Integrating migratory marine connectivity into shark conservation

Abstract

Understanding migratory connectivity is important for the conservation of highly mobile marine species facing escalating threats. Establishing baseline information on migratory connectivity is important to identify species and regions requiring transboundary cooperation for their conservation. Despite efforts to track migratory sharks and rays, information on transboundary movements is limited and often inaccessible to managers and policymakers. Here, we synthesised multimethod movement data for Australian shark and ray species listed under the Convention on Migratory Species (CMS), investigating which species require international engagement to support their population recovery. Based on data from a systematic literature review, we built connectivity networks from telemetry and mark-recapture studies that provide a first transboundary connectivity baseline for Australian sharks and rays. Of the 29 CMS-listed shark and ray species reviewed, we identified 5 species linking the Australian Exclusive Economic Zone to other national jurisdictions via multispecies migratory connections through the Tasman Sea to New Zealand, through the Tasman and Coral Sea to New Caledonia, and north across the Timor Sea and Torres Strait. White sharks (*Carcharhinus carcharias*) and whale sharks (*Rhincodon typus*) were the most data rich, while 18 (62%) of species had no movement information. Of note, nearly two-thirds of Endangered or Critically Endangered migratory shark and rays had only one or no published studies. We also show the applicability of this framework to support (or not) listing of migratory species under CMS. We demonstrate that migratory connectivity baselines can support international reporting, direct international collaboration, and focus research efforts on critical knowledge gaps.

Keywords: Chondrichthyans; elasmobranchs; satellite telemetry; acoustic telemetry; biogeography; movement ecology; photo-identification

Introduction

Migration, the broad-scale movement of populations (Wiens 1997), can transcend ecosystem, national, economic, and cultural boundaries (Harrison et al. 2018; McLean et al. 2023). By connecting distant habitats, migrations contribute to ecosystem function and resilience (Alerstam & Bäckman 2018; Davidson et al. 2020). While migrations can facilitate access to seasonally abundant resources required for key biological processes (Alerstam et al. 2003), they also expose animals to a variety of threats and uncoordinated governance regimes (Roberson et al. 2021). This often results in population declines (Teitelbaum & Mueller 2019; Kubelka et al. 2022). Indeed, nearly half of all migratory species are in decline, and 20% are at risk of extinction (UNEP-WCMC 2024). Improved management of migratory species is urgently needed.

Migratory sharks and rays often exhibit breeding-site philopatry, in which they return to specific regions for parturition or mating, after long-distance migrations (Dudgeon et al. 2013; Chapman et al. 2015). These movements link biologically important areas that often span national boundaries, either between adjacent countries or between distant regions connected by extensive transnational migrations (Francis & Jones 2017). This phenomenon, of the geographic linking of individuals and populations across their migratory cycles, is known as migratory connectivity (Webster et al. 2002). Understanding migratory connectivity provides insights into the various stressors an animal encounters during its migration, and how these stressors may accumulate and shape population structure, genetic diversity, and survival rates (Heupel et al. 2015; Somveille et al. 2021; Flack et al. 2022). Therefore, enhancing our knowledge of migratory connectivity underpins the development of effective conservation and management practices aimed at mitigating the decline of migratory species.

This is particularly true for elasmobranchs (hereafter sharks and rays) – many of which are both highly migratory and under unprecedented threat (Pacoureau et al. 2021; Juan-Jordá et al. 2022), with many populations in decline (Roff et al. 2018; Dulvy et al. 2021; Yan et al. 2021; Simpfendorfer et al. 2023). Globally, approximately one-third of sharks and rays are threatened with extinction (Dulvy et al. 2021). Oceanic populations are more threatened compared to species in other habitats and have declined by 71% over recent decades (Pacoureau et al. 2021).

The Indo-West Pacific, and Australia in particular, is a global biodiversity hotspot for sharks and rays (Pimiento et al. 2023). Australia is frequently cited as a high-priority country for conservation of shark and rays due to their diversity, species richness and threatened status (Dulvy et al. 2017; Stein et al. 2018; Neubauer et al. 2024). Many of these species are dependent on specific habitats in disparate locations and often migrate within the Australian Exclusive Economic Zone (EEZ) (Stevens et al. 2010; Heupel et al. 2015), and beyond (Chin et al. 2017; McMillan et al. 2019). While several highly mobile shark species that use Australian waters, such as the white shark (*Carcharodon carcharias*), whale shark (*Rhincodon typus*), and tiger shark (*Galeocerdo cuvier*), have been extensively studied and are known to cross international boundaries, other species of conservation concern remain poorly understood. For example, the blue shark (*Prionace glauca*) and shortfin mako (*Isurus oxyrinchus*), both commonly caught as bycatch in pelagic fisheries, require improved understanding of their large-scale movements to inform coordinated, cross-jurisdictional management (Brouwer & Hamer

81 2024). Further, regardless of how well-studied a species is, the information available is
82 dispersed and not readily available and accessible to managers.
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Here we review and quantify published information on migratory connectivity for
Australian shark and ray species listed under the Convention on the Conservation of
Migratory Species of Wild Animals (CMS) to aggregate evidence of migratory patterns
and transboundary movement requiring international collaboration, and to support more
effective management. We build on the Action Plan for Australian Sharks and Rays
2021 that reviewed the extinction risk of all 328 Australian species (Kyne et al. 2021).
We conducted a data synthesis of over 30 years of literature on biotelemetry, mark-
recapture, and photo-identification studies to establish the first baseline for migratory
connectivity of globally at-risk sharks and rays in Australian waters. We also produced
network models for migratory shark and ray species, compiling movement information
to reveal species-level migratory connections (Bentley et al. 2025). Our aim is to
establish an initial baseline of migratory connectivity for Australian sharks and rays to
guide their effective conservation and management. We hope that this will support
Australia's commitments and reporting obligations under international conservation
agreements, including the CMS, and the Convention on Biological Diversity. This
baseline will determine areas supporting migrations of multiple species, highlight
regional and taxonomic data gaps, and help identify nations whose cooperation is
needed to improve the conservation and management of individual species.
102
103 **Methods**
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105 *Species selection criteria*
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Species selection was designed to support reporting by Australia under its
international commitments. International cooperation on the conservation of migratory
species is coordinated through bilateral and multilateral agreements, and more broadly
via the CMS and the Sharks Memorandum of Understanding (MoU) that sits underneath
it. CMS Appendix I requires binding protection measures with limited scope for
exceptions, while Appendix II, where most sharks and rays are listed, only requires
cooperation from signatories on management (Lawson & Fordham 2018). There are 29
species of sharks listed under the CMS that use Australian waters (Table S1). Within
Australian waters, the Environment Protection and Biodiversity Conservation (EPBC)
Act of 1999 is the primary legislation that provides protection for flora, fauna, and
ecological communities. The EPBC Act lists eight shark and ray species as threatened,
including the whale shark, white shark, grey nurse shark, two river shark species, three
sawfish species and Maugean skate. The Act further lists 17 species of sharks and rays
from the CMS Appendices as migratory, but does not list 12 other CMS-listed species
because Australia took a formal exception to those listings (and thus is not compelled to
address them as it does other CMS-listed species). It is also important to note that the
definition of a migratory species under CMS extends to any species that periodically
cross national boundaries (e.g., wolves, lynx, and some primates), and not solely to
species undertaking true migrations for reproductive or other purposes (Lewis &
Trouwborst, 2019).
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To provide an evidence base for engagement (including taking exceptions) and
reporting on migratory sharks, we include all Australian sharks and rays listed under the
Convention on the Conservation of Migratory Species of Wild Animals (CMS)

Appendices I and II, and the Memorandum of Understanding on the Conservation of
Migratory Sharks (Shark MoU) (Table S1). However, listing of species under CMS and
the Shark MoU is not a systematic process and there are likely to be many species that
could be listed that simply have not been included yet due to lack of capacity by a CMS
member state to nominate them, or lack of available data. As such, we include a case
study to show that the development of migratory connectivity baselines can support new
listing proposals. For this purpose, we chose two further species due to their known
large-scale movements and the large number of individuals tagged; the tiger shark
(*Galeocerdo cuvier*) and the bull shark (*Carcharhinus leucas*). The conservation status
of these two species (Vulnerable, and Near-Threatened, respectively) also support their
potential listing under CMS if transboundary movements can be identified. The spiny
dogfish *Squalus acanthias* was not included in our study because only the northern
hemisphere populations are listed under CMS.

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145 *Systematic Literature Review Protocol*

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We followed the PRISMA (Preferred Reporting Items for Systematic Reviews and
Meta-Analyses) framework to select and screen peer-reviewed literature for this study
(Moher et al. 2009). The PRISMA framework outlines a series of steps, beginning with
the identification of relevant studies through comprehensive database searches.
Subsequently, references meeting inclusion criteria undergo screening and eligibility
assessment based on predefined criteria (here, studies with a migratory connection with
Australia). Data are extracted only from selected references (Moher et al. 2009). For this
study, we compiled peer-reviewed studies that used biotelemetry, mark-recapture, and
photo-identification methods or derived products (e.g., kernel density estimates or state
space models) to describe the movements of the 29 CMS-listed species, and two data-
rich unlisted case study species (31 species total).
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All searches for references were conducted between June and November 2023. We used
a broad set of search terms (Appendix 1) related to movement ecology including general
descriptors (e.g., movement, biogeography, population structure, corridor or
connectivity), sampling methods (e.g., satellite, tracking, telemetry, photo-ID, mark-
recapture, acoustic, isotope, genetic and eDNA), behaviours (e.g., migration, feeding,
foraging, breeding, dispersal, aggregation, site fidelity, seasonal movement), and more
specific tag or technology terms (e.g., Argos, GPS, PAT, geolocate). We tested the
relevance of search strings for a subset of shark and ray species using the Web of
Science and Scopus abstract and citation databases (Appendix 1). We noted whether
relevant reference ("control") literature was captured, the total number of references,
and how many of the initial papers identified would meet the screening criteria. Within
the Web of Science database, all search strings were used to conduct topic searches in
English for indexed literature within subscribed databases (WOS, BCI, CCC, DRCI,
DIIDW, KJD, MEDLINE, RSCI, SCIELO, ZOOREC), published until June 2023.
Within Scopus, all search strings were used to search by keyword, title, and subject
area. To focus on developing a connectivity baseline for Australian CMS-listed sharks,
we removed studies with no individuals moving within Australia's EEZ (Figure 1).

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177 *Site aggregations and network models*

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To determine the connectivity of migratory sharks and rays, the information from
the systematic literature review was aggregated into network models following the
methods used to develop the MiCO system (www.mico.eco/system; Bentley et al.

2025). The general approach is to use network models to aggregate multiple data types
describing connectivity. In this approach, individuals reviewing the literature identified
areas used by a tagged/visually identified animal (hereafter "sites"), along with
"connections" to other sites. The size, period, behaviour, number of animals, sex, and
age-class were recorded for each site and connection, if available. The methodology is
meant to support description of regional connectivity and sites are categorised into three
coarse size classes with 1°, 5° or 10° radii. If no specific animal behaviour was
described in the reference reviewed, it was listed as an "observation".

To generate network models from the many sites and connections identified across
various studies, we aggregated overlapping sites into "metasites" (sites made up of
multiple sites) and removed studies that appeared to use data employed in other studies.
The aggregation and data deduplication process followed Bentley et al. (2025), and has
the same four objectives: "1) aggregate information across multiple sites that identify
species' activities in the same location; 2) maintain information on large-scale (> 500
km) connections generated by animal movements; 3) maintain the resolution of
information on critical reproductive life history stages; 4) provide a minimum level of
known animals sampled within a site and moving between sites".

The process of generating network models for shark species entailed five key
stages: data preparation, site selection, metasite centroid definition, data duplication
checks, and metasite aggregation. In the data preparation stage, sites for each species are
compiled and organised based on behaviour, such as reproduction or feeding, as well as
factors such as size and number of nearby sites. The ordering of sites ensures that the
resolution of reproductive sites is maintained, but that overlapping foraging areas are
merged to simplify networks. Subsequently, during site selection, sites are iteratively
chosen (i.e., the script examines one at a time based on the ordering) to identify
overlapping sites. The metasite centroid definition stage iteratively calculates a new
centroid for sites to be aggregated, and then removes any sites whose centroid is no
longer within the radii of the new metasite. The centroid is repeatedly recalculated
whenever a site is dropped until no further sites are dropped from the metasite. In an
effort to maintain long distance connections, any sites that have a connection of >500
km were not allowed to be aggregated. The data duplication stage ensures the integrity
of the dataset by checking for similarities such as identical coordinates, route
connectivity, authorship, and temporal scope. Duplicate sites informed the location of a
centroid of the new metasite, but were left out of calculations of the minimum numbers
of individuals in a given metasite in the final metasite aggregation stage. Once all sites
had been aggregated to a metasite, connections between sites were assigned to their
respective metasites, resulting in metaconnections (a connection made up of
connections). All code used to develop the network models is available on GitHub.

We exported the metasites and metaconnections from the MiCO system
(www.mico.eco/system), where they are freely available to the public. All subsequent
analyses were undertaken in R version 4.3.0, using the packages tidyverse, circlize,
ggOceanMaps, jsonlite, and ggExtra *(Wickham et al. 2019; Attali & Baker 2022; R*
Core Team 2023). The geodatabase files from the system were used to develop maps of
migratory connectivity for all shark and ray species where sufficient information was
available. Metasites were also allocated to an exclusive economic zone based on the
latitude and longitude of the metasite centroid. Adjacency matrices were then

constructed from the data on metaconnections that crossed EEZs and were used to
generate chord diagrams describing regional connectivity.

Results

Our data synthesis of 29 CMS-listed shark and ray species that use Australian
waters identified 64 relevant peer-reviewed references for twelve species (41%; Table
S1). Eighteen shark and ray species (62%) in our review had no published movement
information, and another four species had only one relevant publication (Table S1).
Nearly two-thirds (64%) of the 22 endangered species in this study (i.e., those CMS-
listed species that were also classified as Endangered or Critically Endangered globally
by the IUCN Red List; Table S1) had no published movement information. Another
three endangered species (14%) had only one published movement study, primarily
about fine-scale movements in estuaries. Despite the number of data-deficient species,
our study did identify 140 individuals of 5 migratory shark CMS-listed species that
engaged in movements either into or out of Australian waters to seven other national
jurisdictions and the ABNJ (Table 1, Figure 2).

Across these species, we identified 120 metasites and 161 metaconnections based
on individual movement data from CMS-listed species (Table 1). The number of sites
and routes identified rose proportionally to tagging efforts and were heavily biased
towards iconic species, including white sharks, whale sharks, and makos. Sampling
methods used vary greatly between species (Figure S3a), but the methods that
underpinned accessible large-scale connectivity information aggregated in this study as
metaconnections were dominated by satellite telemetry (Figure S3b). On average, 79%
of the connectivity information for five of the seven CMS-listed Australian migratory
sharks and rays with identified large-scale movements came from satellite telemetry.
Only two of the species (white shark and dusky shark) had a majority of connectivity
information coming from acoustic or mark-recapture data. Importantly, the connectivity
identified through acoustic and mark-recapture methods was largely within Australian
waters, not transboundary connections (e.g., all dusky shark movements; Figure S1c).

International transboundary movement of Australian sharks

While we did not find any ray crossing an international border with Australia, the
five CMS-listed migratory shark species in Australian waters that exhibited
international transboundary movements were shortfin mako (*Isurus oxyrinchus*), white
sharks (*Carcharodon carcharias*), whale sharks (*Rhincodon typus*), blue sharks
(*Prionace glauca*) and school sharks (*Galeorhinus galeus*). These species demonstrate
complex patterns of habitat use, moving across various habitats, from coastal areas to
oceanic habitats, and moving through numerous governance regimes. New Caledonia
had the highest number of species with connections shared with Australia, which
included the shortfin mako, blue shark, and white shark. White sharks were the most
connected species, with movements linking multiple jurisdictions: New Zealand, New
Caledonia, Papua New Guinea, Indonesia, South Africa and Solomon Islands. A total of
34 individual sharks of various species moved between Australia and New Zealand,
indicating strong trans-Tasman migratory connectivity.

<u>White sharks</u>

Strong white shark connectivity was found between eastern Australia and New
Zealand, with 18 individuals migrating to New Zealand and 14 individuals migrating to
Australia. White sharks have also shown transboundary connectivity between Australia
and Papua New Guinea, New Caledonia, and South Africa (Figure 2). Our network
models for white shark migratory connectivity show broad-scale movements along the
Australian east and west coasts (Figure 3a), and, in general, wide-ranging longitudinal
and latitudinal movements.

<u>Shortfin mako</u>
This species demonstrated extensive and diverse movements (Figure 3b): some
migrated to New Zealand and New Caledonia, while one individual travelled from the
Bonney Upwelling Region in southern Australia to the Southwest Indian Ridge in
ABNJ. Extensive movements within Australian waters were also observed.

<u>Whale sharks</u>
Published studies on whale shark movements centred around the coastal hotspot of
Ningaloo National Marine Park in Western Australia, where they aggregate seasonally
to feed (Figure 3c). There were migratory movements into the high seas of the Indian
Ocean and 27 individuals exhibited transboundary movements between Australia,
Indonesia, Papua New Guinea and passed through ABNJ in movements from
continental Australia to overseas Australian territories. Additionally, individuals were
recorded migrating from Ningaloo Reef and the Great Barrier Reef to Micronesia.

<u>Blue sharks and school sharks</u>
Blue sharks were observed migrating to Indonesia, New Caledonia and ABNJ
(Figure 3d). School sharks made extensive long-distance partial migrations using
protected pupping areas along the south coast of Australia, with documented
movements reaching the New Zealand EEZ evidenced by mark-recapture, acoustic and
satellite telemetry methods (Figure 3e).

Large-scale movements within Australian waters

While this study is focused on aggregating information on transboundary
movements of Australian sharks and rays, many species undertook large-scale
movements within Australia waters. Reef manta rays along the Great Barrier Reef in
Eastern Australia and Ningaloo Marine Park in Western Australia are also well-studied
and exhibited well-defined migration patterns that remain within Australian national
waters. These populations engaged in seasonal movements between northern and
southern reef sections (Figure S1). Despite these insights, tracking data for other
Mobulidae remains limited, with no data on their broader oceanic connectivity and no
examples of transboundary movements beyond Australian waters in peer-reviewed
literature. 473 (out of n = 2478) acoustically-tagged dusky sharks migrated between
western and southern Australian waters, and eight individuals displayed shorter-range
movements between Queensland and New South Wales. A single study of great
hammerheads showed primarily short-range movements, indicating that they are mostly
resident in shallow inshore areas, relying on local resources (Figure S1.a). Finally, there
are also movements from waters around the Australian mainland to overseas Australian
territories. Specifically, whale sharks cross international waters to other Australian
remote oceanic islands, such as Christmas Island and Cocos Keeling Island (Figure 3c).
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Unlisted data-rich species case studies

We identified 21 and 5 metasites for tiger and bull sharks, respectively, and 31 and 7 metaconnections. Tiger sharks were studied using acoustic tags (66.5%) and satellite telemetry (33.5%), while bull sharks were predominantly studied using acoustic telemetry (98.4%). Tiger sharks were found to have movements linking multiple jurisdictions: New Zealand, New Caledonia, Papua New Guinea, Indonesia, South Africa and Solomon Islands (Fig S3). Movements of bull sharks were restricted to euryhaline and coastal ecosystems, extending from far North Cape York Peninsula to Tollgate Islands in Southeast Australia, and were not recorded moving among national jurisdictions or into the high seas (Fig S3).

Multi-species connections

We identified several key transboundary connections which were important for multiple species. Firstly, the trans-Tasman pathway represents a key migratory connection for several sharks (white shark, shortfin mako, and school shark). These species migrate across the Great Australian Bight and Bass Strait, extending their migratory pathways through the Tasman Sea to New Zealand. Additionally, shortfin mako, white sharks, and blue sharks shared similar connections extending from the trans-Tasman region to New Caledonia (Figures 3 & 4). In addition to these CMS-listed species, tiger sharks exhibited longitudinal migratory pathways further north, transiting the Coral Sea to New Caledonia. A final area of multispecies migratory connections was found in northern Australia, particularly between Western Australia and Indonesia across the Timor Sea. Both tiger sharks and whale sharks migrated throughout the Timor Sea, travelling from Ningaloo Reef to Indonesia. Moreover, there were connections from waters south of Australia to Indonesia for both shortfin mako and blue sharks.

Discussion

We provide a baseline for the movement of globally at-risk migratory shark species to support conservation policy in the Indo-West Pacific. Among the nine species requiring international engagement to manage their populations mentioned in The Action Plan for Australian Sharks and Rays (Kyne et al. 2021), only whale sharks and shortfin mako have sufficient data to develop migratory connectivity networks. By synthesising information from 64 published references on CMS-listed migratory sharks and rays in Australian waters, we identified transboundary movements for five species: white sharks, whale sharks, shortfin mako, blue sharks, and school sharks. These species visited the EEZs of seven countries or territories, as well as areas beyond national jurisdiction. Our case study of unlisted, data-rich species also identified transboundary movements of tiger sharks. The regional and global scales of animal migrations necessitate an international collaborative approach to conservation and management (Runge et al. 2017).

Identification of multispecies migratory connections

The trans-Tasman migratory pathway was identified as important for multiple species in this review. Our network models align with our knowledge of genetic

structuring in both white and tiger shark populations across the Tasman Sea and broader West Pacific (Holmes et al. 2017; Clark et al. 2025). However, genetic information cannot confirm contemporary connectivity or inform spatial management to reduce mortality during migrations, underscoring the importance of tagging data and connectivity syntheses such as this work (Figures 3 &4) (Devloo-Delva et al. 2019; McMillan et al. 2019). Multiple species also continued from the Tasman Sea through to New Caledonia. The region has been recognised under the Important Shark and Ray Areas (ISRAs) Subcriterion C4 as a critical movement area linking Norfolk Island and New Caledonia (Jabado et al. 2024), and was identified as both a fish and a multi-taxa important area by the largest assessment of tracking data to date (Sequeira et al 2025). The number of shark species and individuals migrating across the Tasman Sea suggests the need for strengthened bilateral management between Australia and New Zealand.

Multispecies use of the waters from northern Australian through the Timor Sea was also evident. Despite the presence of the Timor Trench, which is up to 3300 m deep and known to limit the dispersal and connectivity of shark populations (Hirschfeld et al. 2021), both tiger sharks and whale sharks were seen to migrate from Ningaloo Reef to Indonesia. Further research could elucidate the degree to which the Timor Trench may act as a barrier for movements of coastal sharks, particularly in comparison to the Torres Strait, which may represent a migratory corridor for species that prefer shallow waters but act as a barrier for deep-dwelling species. While tracking data on megavertebrate movement in the Timor Sea and Torres Strait are scarce, Sequeira et al (2025) did identify the area as of importance to marine megafauna – in particular fish – and genetic data have provided valuable insights into transnational elasmobranch populations across the Torres Strait (Chin et al. 2017). Prioritising data collection for poorly studied species in this region is imperative to better understand connectivity, given that Indonesia is one of the world's largest shark-fishing nations (Sherman et al. 2023). There is a particular need to understand population connectivity for the critically endangered largetooth sawfish *Pristis pristis,* which is likely to move from Australia into Papua New Guinea, as indicated by their distribution, geographical proximity between populations and genetic studies (Feutry et al. 2015). Given the shallow nature of the Torres Strait, we recommend expanding the IMOS acoustic network to develop a curtain of receivers across the Strait to capture the potential movement of shallow-obligate sharks and rays moving between Australia and Papua New Guinea. While this approach should work in that region, it is less suitable for the deeper and larger Timor Sea or the open ocean areas in the West Pacific. For those regions we recommend expansion of satellite tagging programs and archival tagging for species caught and retained by fisheries managed through the WCPFC.

We found less evidence for multispecies connections with Melanesia and islands east of New Caledonia, though this may be due to lower sampling effort in these regions rather than an actual lack of connectivity (Francis & Jones 2017). Of note, whale sharks were identified to move from southwest of Papua New Guinea to Kirabati, indicating that while no connection directly from Australian waters was identified, movements from the region to the Central Pacific do occur (Womersley et al. 2022). Among the five devil ray species assessed, no data were available from Australian waters. However, two *Mobula mobular* individuals were documented migrating 1,400–1,800 km from New Zealand to tropical regions near Vanuatu and Fiji, providing evidence of their long-range migratory capacity (Francis & Jones 2017).

We expect that lack of large-scale connectivity and transboundary movements for
many species are driven by a similar lack of sampling, not the actual movements of
those populations. The lack of information on blue shark movement likely conceals
larger-scale movement in this region, as although there were few references in the
literature for blue shark in Australian waters, there is extensive information on their
ontogenetic habitat shifts across large spatial scales in multiple ocean basins (Maxwell
et al. 2019; Fujinami et al. 2021; Madigan et al. 2021; Elliott et al. 2022; Poisson et al.
2024). Similarly, there is a lack of understanding of shortfin mako movements in the
region, leading the WCPFC to describe the degree of connectivity as "unclear" and to
suggest that the population may be made up of "geographically relatively distinct stocks
or migratory contingents" (Large et al. 2022).
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The type of sampling method used also impacts our ability to understand large-
scale or transboundary movements. Mark–recapture and acoustic tracking approaches
typically involve tagging large numbers of individuals but yield relatively few
recaptures. This low recapture rate reflects limited detection probability rather than an
absence of large-scale movements. For species like reef manta ray, dusky sharks and
bull sharks, large sample sizes may not translate to identified transboundary movements
because of low recapture rates and the coastal distribution of acoustic receivers. For
example, while no transboundary connectivity was found for bull sharks, they have
recently been recorded travelling 7,290 km across ocean basins (Daly et al. 2025).
Indeed, acoustic-tagged bull sharks have migrated from New South Wales to the eastern
tip of Cape York (Barnett et al. 2024). However, there is limited to no acoustic array
coverage throughout the Torres Strait and into Papua New Guinea or Indonesian (at
least any that have been uploaded to IMOS Animal Tracking Facility's acoustic
telemetry database). Most bull sharks in this study were tagged using acoustic telemetry
(93%), making it unlikely that we would find documentation of movements across
international lines. Even for well-studied transboundary migrants like whale sharks,
reliance on mark-recapture methods can make those transboundary movements look like
rare events, when in fact it may just be the recapture rate.
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457   *Transboundary management of migratory sharks*
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Regional baselines are useful tools for understanding the international
transboundary movements of migratory species and, consequently, shared responsibility
for the management of migratory populations (Harrison et al. 2018). One existing
pathway for multinational collaboration on the conservation of migratory sharks is the
CMS and the Sharks MoU that sits beneath it. Of the countries connected by shark
movements identified in our study, Australia, New Zealand, New Caledonia (France),
and South Africa are signatories to the CMS and the Shark MoU, while Indonesia,
Papua New Guinea, the Federated States of Micronesia, and the Solomon Islands are
not, nor are they signatories to the Shark MoU. An important step toward better
governance of migratory sharks in the region would be for all countries to develop
mechanisms to cooperate (e.g., becoming parties to CMS or signatories to the Shark
MOU) or through the development of bilateral agreements where they do not exist. This
could then provide political momentum for greater support of research into regional
connectivity for sharks and rays. Although the CMS signatory status alone cannot fully
address governance gaps for migratory sharks and rays, it plays a constructive role in
driving efforts to implement and coordinate agreed-upon conservation measures.
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Domestically within Australia, the EPBC Act identified threatened and migratory
species in Australian waters. While the EPBC Act provides the overarching
environmental protection for threatened sharks and rays in Australia, managing their
major threat (fishing), including sustainable harvesting and bycatch regulation, is
undertaken by state agencies, the Australian Fisheries Management Authority at a
national level, and through regional fisheries management organisations (RFMOs) for
species taken in shared-stock fisheries on the high seas. Thus there will be a need to
close cooperation between environmental regulators and fisheries managers to achieve
good outcomes for CMS listed species.
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RFMOs play a central role in monitoring and managing the sustainability of
fisheries across vast oceanic areas. RFMOs implement a variety of measures to mitigate
threats to these species, such as setting catch limits, enacting fishery closures, enforcing
gear restrictions to reduce bycatch, and designating "no retention" species to prohibit
their landing. All West Pacific countries for which transboundary connections with
Australia were identified in this study are members of the Western and Central Pacific
Fisheries Commission (WCPFC). The WCPFC has a Conservation and Management
Measure for Sharks that, among other things, specifically prohibits: shark finning;
retention of whale sharks, oceanic whitetip sharks or silky sharks; the use of shark lines
in longlining; and the setting of purse seines on tuna associated with whale sharks
(Neubauer et al. 2024). In addition to the Conservation and Management Measure for
Sharks, the WCPFC also have a 2021-2030 Shark Research Plan that provides a
timeline for assessment of various shark species and a list of prioritised projects
(Brouwer & Hamer 2024). Of interest, the Shark Research Action Plan includes a
scoping study to understand stock structure and natal homing across all shark species.
Similarly, to address uncertainty in the stock assessment for silky sharks, there is a call
for more satellite tagging studies to be undertaken to "resolve fundamental questions…
about the degree of natal homing and limited mixing of the stock" (Neubauer et al.
2024). For the same reasons, the stock assessment for shortfin mako recommends
"additional tagging should be carried out… especially [in] known nursery grounds off
southeast Australia and New Zealand, as well as high seas areas to the north and east of
New Zealand, where catch-rates are high." The baseline connectivity models presented
here can enhance the understanding of metapopulation dynamics critical to RFMO
management, as well as underpin future risk-assessments by allowing cumulative
impacts to be accounted for across the known migratory movements of these species.
They also provide a framework for how information from various sampling methods
can be brought together to describe regional connectivity for sharks and rays.
513
It is important to note that while, in this manuscript, we use the term
"transboundary" to refer to movements that cross international borders, animals moving
across multiple management jurisdictions at any scale face similar challenges. For
example, bull sharks demonstrate large movements across Australian state lines. As bull
shark management is inconsistent across Australian states and territories, these
movements are a microcosm of the broader challenge of effectively managing highly
migratory species. It is also important to note that the scale of these movements could
easily have resulted in transboundary movement in regions with more or smaller EEZs.
Indeed, while the published movement data for bull sharks and reef manta rays did not
show evidence of international transboundary movements, this may be influenced by the
limited use of satellite telemetry for bull sharks and/or the predominantly coastal

behaviour observed in reef manta rays (confirmed through aggregated photo-
identification data (Armstrong et al. 2019).
527
528 *Data limitations for migratory sharks and rays*
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Listings of species under CMS and the EPBC Act, and management of sharks and
rays by relevant fisheries organisations, are dependent on information on the movement
of animals and status of populations being monitored and provided to management and
policy fora in an accessible and actionable manner. However, understanding
elasmobranch movement at large scales is hampered by major sampling obstacles.
Conventional mark-recapture studies are cost-effective and tag many animals, but the
likelihood of recapturing tagged individuals is low, and biased towards highly populated
areas and areas of high tourism (Kohler & Turner 2001; Rowat et al. 2009; Mas et al.
2022). Acoustic telemetry can capture local movements, particularly in estuarine or reef
ecosystems, but detection probabilities are low across vast geographic areas (Bradford
et al. 2019; Spaet et al. 2020). When migratory locations are unknown, or species are
highly pelagic, it is usually necessary to undertake expensive satellite tracking (Jaine et
al. 2014). However, sharks and rays spend limited time at the surface, reducing the
utility of satellite tracking, and increasing the reliance on archival pop-up light-level
tags with far greater location uncertainty. Despite transnational collaborations
expanding acoustic receiver networks, mark-recapture and archival pop-up tags remain
the main sources of information on large-scale connectivity for elasmobranchs. All of
these obstacles can and have been overcome for species of commercial interest, but the
vast majority of sharks and rays do not fall into this category. Thus, difficulties in
collecting data on elasmobranch movements persist and have limited our understanding
of migration paths and areas of importance for various life-history stages, which
impedes their management and conservation both nationally and internationally. These
obstacles increase the importance of aggregating and making use of all available
information on shark and ray connectivity.
554
Existing research also shows a marked geographic bias, with most data focusing on
iconic species in wealthier countries, such as Australia, New Zealand, and New
Caledonia. In contrast, less-studied species in poorer countries often lack sufficient data
and have weaker management frameworks. To support the implementation of CMS
agreements, it is crucial to prioritise research on the 22 shark and ray species listed
under the CMS that had one or no connectivity studies. With its substantial research
capacity and economic resources, Australia is well-placed to lead efforts in addressing
these disparities by generating critical data domestically and supporting research
initiatives in connected neighbouring regions with limited resources and capacity. In
particular, the Australian government could focus on the seventeen shark and ray
species listed under the EPBC Act as migratory. Particular attention should be paid to
the three sawfish species listed as Threatened under the Act that had three connectivity
studies across them (two with no studies at all). This compares with the other two
sharks listed as threatened, white sharks and whale sharks, for which there were 38
studies. An emphasis on studies that could clarify movement across the Timor Sea and
the Torres Strait would also reduce geographic bias towards wealthier regions.
571
572 *Using network models to understand migratory connectivity*
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While information on migratory connectivity can be gleaned from many sampling methods, findings are rarely integrated (Bentley et al. 2025). Our approach identifies sites and connections across methods and integrates them into a single network of the minimum known connectivity for each species. For example, acoustic telemetry data were previously used to describe school shark movement in national waters throughout southern New South Wales, Victoria and eastern Tasmania (Lédée et al. 2021). Our network connectivity models, incorporating satellite telemetry studies, extend these findings by describing transboundary migrations from South Australia to New Zealand waters, and are corroborated by a vast amount of mark-recapture tag data (Hurst et al. 1999). This supports the recent listing of school sharks (also known as tope) under Appendix II of the CMS. Establishing a baseline for migratory connectivity facilitates international collaboration and supports the identification of interested parties, from national stakeholders to intergovernmental organisations, with management mandates related to sharks and rays. These baselines also identify gaps in listings and the regions and species for which data gaps persist, providing evidence to guide the prioritisation of future research and policy efforts. For example, our case study examining two data-rich sharks and rays with known long-distance movements provides strong evidence for the listing of tiger sharks under CMS Appendix II, while the evidence from our bull shark model suggests further research is needed – particularly focusing on expanding acoustic array coverage through cooperative arrangements in PNG and Indonesia. Benchmarks for well-studied species (e.g., the white shark in southeastern Australia) also demonstrate the power and feasibility of this method, and provide a way to measure changes in connectivity into the future. The approach adopted here offers a transferable model to help develop baselines for migratory connectivity in sharks and rays in other regions, which is critical to conserving these threatened taxa.

Some caveats should also be considered when interpreting our results. Network models demonstrate movement patterns from known data, but also reflect biases in the location of tagging or acoustic receivers, which can potentially skew results. Our results mostly relied on satellite telemetry data and passive acoustic telemetry studies, methods which are commonly deployed in coastal regions (Hussey et al. 2015). Another key limitation is that network models do not capture the precise routes individuals take between nodes. Connections between nodes represent observed migratory links, not a precise movement path. As such, the models provide a simplified representation of complex migratory behaviours and cannot readily inform spatial management of migratory corridors without further interrogation of the underlying data.

It is important to acknowledge that unpublished data, including telemetry studies not yet available in the public domain, were not included here but could provide additional insights into migratory patterns and further inform our understanding of species connectivity. Many research efforts are never published, are not published in English (resulting in barriers to their use and indexing), or are published in un-indexed grey literature that was not reviewed in this study, potentially resulting in apparent "gaps" in which studies have indeed been undertaken (Heng et al. 2025). As such, this study should be viewed as an assessment of the minimum known connectivity for Australian sharks and rays, and further work should be undertaken to incorporate any available information on shark and ray movements. Together with improvements in spatial resolution and gap-filling to address geographic biases, these measures could offer a more comprehensive view of shark and ray migratory connectivity.

Further tagging and tracking efforts (including expansion of acoustic arrays) are
needed to address the significant data gaps that persist within Australia and
neighbouring countries. Critically, given the transboundary nature of many shark and
ray migrations and distributions, regional funding to raise capacity across all
neighbouring countries is essential to support Australian shark and ray populations and
their important habitats. Our synthesis of available evidence identifies several key
opportunities for international partnerships to strengthen migratory sharks and ray
conservation in the Indo-West Pacific. Of particular interest are multispecies migratory
connections between countries shared by multiple shark and ray species, such as
Australia and Indonesia, Papua New Guinea, and New Zealand. Aggregation of such
shared connections in unified models of migratory connectivity could help foster the
cooperative transboundary management required to sustain shark and ray populations.
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836   **Table 1.** The proportion of individuals sampled by sex and life stage in publications that included accessible information on connectivity, and the number of
837   metasites generated, for the eight CMS-listed Australian shark species for which network models could be developed. The total number of individuals
838   includes those sampled using acoustic and satellite telemetry, and mark-recapture studies. See Figure S3 for details of sampling methods used across species.

Common name	Total metasites	Total meta-connections	Male	Female	Unknown sex	Adult	Juvenile	Sub-Adult	Unknown life stage	Transboundary Movement
White Shark	30	56	40%	43%	17%	7%	35%	9%	49%	Yes
Whale Shark	27	40	21%	9%	71%	0%	1%	0%	99%	Yes
Shortfin Mako	17	30	20%	55%	26%	3%	95%	0%	2%	Yes
Blue Shark	18	13	27%	45%	27%	36%	9%	0%	55%	Yes
Reef Manta Ray	9	7	39%	52%	9%	0%	0%	0%	99%	No
School Shark	8	6	7%	93%	0%	68%	0%	0%	32%	Yes
Great Hammerhead	6	6	40%	60%	0%	86%	14%	0%	0%	No
Dusky shark	5	3	49%	47%	4%	15%	7%	5%	73%	No

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841 *Figure 1. Schematic of the systematic literature review screening protocol illustrated*
842 *using the white shark (Carcharodon carcharias).*
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847 *Figure 2. Species with known transboundary movements between the Australian EEZ*
848 *and other jurisdictions (including areas beyond national jurisdiction; ABNJ). Diagram*
849 *generated using R package circlize (Gu et al. 2014).*
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Figure 3. Network connectivity models showing the transboundary movements of six shark species: (a) White shark (b) Shortfin mako, (c) Whale shark, (d) Blue shark, and (e) School shark. These models depict connectivity across Australia's Exclusive Economic Zone (EEZ) and into adjacent international waters. Maps were generated using additional data from rnaturalearth (Massicotte and Young, 2023) and EEZ boundaries from Flanders Marine Institute (2023).