sample viewed under transmitted LED light (b). Arrows indicate the location of the fluorochrome marks.

Growth banding was not always clearly visible (Figure D3), which introduced uncertainty of growth band counts. The number of bands between the fluorochrome marks and the growing edge was highly variable among individuals and did not match the number of days at liberty (Figure D4a). Alternation of wide translucent and thin opaque bands were apparent on some opercula, however, these were not consistent between individuals and no clear patterns were observed (i.e., moon cycles or season). There was considerable variability in band counts among individuals (Figure D4a), further complicating their reliability as a measure of age. Additionally, there was no clear relationship between the shell height (mm) or the growth increase (mm) and the number of bands between the calcein mark and the growing edge (Figure D4b).

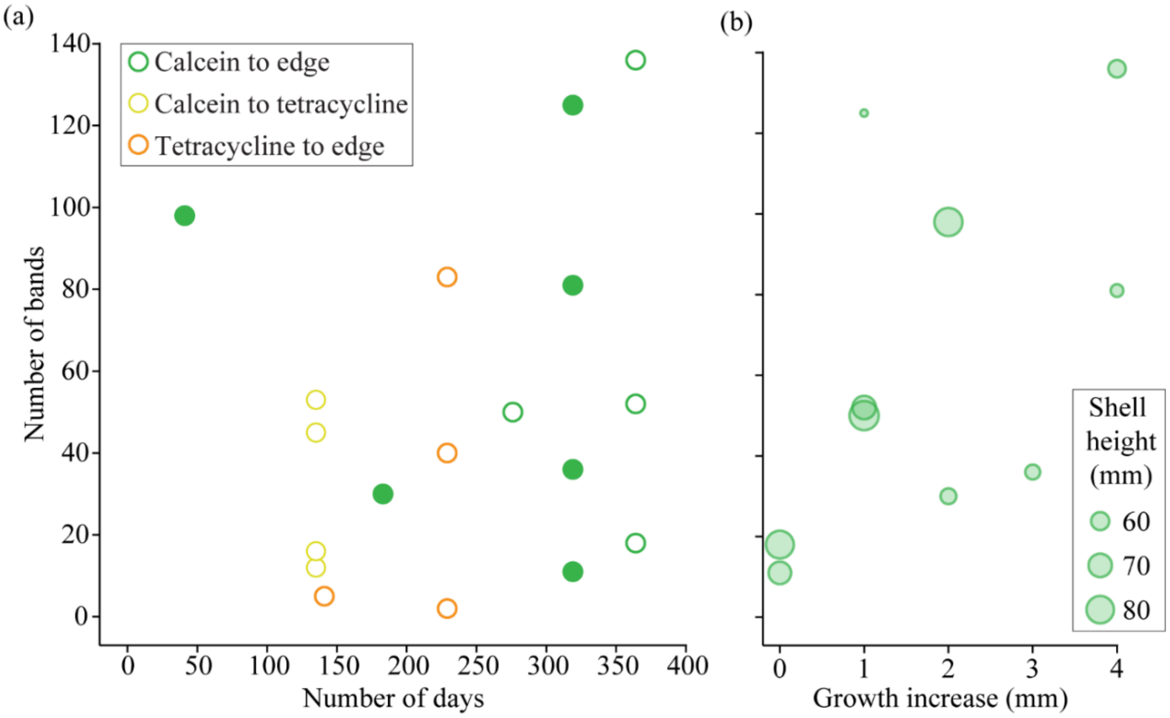

Figure D4. The number of bands between fluorescent marks and the growing edge of *Turbo militaris* opercula and the number of days at liberty (a). Closed points represent samples with only a calcein mark (n = 6) and open points represent samples with both calcein and tetracycline marks (n = 4). The number of bands between calcein marks and the growing edge and the growth increase (shell height – mm), and initial shell height (mm) depicted by bubble size (b).

APPENDIX E. Laser ablation inductively-coupled mass-spectrometry of *Turbo militaris* opercula

Opercula preparation

Turbo militaris were collected from seven rocky shores along the New South Wales coast: Hastings Point (29.2° S, 153.3° E), Woody Head (29.2° S, 153.2° E), Nambucca Heads (30.4° S, 153.0° E), Crowdy Head (31.5° S, 152.5° E), Big Rocky (32.8° S, 152.1° E), Sydney (34.0° S, 151.2° E), and Jervis Bay (35.1° S, 150.4° E). Samples were collected in collaboration with a study on genomics (Nimbs et al., 2023), a method development study (Woody Head samples) (Chapter 2) and a tagging study (Sydney samples) (Hamer, 2024). Three large individuals (shell height <80 mm) were selected from the snails collected at each site for opercula studies.

Measurements, dissections and preparation of the thin opercula sections were carried out as per the method outlined in Appendix D. The thin sections were adhered to glass slides using the clear bonding agent, Crystal Bond, and then each section was polished (as per Appendix D). One additional sample was sectioned parallel to the foot attachment edge, including the centre growth spiral (Figure E1a). Each opercula slide was viewed using a dissecting microscope (Nikon SMZ745T) using 3 x magnification. Multiple photomicrographs across the whole sample were taken of each sample using a microscope-fitted camera (MIcrome 20 Pro). The set of images for each sample was imported into Adobe Lightroom (v28.3), where the photo merge tool was used to merge the photos into one image for each opercula (Figure E1).

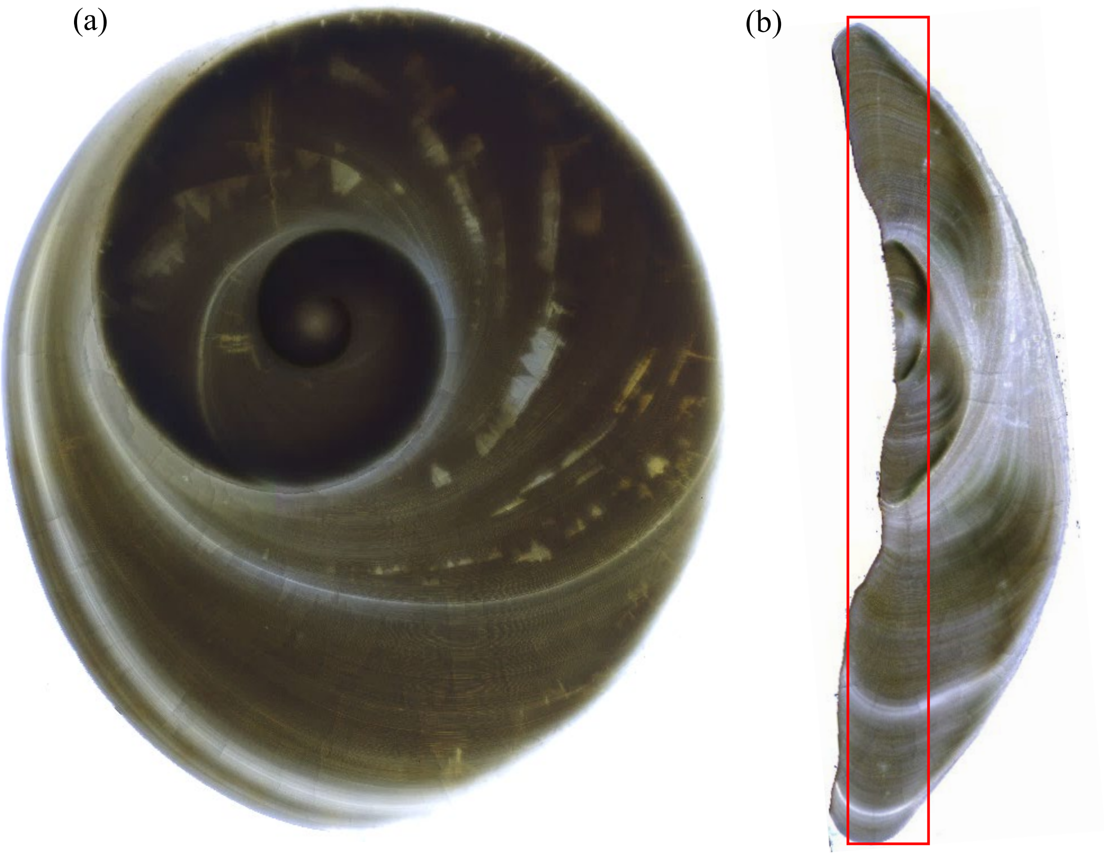

Figure E1. *Turbo militaris* opercula on the axis parallel to the foot attachment (a) and the perpendicular axis (b), derived from a series of merged photomicrographs taken with a dissecting microscope. Samples were collected from Jervis Bay, New South Wales, Australia. The red box denotes the approximate region for laser ablation mapping.

Proposed method

The proposed method includes analysis of the opercula sections using Laser Ablation Inductively-Coupled – Mass-Spectrometry (LA ICP-MS). The perpendicular sectioned samples will be ablated using a mapping technique over a region encompassing all growth directions (Figure E1b). The whole surface will be mapped from the parallel section (Figure E1a) and one perpendicular section to visualise the growth pattern from the two perspectives. Elements to consider in the LA ICP-MS to analyse growth include strontium, magnesium, and calcium. Ratios of strontium:calcium and magnesium:calcium will then be used to assess growth cycles. Other trace elements including barium, copper, iron, manganese and nickel will be included in the LA ICP-MS analysis to potentially detect environmental perturbations.

APPENDIX F. Statements of co-authorship

Authorship details

The following people and institutions contributed to the publication of work undertaken as part of this thesis:

Author #	**Name**	**Role**	**Affiliation**
Author 1 (candidate)	Kate Seinor	Candidate	National Marine Science Centre, Southern Cross University
Author 2	Prof. Kirsten Benkendorff	Primary supervisor	National Marine Science Centre, Southern Cross University
Author 3	Prof. Steven W. Purcell	Co-supervisor	National Marine Science Centre, Southern Cross University
Author 4	Prof. Stephen D. A. Smith	Co-supervisor	National Marine Science Centre, Southern Cross University Aquamarine Australia
Author 5	Dr. Hamish Malcolm	Industry supervisor	NSW Department of Primary Industries and Regional Development (Fisheries)
Author 6	Dr. Robert G. Creese	Collaborator	NSW Department of Primary Industries and Regional Development (Fisheries)

Proportion of work undertaken

Paper 1 (Chapter 2):

Seinor, K., & Benkendorff, K. (2023). Shell drilling and gonad biopsies provide a rapid, non-lethal method for in-situ assessment of reproductive periodicity in Turbinidae. *Journal of Molluscan Studies*, 89(2): e012. doi:10.1093/mollus/eyad012

The candidate was the primary author and, alongside Author 2, formulated the research. The candidate planned and conducted the fieldwork and laboratory work and analysed and interpreted the data with the guidance of Author 2. The candidate prepared the first draft of the manuscript. Overall, the candidate contributed approximately 90% of the planning, execution and preparation of the work for the paper.

Author 2 contributed to the formulation of the research and method development. Author 2 assisted with interpreting the data and provided inputs and feedback on the manuscript for publication. Author 2 assisted with the post-review revisions.

Paper 2 (Chapter 3):
Seinor, K., Purcell, S. W., Malcolm, H., Smith, S. D. A., & Benkendorff, K. (2023). Extended and spatially asynchronous reproductive periodicity in a harvested, warm-temperate rocky-reef gastropod (Turbinidae). *Fisheries Oceanography, 33(1)*: e12653. doi:10.1111/fog.12653

The candidate was the primary author and planned and conducted the fieldwork and laboratory analysis. The candidate and Author 2 analysed the data and interpreted the results. The candidate and all authors contributed to the study conception and interpreted the results. The candidate prepared the first draft of the manuscript. Overall, the candidate contributed approximately 80% of the planning, execution and preparation of the manuscript.

Author 2 contributed to the conception of the research, analysed part of the data and guided the interpretation of the results. Author 2 provided input and feedback on the manuscript for publication.

Author 3 contributed to the conception of the research and the interpretation of the results and assisted in the field. Author 3 provided edits and feedback on the manuscript.

Author 4 contributed to the conception of the research and the interpretation of the results. Author 4 provided edits and feedback on the manuscript.

Author 5 contributed to the conception of the research and the interpretation of the results. Author 5 provided edits and feedback on the manuscript.

Paper 3 (Chapter 4):
Seinor, K., Purcell, S. W., Malcolm, H., Creese, R. G., & Smith, S. D. A. (2025). Long-term mobility of a harvested, rocky-reef gastropod. *Fisheries Management and Ecology*, e12794. doi:10.1111/fme.12794

The candidate was the primary author, planned and conducted the fieldwork and analysed the data. The candidate and all authors contributed to the study conception and interpreted the results. The candidate prepared the first draft of the manuscript. Overall, the candidate contributed approximately 80% of the planning, execution and preparation of the manuscript.

Author 3 contributed to the formulation of the research and field methodology. Author 3 assisted in the field and provided support for the analysis and interpretation of the results. Author 3 contributed to drafting of the manuscript and provided edits and feedback on the manuscript for publication. Author 3 assisted with the post-review revisions.

Author 4 guided the formulation of the research, assisted in the field and provided guidance with analysis and interpretation of the results. Author 4 contributed to drafting the manuscript and provided edits and feedback on the manuscript for publication.

Author 5 contributed to the conception of the research, assisted in the field and provided edits and feedback on the manuscript.

Author 6 contributed to the conception of the research, assisted in the field and provided edits and feedback on the manuscript.

Chapter 5 – *in preparation for submission to an academic journal*:
Seinor, K., Malcolm, H., Benkendorff, K., Smith, S. D. A., Creese, R., & Purcell, S. W. Latitudinal variation in age and growth of a harvested, marine gastropod (Turbinidae)

The candidate was the primary author and contributed to the research design. They planned and conducted the fieldwork and analysed the data. The candidate interpreted the data and prepared the first draft of the manuscript. Overall, the Candidate contributed approximately 75% to the planning, execution and preparation of the manuscript.

Author 2 provided guidance on the conception of the research, interpretation of results and inputs on the draft feedback on the manuscript.

Author 3 contributed to the formulation of the research and field methodology and assisted in the field. Author 3 provided feedback on data analysis and interpretation of the results.

Author 3 contributed to drafting the manuscript and provided edits and feedback on the manuscript.

Author 4 contributed to the conception of the research and interpretation of results, assisted in the field and provided edits and feedback on the manuscript.

Author 5 contributed to the conception of the research, assisted in the field and provided edits and feedback on the manuscript.

Author 6 contributed to the conception of the research, assisted in the field and provided edits and feedback on the manuscript.

Co-author declarations

We, the authors, agree with the above-stated "proportion of work undertaken" for each of the above published (or submitted) peer-reviewed manuscripts contributing to this thesis:

Author 1 (candidate)
Kate Seinor

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Author 3
Prof. Steven W. Purcell

Author 4
Prof. Stephen D. A. Smith

Author 5
Dr. Hamish Malcolm

Author 6
Dr. Robert G. Creese